JCU ePrints

This file is part of the following reference:

Hazel, Julia (2009) ***Turtles and vessels: threat evaluation and behavioural studies of green turtles in near-shore foraging grounds.*** **PhD thesis, James Cook University.**

Access to this file is available from:

http://eprints.jcu.edu.au/10680

JCU
JAMES COOK UNIVERSITY

Turtles and vessels: threat evaluation and behavioural studies of green turtles in near-shore foraging grounds

Thesis submitted by

Julia Hazel B.Sc. G.Dip.Res.Meth.

October, 2009

For the degree of Doctor of Philosophy

In the School of Earth and Environmental Sciences

James Cook University

Townsville, Queensland, Australia

Statement of access

I, Julia Hazel, author of this work, understand that James Cook University will make my thesis available for use within the university library and, via the Australian digital thesis network, for use elsewhere.

I understand that, as an unpublished work, a thesis has significant protection under the Copyright Act.

I do not wish to place any further restriction on access to this work.

....

Julia Hazel Date

Statement of sources

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. I note that Chapter 2 builds upon preliminary work I conducted as a minor project for my Graduate Diploma in Research Methods at James Cook University. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given. I would be pleased to hear from any copyright owner who has been accidentally omitted or incorrectly acknowledged.

....

Julia Hazel Date

Declaration on Ethics

The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997), the *James Cook University Policy on Experimentation Ethics. Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001). The proposed research methodology received clearance from the James Cook University Ethics Review Committee (approval numbers A843, A898 and A948).

....

Julia Hazel Date

Statement on the contribution of others

Funding for field research

CRC Reef Research Centre

Sea World Rescue and Research Foundation

Tangalooma Marine Research and Education Foundation

James Cook University

Anonymous private donor

In-kind support for field research

Tangalooma Marine Research and Education Foundation

James Cook University

Project initiation

Professor Helene Marsh, Graduate Research School, James Cook University

Supervision

Dr Ivan Lawler, School of Earth and Environmental Sciences, James Cook University

Associate Professor Simon Robson, School of Marine and Tropical Biology, James Cook University

Turtle stranding records (Chapter 2)

Queensland Environment Protection Authority

Acknowledgements

I am deeply grateful to everyone who helped me reach the starting point for this PhD and then get through its trials and tribulations during my six years of part-time candidature. There have been so many people in total that it is impossible to thank everyone individually here. Most of all I thank my parents, siblings, extended family and friends who supported and encouraged me and suppressed their occasional doubts about my sanity. I am also indebted to the many inspirational marine scientists and wildlife researchers I've 'met' through their writings and a few I've been fortunate to meet in person, particularly those working in remote islands of the tropical Pacific and the icy South Atlantic Ocean.

In the academic arena I am most grateful to Professor Helene Marsh for obtaining funding to initiate this project and I particularly thank my supervisors Dr Ivan Lawler and Associate Professor Simon Robson for their knowledge, patience and goodwill in seeing my PhD through to completion. Thanks also to Dr Emma Gyuris for important input during the early stages and to Dr Mark Hamann for much appreciated discussion and advice during the later stages of my project. For editorial input I thank all the aforementioned, as well as anonymous reviewers and editors of journals that accepted papers based on some of my thesis chapters. I thank Associate Professor Jamie Seymour for encouragement to tackle the 'black art' of acoustic tracking, and thank my post-graduate colleagues at James Cook University (TESAG/EES) for interesting conversations and cheerful company on campus.

I sincerely thank marine turtle experts Dr Colin Limpus and Ian Bell for their invaluable help and advice on all things turtle. I appreciate Queensland Environmental Protection Agency allowing me to review their stranding records and thank Dr Limpus for facilitating this process. I thank Maritime Safety Queensland for providing bathymetry and tidal data for Moreton Bay. I am forever grateful to fieldwork volunteers Rachel Groom, Deb Bower, Leanne Ezzy, Kristina Boeck, Celia Schunter, Kerryn Johns, Natalie Reed, Bianca Casimaty, Kerrily Hooper, Tim Harvey, Laura Middelmann and Pat Woolley for their time, energy, skill and good humour throughout many long days in a small research vessel. Many thanks also to additional volunteers who helped for brief periods, and to professional fishers of Moreton Bay who provided information, insights and practical assistance, especially John Page and Dave Thompson.

This project would not have been possible without funding provided by CRC Reef Research Centre, Sea World Rescue and Research Foundation, Tangalooma Marine Research and Education Foundation, James Cook University and an anonymous private donor. In-kind fieldwork support provided by Tangalooma Marine Research and Education Foundation was invaluable and, best of all, included generous on-site help from Trevor Hassard and his team at Tangalooma.

I am indebted to many technical and administrative staff at James Cook University for their help with everything from computer connections and recalcitrant outboard motors to grant applications and thesis printing. Many thanks also to JCU library staff, especially those who sent me reference material during my extended fieldwork sessions far from the university campus. I received great support from the suppliers of my telemetry equipment and particularly thank Kevin Lay and Colin Hunter at Sirtrack, Dr Ed Bryant at Wildtrack Telemetry Systems and Baldur Sigurgeirsson at Star-Oddi for prompt and helpful advice. Finally I am enormously grateful to the R Development Core Team (my analysis would not have been possible without their excellent free software) and many other skilled and generous people who routinely share computer code, specialist expertise and interesting ideas with total strangers via the internet.

Publications associated with this thesis

The four papers listed below are based on Chapters 2, 4, 6 and 7 respectively.

- HAZEL, J. & GYURIS, E. (2006) Vessel-related mortality of sea turtles in Queensland, Australia. *Wildlife Research* 33, 149-154
- HAZEL, J., LAWLER, I. R., MARSH, H. & ROBSON, S. (2007) Vessel speed increases collision risk for the green turtle *Chelonia mydas*. *Endangered Species Research* 3, 105-113
- HAZEL, J., LAWLER, I.R.. & HAMANN, M, (2009) Diving at the shallow end: Green turtle behaviour in near-shore foraging habitat. *Journal of Experimental Marine Biology and Ecology* 371, 84–92
- HAZEL, J. (2009) Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. *Journal of Experimental Marine Biology and Ecology* 374, 58-68

Abstract

This study aimed to (1) evaluate vessel strike as a threat to marine turtles in Queensland, Australia, (2) investigate behavioural responses of free-living green turtles to vessel traffic, (3) study diving behaviour of green turtles in foraging grounds adjacent to vessel traffic, (4) test established and novel methods for recording fine-scale geographic movement by green turtles and gain insight into the spatial behaviour of turtles in shallow foraging habitat.

Analysis of stranding records collected by the Queensland Environment Protection Authority indicated that, for the Queensland east coast during the period 1999-2002, an average of 65 documented turtle deaths annually were ascribed to collisions with vessels. This number represented an extremely conservative indication of actual mortality because no systematic surveys for stranded animals were conducted and records were contingent on chance discoveries and on motivation of members of the public to report findings. The records showed a high degree of geographic concentration, green turtles comprised the majority of vessel-related records, followed by loggerhead turtles, and the majority of cases concerned adult and sub-adult turtles. Based on these findings, subsequent behavioural research in pursuit of aims 2 to 4 focussed on green turtles of adult and sub-adult age classes in Moreton Bay, which wass the area with the highest recorded incidence of turtle mortality from vessel strike.

Field research investigated behavioural responses of green turtles to an approaching vessel. Visual observations were conducted from a moving vessel that served a dual role as stimulus for potential turtle responses and as observation platform. During experimental vessel transits the proportion of turtles that fled to avoid the vessel decreased significantly as vessel speed increased and turtles that fled from moderate and fast approaches did so at significantly shorter distances from the vessel than turtles that fled from slow approaches.

For telemetry studies, green turtles were captured individually and equipped with time-depth recorders and ultrasonic transmitters. Ten telemetry sessions were distributed over 2 years to cover seasonal variation in sea temperature from 14ºC to 30ºC. These sessions provided diving data for a total of 19 turtles with curved carapace lengths in the range 49 to 118 cm. Three of the study turtles were additionally equipped with a Fastloc GPS (FGPS) device that used novel technology, specifically designed to record fine-scale movements of marine animals that surface too briefly for effective use of standard GPS. Detailed data were obtained for FGPS accuracy and efficiency, tested during extensive stationary trials. FGPS performance during live deployment was compared with two alternative methods, namely boat-based ultrasonic tracking and Argos Platform Transmitter Terminals.

Overall findings of telemetry sessions revealed that dive duration increased as sea temperature decreased, showing strong negative correlation by day and by night. Study turtles made resting dives that were 3 to 4 times longer in median duration, and six times longer in maximum duration, at cool temperatures than dives made at warm temperatures, but there was no evidence of winter diapause or location shift to avoid cold water. Diurnal dives were shallower and shorter than nocturnal dives, with diel patterns also evident in dawn and dusk peaks in occupation of depths within 1 m of the surface, elevated diurnal occupation of depths 1 to 2 m below the surface and elevated nocturnal occupation of depths >2 m.

The FGPS-equipped turtles (n = 3) used modest short-term activity ranges, remained within <4.7 km of their capture-release locations and favoured shallow water with 86% of locations at charted depths ≤3 m and the deepest location at 5.9 m. Fine-scale movements of each turtle varied from day to day with respect to tortuosity and areas traversed. Statistically significant day-night differences were evident in average rates of movement (greater by day) and in habitat selection, where diurnal locations had greater seagrass density while nocturnal locations featured deeper bathymetry. Individual turtles revisited some of their centres of activity on multiple occasions although none of the study turtles travelled consistently between the same day-night pair of sites as has been reported elsewhere.

In combination the diving and movement data showed that study turtles consistently and continuously used the shallow margins of the bay where human activities tend to be concentrated, thereby increasing their exposure to anthropogenic threats including vessel strike. Coupled with the evidence that reliable evasion responses occur only with very slow vessels, this thesis confirms the need for management strategies that restrict vessel speed or routes in order to reduce the cumulative risk of vessel strike in key turtle habitat subject to frequent vessel traffic.

Contents

List of tables

List of figures

Chapter 1: General introduction

Australian waters host some of the few remaining large sub-populations of green turtles *Chelonia mydas*, a species whose universal biodiversity value is specifically recognised in two World Heritage areas, the Great Barrier Reef, Queensland (Lucas et al., 1997; DEWHA, 2009a) and Shark Bay, Western Australia (DEWHA, 2009b). Persistence of large stocks at a time when green turtles have been severely diminished on a global scale (IUCN Marine Turtle Specialist Group, 2004) attests to favourable habitat available along Australia's extensive tropical and sub-tropical coasts and to early abolition of commercial harvests in recognition of marine turtles' biological vulnerability to human impact (Bustard, 1972; Limpus, 1983; Limpus et al., 2003).

The future of Australian green turtle populations is, however, by no means assured. Already signs of impending decline in the Northern Great Barrier Reef sub-population have been inferred from the decreasing average size of breeding female turtles, their increasing remigration intervals and a low recruitment rate (Limpus et al., 2003) while stability of the Southern Great Barrier Reef sub-population remains uncertain (Dobbs, 2001). Both sub-populations face an array of anthropogenic threats (Dobbs, 2001; Environment Australia Marine Species Section, 2003) and additional concern has recently been raised about the vulnerability of green turtles and other species to climate change (Hamann et al., 2007).

Although the commercial harvest of green turtles has long been prohibited under Australian jurisdiction, it has continued under the jurisdiction of neighbouring countries whose waters host shared green turtle stocks (Kwan, 1991; Kennett et al., 1998; Dobbs, 2001). Non-commercial green turtle harvests have also continued within Australia where traditional hunting by Indigenous people is exempt from no-take regulations. Although not quantified, these combined harvests are substantial and are considered likely to exceed biologically sustainable levels (GBRMPA, 2009). In addition turtle populations suffer the cumulative effects of incidental and accidental turtle mortality that remain largely unquantified.

New management initiatives are now under way in Australian Indigenous communities with the goal of achieving sustainable harvest practices because the long-term continuation of customary hunting is of great cultural importance to these communities (Marine And Coastal Committee, 2005; NAILSMA., 2009). At the same time, management agencies must strive to reduce incidental and accidental turtle mortality from multiple causes including habitat degradation, incidental capture in fisheries and shark control programs (the latter intended to protect bathers from risk of shark attack), entanglement in and ingestion of marine debris, and accidental collisions with boats (Dobbs, 2001; Environment Australia Marine Species Section, 2003). My thesis specifically addresses the latter threat.

1.1 Vessel traffic as a threat to marine turtles

At the commencement of my research on this topic in 2004, vessel traffic was already well-recognised as a major threat to some species, notably right whales *Eubalaena glacialis* in the North Atlantic Ocean (Knowlton and Kraus, 2001; Laist et al., 2001) and manatees *Trichechus manatus latirostris* in Florida, USA (Ackerman et al., 1995; Wright et al., 1995). However, I found only scant information in the scientific literature about any comparable threat to marine turtles.

An authoritative 1997 review of human impacts on turtles cited ‘grey literature’ indicating that in some areas of US jurisdiction up to 18% of stranded turtles (predominantly loggerheads *Caretta caretta*) were found to have boat strike injuries (Lutcavage et al., 1997). The topic received only cursory mention (3 sentences) among many other impacts addressed at greater length, but these authors described vessel traffic as “an important cause of sea turtle mortality” (Lutcavage et al., 1997). In this context they evidently referred only to US sub-populations of turtles and did not mention vessel-related impacts in other parts of the world. However, vessel strike had already been identified as a problem for loggerhead turtles at a nesting beach in Greece, as noted in a very brief report by Venizelos (1993).

Within Australia, during the early 1990s about 1% of green turtles (9 out of the 784 individuals captured and released) at one Queensland site carried scars apparently caused by prior vessel strikes (Limpus et al., 1994). The finding referred only to turtles that had survived collisions with vessels, whereas the level of mortality from collisions remained unknown. Vessel strike was subsequently included in a 2001 list of human impacts on turtles in the Great Barrier Reef Marine Park, based on unpublished data (Dobbs, 2001). Finally the 2003 Australian Recovery Plan for Marine Turtles provided the nation’s first formal recognition of vessel traffic as a threat to turtles under its jurisdiction (Environment Australia Marine Species Section, 2003).

The recovery plan relied on expert knowledge and unpublished data when it referred to boat strike as an issue in Queensland waters, but it did not quantify the problem in absolute or relative terms. In contrast to official recognition, there was public scepticism about the existence of a vessel strike problem. Opinions of Queensland boat operators, expressed during informal interviews I conducted between 2003 and 2005, are summarised in Table 1.1.

Professional and recreational boat operators who spoke with me believed it to be extremely rare for any boat to collide with a turtle. Several interviewees asserted that even if a boat driver intended to hit a turtle, actually doing so would be much more difficult than the proverbial challenge of hitting a needle in a haystack. The majority of respondents said they seldom saw turtles while boating and almost all believed turtles would reliably evade an approaching vessel.

1.2 Turtle behaviour in proximity to vessel traffic

Links between behavioural ecology and conservation biology are well established and it is clear that detailed knowledge of a species' behaviour can play a crucial role in successful conservation programs (Clemmons and Buchholz, 1997; Caro, 1998; Gosling and Sutherland, 2000). In support of chelonian conservation there is a corresponding need for behavioural data, particularly for green turtles in near-shore foraging grounds where individuals spend the major part of their lives with a potentially high level of exposure to human impacts.

The best known aspect of chelonian behaviour is their reproductive activity. Comprehensive descriptions are available of marine turtle mating, female emergence on land, nest construction and deposition of eggs (e.g. Carr, 1967; Bustard, 1972; Miller, 1997). This information has been supplemented by brief observations of the underwater behaviour of female and male turtles near nesting beaches (Booth and Peters, 1972; Houghton et al., 2003; Schofield et al., 2007). The broad-scale migratory movements of adult turtles have also attracted research interest since the earliest tagging and tracking studies (Miller, 1997), with recent burgeoning effort due to technical advances in satellite tracking equipment (see Godley et al., 2008 and references therein). Tracking has focussed mainly on female turtles departing from nesting beaches and similarly investigation of turtle diving behaviour by means of electronic depth recorders has been conducted predominantly in the vicinity of nesting beaches and during post-nesting migratory movements (e.g. Hays et al., 2000; Hays et al., 2001; Houghton et al., 2002).

Turtles in neritic foraging areas have received less attention than those at nesting sites. A modest amount of behavioural data is available for green turtles (e.g. Bjorndal, 1980; Mendonca, 1983; Whiting and Miller, 1998; Seminoff et al., 2002; Southwood et al., 2003; Meadows, 2004; see also citations in Chapters 4 to 7). However these data derive from disparate methods and span diverse time scales and widely divergent locations such that inference beyond study-specific circumstances is tenuous. For example, green turtle range of movement is one of the few aspects of behaviour investigated at several foraging sites, yet location, duration and individual differences remain confounded. Study turtles at Bahia de los

Angeles in Mexico used an area <4,000 ha over 96 days (Seminoff et al., 2002) while those at Shoalwater Bay, Australia foraged within <1,000 ha over 26 days (Whiting and Miller, 1998). Turtles in the latter study showed notable variation between individuals, some of which remained within less than 2 km of an apparently preferred position, while others moved up to 25 km, the latter being interpreted as use of multiple disjunct foraging ranges by some individuals (Whiting and Miller, 1998).

Turtle behaviour in direct responses to humans, as recorded in sparse data and anecdotal reports, appears diverse. At one site in Hawaii green turtles tolerated relatively close proximity of swimmers (~3 m) without overt reaction (Meadows, 2004) whereas a Caribbean study noted that turtles fled from an approaching diver (Ogden et al., 1983). My own observations while diving and snorkelling indicate that green turtles in Queensland waters sometimes flee abruptly from a person at >10 m, sometimes tolerate underwater humans within 2 m, and often move away slowly at intermediate distances. Turtles flee rapidly when startled by sudden human movements (personal observation) and when chased by boat-borne researchers intent on capturing turtles for study purposes (e.g. Heithaus et al., 2002). Generalised avoidance of people, boats and fishing activity has been proposed in explanation for green turtles' nocturnally biased use of some near-shore waters (Balazs, 1996; Seminoff et al., 2002). However in literature searches I found no systematic studies of turtle responses to vessel movements.

1.3 Research objectives

With a broad goal of gaining insight into the threat of vessel strike for marine turtles and relevant aspects of green turtle behaviour, I defined four major objectives.

1.3.1 Objective 1

- To evaluate vessel strike as a threat to marine turtles in Queensland

Noting the paucity of published data about a threat identified as important in at least two national jurisdictions (Lutcavage et al., 1997; Environment Australia Marine Species Section, 2003), my first objective was to seek evidence of vessel-turtle collisions in Queensland and to assess the severity of this threat. It was also relevant to determine which turtle species and life stages were most often involved in vessel collisions and if possible to establish the local geographic distribution of the problem.

1.3.2 Objective 2

- To investigate the immediate behavioural responses of free-living green turtles to vessel traffic

The belief of vessel operators that turtles almost invariably evade vessels (Table 1.1) was clearly at variance with formal recognition that turtle mortality from vessel strike is important (Environment Australia Marine Species Section, 2003). My second objective was therefore (a) to devise a methodology for observing turtle responses to vessel approaches, and (b) under natural conditions to investigate whether turtles display reliable evasion responses and whether vessel speed influences their evasion behaviour.

1.3.3 Objective 3

- To study diving behaviour and vertical space use by green turtles in foraging grounds adjacent to vessel traffic

Logically turtles will be immune to collision as long as they remain deeper in the water column than the maximum underwater projection of passing vessels. In contrast, collision risk can arise when a turtle occupies a shallower position in the water column. The capacity of turtles to dive to 10s of meters, and in some instances deeper, is well established (Lutcavage and Lutz, 1997). However temporal variation in their diving patterns and consequent occupation of vertical space is insufficiently known, particularly within near-shore foraging areas where vessel traffic is concentrated. A study of turtle diving behaviour in relevant habitat thus constituted my third objective.

1.3.4 Objective 4

- To test established and novel methods for recording fine-scale geographic movement by green turtles and thereby gain preliminary insight into the spatial behaviour of turtles in shallow foraging habitat.

Detailed knowledge of turtles' spatial movements could potentially support the design of local vessel traffic routes to minimise collision risk. However substantial technical challenges had hitherto precluded continuous tracking of turtles with sufficiently high temporal and spatial resolution over multiple days or longer. I undertook to develop methods for this purpose, both to gain preliminary insights about habitat use by a small sample of turtles in my study area and to facilitate future research of this nature.

1.4 Structure of this thesis

I prepared this thesis with the dual aim of reporting a large body of work to a specialist academic readership and at the same time making coherent segments of my research available separately to more diverse audiences. The introductory and final chapters set out research objectives and discuss findings of my entire PhD project while chapters 2, 4, 6 and 7 present distinct components of the project in a format suitable for stand-alone journal papers. Consequently in Chapters 2, 4, 6 and 7 the Introductions and Discussions reflect a broader context for each topic and the Methods sections of those chapters are concise. Chapters 3 and 5 provide additional background and methodological detail but in some instances refer to subsequent chapters to avoid repetition. I have placed relevant tables, figures and references at the ends of chapters to facilitate the reading of each chapter as a complete document when required. Following recommendations of the JCU Graduate Research School this thesis contains my original chapters rather than the published papers derived from some chapters. Publications associated with this thesis are listed in the front matter.

Chapter 1 (this chapter) presents an introduction to my PhD project, my research objectives and an overview of my thesis structure.

Chapter 2 evaluates the threat of vessel strike to marine turtles in Queensland. Here I review the available evidence, assess the level of mortality ascribed to vessel-related injury and investigate its spatial distribution.

Chapter 3 explains my selection of two sites in Moreton Bay and describes several alternative methods for visual observation of green turtle behaviour. This chapter amplifies the context of chapters 4 to 7 and includes detail of potential relevance for other researchers considering similar behavioural studies.

Chapter 4 describes the behavioural responses by free-living green turtles to vessel approaches at three different experimental speeds and offers new insights into the limitations on their capacity to evade fast-moving vessels.

Chapter 5 addresses analytic issues for time-depth recorder data, including the potential for sub-optimal sampling frequency to bias quantitative measures of green turtle diving behaviour based on such data, and validates methods used in Chapter 6.

Chapter 6 describes green turtle diving behaviour in near-shore foraging habitat as determined from time-depth recorders deployed on study turtles in multiple sessions covering seasonal variations in sea temperature.

Chapter 7 presents my evaluation of a novel fast-acquisition GPS system, based on my field tests in stationary positions and during live tracking of green turtles. I compare the accuracy and utility of fast-acquisition GPS with that of Argos-linked satellite transmitters and boat-based acoustic tracking. I also report the fine-scale movements of study turtles as revealed by fast-acquisition GPS.

Chapter 8 provides a synthesis of my findings and a general discussion.

1.5 Tables

Table 1.1 Responses expressed by Queensland boat operators during informal interviews between 2003 and 2005. Respondents (n = 72) comprised 14 professionals (19%), 50 recreational boaters (69%) and 8 (11%) people who operated both recreational and professional boats.

	Never	Seldom	Sometimes	Often	Always
Do you see turtles while you are out on your boat?	15 (21%)	38 (53%)	19 (26%)		
Have you seen a boat hitting a turtle or received a first-hand report of such an event?	70 (97%)	2 (3%)			
Do you expect turtles will get out of the way when a boat approaches them?				1 (1%)	71 (99%)
Do you think boat collisions are a problem for Queensland turtles?	71 (99%)	1 (1%)			

1.6 References

ACKERMAN, B. B., WRIGHT, S. D., BONDE, R. K., O'DELL, D. K. & BANOWETZ, D. J. (1995) Trends and patterns in mortality of manatees in Florida, 1974–1992. In O'SHEA, T. J., ACKERMAN, B. B. & PERCIVAL, H. F. (Eds.) *Population biology of the Florida manatee.* Washington, DC, National Biological Service.

BALAZS, G. H. (1996) Behavioral changes within the recovering Hawaiian green turtle population. In KEINATH, J. A., BARNARD, D. E., MUSICK, J. A. & BELL, B. A. (Eds.) *Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation.* Miami, NOAA.

BJORNDAL, K. A. (1980) Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Marine Biology,* 56**,** 147-154.

BOOTH, J. & PETERS, J. A. (1972) Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Animal Behaviour,* 20**,** 808-812.

BUSTARD, R. (1972) *Sea turtles: natural history and conservation,* London, Collins.

CARO, T. (Ed.) (1998) *Behavioural Ecology and Conservation Biology,* Oxford, Oxford University Press.

CARR, A. (1967) *So Excellent a Fishe,* New York, The Natural History Press.

CLEMMONS, J. R. & BUCHHOLZ, R. (1997) *Behavioral Approaches to Conservation in the Wild,* Cambridge, Cambridge University Press.

DEWHA, A. G. (2009a) The Great Barrier Reef World Heritage values. Canberra, Department of the Environment, Water, Heritage and the Arts.

DEWHA, A. G. (2009b) Shark Bay, Western Australia, World Heritage values. Canberra, Department of the Environment, Water, Heritage and the Arts.

DOBBS, K. (2001) *Marine turtles in the Great Barrier Reef World Heritage Area,* Townsville, Great Barrier Reef Marine Park Authority.

ENVIRONMENT AUSTRALIA MARINE SPECIES SECTION (2003) Recovery plan for marine turtles in Australia. Canberra, Environment Australia.

GBRMPA (2009) Environmental Status: Marine Reptiles. Townsville, Great Barrier Reef Marine Park Authority.

GODLEY, B. J., BLUMENTHAL, J. M., BRODERICK, A. C., COYNE, M. S., GODFREY, M. H., HAWKES, L. A. & WITT, M. J. (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endangered Species Research,* 4**,** 3-22.

GOSLING, L. M. & SUTHERLAND, W. J. (Eds.) (2000) *Behaviour and Conservation,* Cambridge, Cambridge University Press.

HAMANN, M., LIMPUS, C. J. & READ, M. A. (2007) Vulnerability of marine reptiles in the Great Barrier Reef to climate change. In JOHNSON, J. & MARSHALL, P. (Eds.)

Climate change and the Great Barrier Reef: A vulnerability assessment. Australia, Great Barrier Reef Marine Park Authority and Australian Greenhouse Office.

HAYS, G. C., ADAMS, C. R., BRODERICK, A. C., GODLEY, B. J., LUCAS, D. J., METCALFE, J. D. & PRIOR, A. D. (2000) The diving behaviour of green turtles at Ascension Island. *Animal Behaviour,* 59**,** 577-586.

HAYS, G. C., AKESSON, S., BRODERICK, A. C., GLEN, F., GODLEY, B. J., LUSCHI, P., MARTIN, C., METCALFE, J. D. & PAPI, F. (2001) The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *Journal of Experimental Biology,* 204**,** 4093-4098.

HEITHAUS, M. R., FRID, A. & DILL, L. (2002) Shark inflicted injury frequencies, escape ability and habitat use of green and loggerhead turtles. *Marine Biology,* 140**,** 229-236.

HOUGHTON, J. D. R., BRODERICK, A. C., GODLEY, B. J., METCALFE, J. D. & HAYS, G. C. (2002) Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Marine Ecology Progress Series,* 227**,** 63-70.

HOUGHTON, J. D. R., CALLOW, M. J. & HAYS, G. C. (2003) Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) around a shallow water coral reef. *Journal of Natural History,* 37**,** 1269-1280.

IUCN MARINE TURTLE SPECIALIST GROUP (2004) 2004 Global Status Assessment: Green Turtle (*Chelonia mydas*). The World Conservation Union (IUCN).

KENNETT, R., MUNUNGURRITJ, N. & YUNUPINGU, D. (1998) Migration patterns of marine turtles in the Gulf of Carpentaria, Northern Australia: Implications for Aboriginal management. *Wildlife Research,* 31**,** 241- 248.

KNOWLTON, A. R. & KRAUS, S. D. (2001) Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean. *Journal of Cetacean Research and Management,* Special Issue 2**,** 193-208.

KWAN, D. (1991) The turtle fishery of Daru, Western Province, Papua New Guinea: insights into the biology of the green turtle (*Chelonia mydas*) and implications for management. Townsville, James Cook University.

LAIST, D. W., KNOWLTON, A. R., MEAD, J. G., COLLET, A. S. & PODESTA, M. (2001) Collisions between ships and whales. *Marine Mammal Science,* 17**,** 35-75.

LIMPUS, C. J. (1983) The Reef: Uncertain Land of Plenty. In LAVERY, H. J. (Ed.) *Exploration North: A Natural History of Queensland.* South Yarra, Lloyd O'Neil Pty Ltd.

LIMPUS, C. J., COUPER, P. J. & READ, M. A. (1994) The green turtle, *Chelonia mydas*, in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum,* 35**,** 139-154.

LIMPUS, C. J., MILLER, J., PARMENTER, C. & LIMPUS, D. (2003) The green turtle, *Chelonia mydas*, population of Raine Island and the northern Great Barrier Reef: 1843-2001 *Memoirs of the Queensland Museum,* 49**,** 349-440.

LUCAS, P., WEBB, T., VALENTINE, P. & MARSH, H. (1997) The outstanding universal value of the Great Barrier Reef World Heritage Area. Townsville, QLD, Great Barrier Reef Marine Park Authority.

LUTCAVAGE, M. E. & LUTZ, P. L. (1997) Diving physiology. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, Fla, CRC Press.

LUTCAVAGE, M. E., PLOTKIN, P., WITHERINGTON, B. & LUTZ, P. L. (1997) Human impacts on sea turtle survival. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, Fla, CRC Press.

MARINE AND COASTAL COMMITTEE (2005) Sustainable harvest of marine turtles and dugongs in Australia – a national partnership approach. Canberra, Australian Government Natural Resource Management Ministerial Council.

MEADOWS, D. (2004) Behavior of green sea turtles in the presence and absence of recreational snorkellers. *Marine Turtle Newsletter,* 103**,** 1-4.

MENDONCA, M. T. (1983) Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia,* 4**,** 1013-1023.

MILLER, J. D. (1997) Reproduction in Sea Turtles. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles.* Boca Raton, CRC Press.

NAILSMA. (2009) NAILSMA dugong and marine turtle project. Darwin, North Australian Indigenous Land and Sea Management Alliance.

OGDEN, J. C., ROBINSON, L., WHITLOCK, K., DAGANHARDT, H. & CEBULA, R. (1983) Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. *Journal of Experimental Marine Biology and Ecology,* 66**,** 199-205.

SCHOFIELD, G., KATSELIDIS, K. A., PANTIS, J. D., DIMOPOULOS, P. & HAYS, G. C. (2007) Female-female aggression: structure of interaction and outcome in loggerhead sea turtles. *Marine Ecology Progress Series,* 336**,** 267-274.

SEMINOFF, J. A., RESENDIZ, A. & NICHOLS, W. J. (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series,* 242**,** 253-265.

SOUTHWOOD, A. L., REINA, R. D., JONES, V. S. & JONES, D. R. (2003) Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. *Canadian Journal of Zoology,* 81**,** 1014-1024.

VENIZELOS, L. (1993) Speed boats kill turtles in Laganas Bay, Zakynthos. *Marine Turtle Newsletter,* 63**,** 15.

WHITING, S. D. & MILLER, J. D. (1998) Short term foraging ranges of adult green turtles (*Chelonia mydas*). *Journal of Herpetology,* 32**,** 330-337.

WRIGHT, S. D., ACKERMAN, B. B., BONDE, R. K., BECK, C. A. & BANOWETZ, D. J. (1995) Analysis of watercraft-related mortality of manatees in Florida, 1979-1991. In O'SHEA, T. J., ACKERMAN, B. B. & PERCIVAL, H. F. (Eds.) *Population Biology of the Florida Manatee.* Fort Collins, USA, National Biological Service.

Chapter 2: Vessel-related mortality as a threat to marine turtles in Queensland

Abstract

Identification of threats is a standard component of conservation planning and the ability to rank threats may improve the allocation of scarce resources in threat mitigation programs. For vulnerable and endangered marine turtles in Australia, vessel strike is recognised as an important threat but its severity relative to other threats remains speculative. Documented evidence for this problem is available only in stranding records collected by the Queensland Environment Protection Authority. With the authority's support I assessed the scope and quality of the stranding data and analysed vessel-related records. The records provided evidence that during the period 1999-2002 on average 65 turtles were killed annually as a result of collisions with vessels on the Queensland east coast. This level of mortality appears broadly comparable to mortality recorded in the Queensland East Coast Trawl Fishery before the introduction of mandatory Turtle Exclusion Devices in that fishery. In both cases, the true level of mortality must be expected to exceed recorded mortality. Green turtles *Chelonia mydas* comprised the majority of vessel-related records, followed by loggerhead turtles *Caretta caretta*, and 72% of cases concerned adult or sub-adult turtles. The majority of vessel-related records came from the greater Moreton Bay area, followed by the Hervey Bay and Cleveland Bay areas. The waters of all three areas are subject to variable levels of commercial and recreational vessel traffic, and their shores comprise both populated and unpopulated coastal land.

2.1 Introduction

Conservation plans routinely identify threats confronting vulnerable and endangered species, with a view to reducing those threats. Where multiple threats exist, evaluation of their relative impacts can inform the allocation of scarce resources in threat mitigation programs. However it is often difficult to quantify impacts, particularly those affecting such long-lived and wide-ranging species as marine turtles.

In the Australian Recovery Plan for Marine Turtles, vessel strike is presented as an important detrimental impact but threats are not ranked in the plan (Environment Australia Marine Species Section, 2003). Vessel strike is also prominent in a review of impacts ‘of greatest relevance to turtle populations in the World Heritage Area’ of the Great Barrier Reef (Dobbs, 2001). But despite formal recognition of the issue, no published assessment is available regarding the severity of vessel strike as a cause of mortality for marine turtles in Australian waters. Here I seek to fill this gap.

Documentation on collisions between vessels and turtles is lacking. However, evidence of collision is inferred when a dead or moribund turtle is found to have massive fractures of the carapace and/or deep parallel cuts, which strongly suggest that a vessel hull or vessel propeller struck the turtle. In Australia the Queensland Environment Protection Authority (QEPA), a state government body, recorded such evidence within a long-standing collection of information on stranded marine wildlife that covers turtles, dugongs and cetaceans found outside their normal environment, on or close to shore.

The QEPA wildlife stranding data have been collected from diverse sources, ranging from reports by staff biologists to newspaper accounts and telephone calls by members of the public (J Greenland, personal communication) but recording remained informal until the late 1970s (Kwan, 2004) and a public telephone hotline to facilitate reporting of stranding events was established only in 1998 (Great Barrier Reef Marine Park Authority, 2003a). I undertook a review of the resulting turtle data, held by QEPA in electronic format, in order to evaluate evidence relating to vessel strike.

2.2 Methods

I received a set of 5,734 records pertaining to marine turtles, extracted from the electronic information system designated by QEPA as their Marine Wildlife Stranding and Mortality Database. I relied on a QEPA manual (Limpus, 2002) to interpret the database fields and the alpha-numeric codes used within them. From the 27 data fields in use I identified items of primary interest for this study: date, species, sex, age-class, curved carapace length, identified primary cause of death, latitude and longitude of stranding location.

I applied a simplified scheme for classifying turtle mortality because 85 different codes had been entered in the data field for primary cause of death. I employed a conservative approach and considered cause of death to be unknown in records with undefined codes (including partial codes followed by a question mark) except where other data fields resolved ambiguity. For vessel-related records I also scanned supplementary information fields, seeking to exclude any cases that might have involved post-mortem collision rather than collision with a living turtle.

To assess spatial components of the turtle stranding data I used ArcView 3.3 Geographic Information System software (Environmental Systems Research Institute, Redlands, California, USA). I prepared shapefiles from the geographic coordinates of stranding records to display recorded locations in relation to the Queensland coastline and defined five areas of interest where stranding records were concentrated. I used locally recognisable names (Moreton Bay, Hervey Bay, Cleveland Bay, Hinchinbrook and Cairns) as convenient labels but note that these areas were diverse in their extent and topography and their boundaries were necessarily arbitrary (Figure 2.1).

2.3 Results and Discussion

2.3.1 Scope and quality of data

Clear criteria for inclusion/exclusion of information in the QEPA Marine Wildlife Stranding and Mortality Database had not been documented. The data set I received appeared notably inconsistent in three respects: some records referred to locations outside the state of Queensland; some records referred to mortality from permitted hunting, apparently at variance with a stated intention to include only cases of non-permitted hunting; (Haines et al., 2000; Haines and Limpus, 2001); some records referred to mortality incidental to dredging and shark control operations. The latter were derived from formal reports on professional activities, in contrast to records of opportunistic discoveries of stranded animals.

This inconsistent recording practice confounded any assessment of long-term trends although the full data set spanned four decades up to 2002. Data for earlier decades were sparse and only a minority of cases actually represented stranding events, with information from the Queensland Shark Control Program dominating the record count prior to 1990. Consequently I limited my study to records for the period 1990 to 2002, and to those pertaining to stranding events along the Queensland east coast only.

Data verification was precluded by the original data collection processes. These involved a wide range of personnel and procedures that varied over the broad temporal and geographic extent of the data. Some implausible entries and internal inconsistencies were evident. Many data fields had been coded as ‘unknown’ or left blank. In many cases it was plausible that carcass decomposition had prevented accurate assessment. In addition, professional staff did not investigate all stranding events due to inaccessible locations and limitations on resources (J. Haines, personal communication). A few geographic locations appeared grossly in error (far inland) and many locations appeared imprecise, being at short distances inland or offshore although supplementary information in the record indicated a beach location. I accepted the lack of precision as a limitation inherent in this type of stranding data.

2.3.2 Frequency of vessel-related records

During the period 1990 to 2002, vessel-related records fluctuated between 12% and 16% of annual stranding records while the total number of stranding records increased almost three-fold (Table 2.1). My term “vessel-related records” includes all cases where the cause-of-death code denoted vessel-related injuries and cases where such injuries (massive fractures and/or deep parallel cuts) were recorded but cause of death had been left unspecified. Taking a conservative stance, I excluded the latter cases from my evaluation of vessel-related mortality for the period 1999 to 2002, when an average of 65 turtle deaths per year were ascribed to injuries caused by vessels on the east coast of Queensland (mean 64.5, standard error 4.646, range 52 to 74).

2.3.3 Biological factors in vessel-related records

The majority of vessel-related records involved green turtles (*Chelonia mydas*, 76%) followed by loggerhead turtles (*Caretta caretta*, 14%) (Table 2.2). This finding, in combination with the geographic locations for these records (see section 2.3.4) suggested that mortality from vessel collisions was probably concentrated on two breeding stocks. Loggerhead turtles recorded as killed by vessel strikes most likely belonged to the single eastern Australian breeding stock of this species (Environment Australia Marine Species Section 2003). Most green turtles killed by vessel impacts were probably from the southern Great Barrier Reef breeding stock (Limpus et al., 1992; Dobbs, 2001). It should be possible to estimate the proportional representation of different breeding stocks in mortality records more precisely when genetic data become available for turtles at different foraging grounds along Queensland’s long coastline.

Turtles from 30 to 65 cm curved carapace length accounted for 13% of vessel related records while turtles larger than 65 cm curved carapace length comprised 60% of vessel related records. The latter group comprised sub-adults and adults according to the size-based classification used by QEPA for green turtles and loggerheads, in the absence of gonad examination (Limpus, 2002). With the addition of cases where curved carapace length was not recorded but adult size class was indicated, 72% of vessel-related records involved sub-adults and adults. Implications of this finding are considered below, under Conclusions.

Sex was not determined for the majority of vessel-related records. Nineteen percent of cases were recorded as female and 16% as male. However, except for a small number of cases (<2%) subjected to an internal examination of reproductive organs, sex was evidently determined by inspection of tail length. Since this method is valid for adult turtles only and may fail to discriminate between large immature males and small mature females (Wibbels, 2003), these data must be viewed with caution. Furthermore a few cases, which indicated sex determination of juvenile turtles without internal examination, implied either errors in recording age class and/or sex, or failure to record internal examinations. Consequently I did not draw inferences based on sex of turtles indicated in the stranding records.

One turtle with a small number of fibropapilloma growths appeared among the deaths ascribed to vessel impact, but no evidence of disease or disability was recorded in any other vessel-related cases. Thus the stranding records did not support a popular view that turtles suffering vessel strike tend to be those that remain at the sea surface due to disability, although the existence of undetected disabilities cannot be ruled out.

The stranding records also lacked support for the suggestion that a surface basking habit and a tendency for turtles to seek warm water in deeper channels (including shipping channels) increase the risk of vessel strike (Dobbs, 2001). On the assumption that turtles would engage in warmth-seeking behaviours more often under colder conditions, I compared the frequency of vessel-related records for periods of lowest water temperature (June to August) and highest water temperature (January to March), relying on long term sea temperature data recorded by government agencies (CSIRO, 2003; Great Barrier Reef Marine Park Authority, 2003b). The proportion of vessel related records did not vary significantly between these two periods (Chi-Square = .868, df = 1, $p = .351$).

Monthly totals for pooled stranding records were notably higher for September, October and November and lower for February to May, and vessel-related records displayed a similar but less prominent pattern. I failed to find any biological explanation for variation in stranding frequency by month. I considered the seasonality of breeding migrations by Queensland green turtles and loggerheads (Limpus, 1983) but found no difference in the proportion of potential breeders (adults) represented in stranding records for migration periods and non-migration periods. Exploration of records classified by years, by seasons, by species and by sex did not suggest other explanatory hypotheses. Since reporting depended entirely on opportunistic discoveries of stranded turtles and no systematic monitoring had been undertaken, I speculated that discovery opportunities might have been greater between October and November (Austral spring and early summer). The absence of data on the circumstances of each discovery precluded any test of this tentative explanation.

2.3.4 Spatial distribution of vessel-related stranding events

The majority of vessel-related stranding events were recorded within the greater Moreton Bay area, followed by Hervey Bay and Cleveland Bay. I calculated spatial density of vessel-related stranding cases using the cumulative total (1999-2002) averaged over a 5km radius. By this measure the most notable area of concentration (0.16 to 0.6 cases per square kilometre) was evident in south-western Moreton Bay in the general vicinity of Coochiemudlo Island, with a small area of concentration (0.12 to 0.18 cases per square kilometre) in northern Moreton Bay, near the southern end of Bribie Island. Cleveland Bay showed a notable area of concentration (0.12 to 0.24 cases per square kilometre) near the port of Townsville.

These areas of concentration suggested the existence of ‘hot spots’ for vessel impacts but must be interpreted with great caution due to the uncertain geographic accuracy of recorded locations (see 2.3.1 Scope and quality of data) and the fact that recorded locations indicate places where turtle carcases were found, not collision sites. No quantitative vessel traffic data were available for these possible ‘hot spot’ areas. However, all are subject to commercial and recreational vessel traffic with relatively high traffic intensity occurring intermittently, although absolute traffic intensity varies greatly between the areas and varies temporally within each area (J Hazel personal observation).

I recognised a potentially confounding factor in my fine scale spatial analysis, in that winds and currents may have contributed to the accumulation of turtle carcasses in some areas but, based on personal observation, I suspect wind and currents were less significant than traffic intensity. This inference remains speculative because assessment of the influence of wind and current is confounded by lack of precision and uncertain reliability of locations recorded in the database (as noted earlier) and the unknown time intervals between each assumed collision and arrival of the turtle carcass at the location of its discovery.

On a broader scale, limited data on vessel traffic restricted me to two numeric comparisons of dubious value. The first, based on the number of large commercial ships (annual average for 1998-2001) arriving at the main port in each area (Queensland Government, 2004b) indicated that the greater Hervey Bay area had the highest proportion of vessel-related records in relation to large ship traffic. This comparison appears of uncertain relevance because, in the areas under consideration, large ships are a variable and numerically small proportion of all vessel traffic. A substantial proportion of commercial traffic is comprised of smaller vessels including ferries, fishing vessels, tourist and charter vessels, and vessels of government agencies and defence forces (J Hazel personal observation) but no suitable data were available for these types of vessels. The second comparison showed vessel-related stranding records were proportionally higher, in relation to recreational boat registration, in the Cleveland Bay, Hervey Bay and Moreton Bay areas. This comparison was based on the number of recreational vessels registered in 1998 by private owners with home addresses in each area (Queensland Government, 2004a). However registration data may be an inadequate proxy for recreational boating traffic because it cannot be ascertained that boats are used consistently in waters close to each owner's registration address.

Assessment of vessel impacts in relation to turtle density would have been valuable but was not possible because no quantitative data were available at a spatial scale relevant to turtle collisions and stranding events. When considering human population density, I found the greater Hervey Bay area recorded far more stranding events and slightly more vessel-related events, relative to numbers of people living along the adjacent coast, than other areas. I based this comparison on Australian census data for the year 2001 (Commonwealth of Australia, 2001) for persons aged 15 years and over, living within 20 km of the coast. Interpretation of this relationship is uncertain. More people living in an area may give rise to more intense vessel traffic and hence greater risk of vessel-turtle collisions. Equally, a local population increase may result in greater use of local beaches and hence greater probability of stranded carcasses being found. Thus any prospect for detecting a potential increase in collision risk would be confounded by a potential increase in the reporting of turtle mortality.

2.3.5 Comparison of vessel-related mortality and trawl mortality

Seeking a context to assess the impact of vessel-related mortality on Queensland's turtle populations, I considered turtle mortality in the Queensland East Coast Trawl Fishery (Robins, 2002) while recognising that the diverse nature of the two data sources precludes any rigorous comparison. Both sources of data nominally cover the same large geographic area but trawl mortality was derived from formal data collection (Robins, 2002) whereas vessel-related mortality depended entirely on opportunistic discovery of stranded animals. Nevertheless I suggest that this inexact comparison provides a relevant and useful context.

I found that turtle mortality ascribed to vessel impact (1999 – 2002) was of broadly similar magnitude to the observed direct mortality in the trawl fishery prior to the introduction of Turtle Excluder Devices (Table 2.2). I note that mortality ascribed to vessel impact may have been inflated by some instances where a post-mortem vessel strike was mistakenly identified as the cause of death. However, even if this error of interpretation had invalidated 10% of cases (a high estimate I believe) the adjusted average of 58 vessel-related deaths would still be comparable in broad terms to the observed trawl mortality of 61 recorded deaths annually.

Both data sources reflect confirmed turtle deaths. Undoubtedly many turtles have died without being recorded, including turtles subjected to trawl capture (Epperly et al., 1996) and turtles involved in collisions with vessels. The true level of mortality in each case can only be assessed by speculative estimates. Therefore I drew on sparse data in literature regarding the proportion of floating turtle carcasses that are subsequently reported as stranded carcasses, and on this basis I calculated two highly speculative estimates of potential vessel-related mortality, to allow comparison with Robins' estimate of true mortality in trawls (Table 2.2).

2.4 Conclusions

Interpretation of QEPA stranding data must be qualified since the records were unverified, data quality appeared compromised, and there is much uncertainty inherent in determining the cause of death of wild animals. In particular the level of vessel-related turtle mortality that I derived from QEPA stranding data may have been slightly inflated by occasional mistaken identification of post-mortem collisions.

On the other hand, it seems highly likely that many dead turtles (from vessel collisions and other causes) are never recorded because stranding reports depend firstly on the chance discovery of a carcass and secondly on motivation of individual members of the public to report a discovery. The likelihood of turtle carcasses being discovered may be further reduced because dense mangrove forests impede access to substantial portions of the shoreline in all the areas where notable vessel-related mortality was recorded. Therefore I suggest that stranding records of 65 annual deaths from vessel impact provide a reasonable indication of the minimum level of mortality from this cause and suspect that the true level would be considerably higher.

The finding, noted earlier, that 72% of vessel related mortality involved sub-adult and adult turtles appears particularly important. Population models demonstrate that population growth rate is much more sensitive to survival in the large juvenile to adult stages than to changes in survival in the earlier life stages or to increases in fecundity. Larger turtles have a higher reproductive value than smaller juveniles, thus increased mortality of larger individuals must be addressed as a matter of highest priority (Heppel et al., 1999).

I conclude that vessel collisions caused a non-trivial level of turtle mortality along the east coast of Queensland between 1999 and 2002 and expect similar or greater mortality to continue in the absence of mitigation measures. Considering that the severity of vessel-related mortality appears broadly comparable to pre-TEDs turtle mortality in the Queensland East Coast Trawl Fishery, which provided the impetus for researching and implementing important mitigation measures in that industry (Robins, 2002), I suggest that comparable effort needs to be applied towards mitigating vessel-related mortality.

Stranding data offer the only source for quantitative assessment of the severity of vessel-related mortality. These records could also support assessment of other anthropogenic impacts and natural causes of mortality. If location and time of finding carcasses had been accurately recorded, together with a reliable evaluation of the stage of decomposition, then records of freshly dead carcasses with vessel injuries, together with readily available weather and tidal data, would support inference regarding likely collision sites for individual cases. Regrettably, existing data are inadequate for this purpose.

I therefore recommend recognition by Federal and State authorities of the potentially significant management value of reliable and accurate stranding data and allocation of resources to upgrade data collection procedures and enhance data quality. Furthermore, it would be valuable to supplement opportunistic discovery by implementing regular systematic searches for stranded animals in suspected ‘hot spot’ areas. I recognise the difficulty of providing resources for systematic searches and suggest consideration might be given to recruiting local teams of volunteers to undertake systematic searches under the guidance of a professional coordinator. This method could have additional benefits by increasing public awareness of anthropogenic causes of turtle mortality and thereby could enhance public support for future mitigation measures. Long term data derived from consistent monitoring effort would be very valuable for identifying potentially changing trends in the frequency of vessel-related mortality and the proportional representation of turtle species and life stages.

2.5 Tables

Table 2.1 Turtle stranding records 1990 to 2002 for Queensland east coast, a summary of data from the Marine Wildlife Stranding and Mortality Database maintained by Queensland Environment Protection Authority.

Year	All turtle stranding records	Vessel-related records
1990	177	27 (15%)
1991	298	36 (12%)
1992	329	50 (15%)
1993	267	42 (16%)
1994	214	33 (15%)
1995	223	30 (13%)
1996	448	70 (16%)
1997	430	53 (12%)
1998	389	53 (14%)
1999	492	79 (16%)
2000	495	65 (13%)
2001	512	77 (15%)
2002	503	60 (12%)
Total	4777	675 (14%)

Table 2.2: Vessel-related mortality of turtles recorded for Queensland east coast compared to turtle mortality in trawl fishing prior to the introduction of Turtle Excluder Devices (TEDs). Data represent the number of turtles killed annually.

	Turtle deaths ascribed to vessel impacts [A]	Potential vessel impact deaths if 33% of actual deaths were recorded [B]	Potential vessel impact deaths if 7% of actual deaths were recorded [C]	Observed direct mortality in Queensland East Coast Trawl Fishery pre TEDs [D]	Observed potential mortality in Queensland East Coast Trawl Fishery pre TEDs [E]
Chelonia mydas	54	163	768	10	101
Caretta caretta	6	17	79	31	149
Unknown/other spp	5	16	75	27	94
All species combined	65	195	929	61	319

[A] Four-year average for Queensland Environment Protection Authority stranding data 1999 – 2002 only

[B] Speculative estimate using percentage derived from Queensland Environment Protection Authority trial (Anon, 1999)

[C] Speculative estimate using low end of 7-13% range derived from Nth Carolina study by Epperly *et al*. (1996)

[D] Annual turtle mortality 1991-1996 in Queensland East Coast Trawl Fishery comprising only those captured turtles reported as dead (Robins 2002);

[E] Annual turtle mortality 1991-1996 in Queensland East Coast Trawl Fishery comprising captured turtles reported as dead plus captured turtles reported as comatose (Robins 2002)

2.6 Figures

Figure 2.1: Evidence of vessel-related mortality of marine turtles was derived from stranding data for the east coast of Queensland, Australia. Labels placed to seaward of the coastline identify the five areas of interest (defined by arbitrary boundaries) where stranding records were concentrated.

2.7 References

ANON (1999) Sea Turtle Strandings 1 January - 31 December 1998. Brisbane, Queensland Environmental Protection Agency.

COMMONWEALTH OF AUSTRALIA (2001) Census of Population and Housing 2001. Australian Bureau of Statistics.

CSIRO (2003) CSIRO Marine Data Center. Commonwealth Scientific & Industrial Research Organisation (CSIRO).

DOBBS, K. (2001) *Marine turtles in the Great Barrier Reef World Heritage Area,* Townsville, Great Barrier Reef Marine Park Authority.

ENVIRONMENT AUSTRALIA MARINE SPECIES SECTION (2003) Recovery plan for marine turtles in Australia. Canberra, Environment Australia.

EPPERLY, S. P., BRAUN, J., CHESTER, A. J., CROSS, F. A., MERRINER, J. V., TESTER, P. A. & CHURCHILL, J. H. (1996) Beach strandings as an indicator of at-sea mortality of sea turtles. *Bulletin of Marine Science,* 59**,** 289-298.

GREAT BARRIER REEF MARINE PARK AUTHORITY (2003a) Marine Wildlife Stranding Listserver. Great Barrier Reef Marine Park Authority.

GREAT BARRIER REEF MARINE PARK AUTHORITY (2003b) Sea Temperature Monitoring. Great Barrier Reef Marine Park Authority.

HAINES, J. A. & LIMPUS, C. J. (2001) Marine wildlife stranding and mortality database annual report, 2000 - III Marine turtles. Brisbane, Queensland Parks and Wildlife Service.

HAINES, J. A., LIMPUS, C. J. & FLAKUS, S. (2000) Marine wildlife stranding and mortality database annual report, 1999 - III Marine turtles. Brisbane, Queensland Parks and Wildlife Service.

HEPPEL, S. S., CROWTHER, L. B. & R., M. T. (1999) Life table analysis of long-lived marine species with implications for conservation and management. *American Fisheries Society Symposium***,** 137-148.

KWAN, D. (2004) Review and refinement of the Queensland marine mammal and turtle stranding and mortality program focused in the Great Barrier Reef World Heritage Area. Townsville, Report to the Great Barrier Reef Marine Park Authority.

LIMPUS, C. J. (1983) The Reef: Uncertain Land of Plenty. In LAVERY, H. J. (Ed.) *Exploration North: A Natural History of Queensland.* South Yarra, Lloyd O'Neil Pty Ltd.

LIMPUS, C. J. (2002) Turtdata Database Manual. *Queensland Turtle Conservation Project & Monitoring of Marine Wildlife Mortality & Strandings.* Brisbane.

LIMPUS, C. J., MILLER, J. D., PARMENTER, C. J., REIMER, D., MCLACHLAN, N. & WEBB, R. (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildlife Research,* 19**,** 347-358.

QUEENSLAND GOVERNMENT (2004a) Office of Economic and Statistical Research: Private vessel registration.

QUEENSLAND GOVERNMENT (2004b) Office of Economic and Statistical Research: Shipping arrivals for selected ports.

ROBINS, J. B. (2002) *A scientific basis for a comprehensive approach to managing sea turtle by-catch: the Queensland east coast as a case study (PhD)*, James Cook University.

WIBBELS, T. (2003) Critical Approaches to Sex Determination in Sea Turtles. In LUTZ, P. L., MUSICK, J. A. & WYNEKEN, J. (Eds.) *The Biology of Sea Turtles Volume II.* Boca Raton, CRC Press.

Chapter 3: Study sites and methods for observing green turtle behaviour in shallow foraging areas

Abstract

Green turtles in natural open water habitat tend to be wary and difficult to observe beyond brief glimpses. They therefore presented challenging subjects for the behavioural studies that I intended to undertake in the area with Australia's highest recorded incidence of turtle mortality from vessel strike (Chapter 2). In this chapter I explain my selection of two study sites separated by approximately 40 km, summarise site features and describe my opportunistic observations of vessel traffic in each area, respectively near the North-Eastern and South-Western sides of Moreton Bay. I also describe various observation methods that I tried and report on their benefits and limitations. Overall this chapter provides additional background and context for my research reported in Chapters 4 to 7 and includes detail that might be of relevance for others considering similar work.

3.1 Introduction

Modern biological study of animal behaviour was established during the middle decades of last century based on careful visual observation. Founding researchers necessarily restricted their focus either to animals that could be raised and maintained in domestic or laboratory environments conducive to naturalistic behaviour or to species that were available for direct observation in the wild (Burkhardt, 2005). Various novel technologies for remote photography and remote digital data acquisition have expanded opportunities for indirect ‘observation’ (in a broader sense) of animals but direct visual observation continues to play a crucial role in current behavioural studies (Dawkins, 2007; Martin and Bateson, 2007).

Wide-ranging marine species like turtles, which are rarely visible to human observers, present particularly challenging subjects for behavioural studies. Their behaviour has been intensively studied only at nesting beaches. During this brief but crucial stage of their life cycle, adult females and hatchlings are exposed to multiple anthropogenic impacts. At the same time they are available for direct observation by scientists whose finding can guide strategies to mitigate negative impacts (e.g. Witherington, 1997).

In contrast to extensive coverage of all aspects of marine turtle reproduction (e.g. see Hamann et al., 2003 and references therein) the literature contains sparse data on turtle behaviour in near-shore foraging grounds. This is the environment where most green turtles are understood to spend many decades during their late juvenile and adult life stages, (Musick and Limpus, 1997; Plotkin, 2003) and where they face potentially high exposure to anthropogenic threats. Confirmation that vessel strike is an important threat to turtles in Queensland waters (Chapter 2) led me to seek new insight into green turtle behaviour at a location with the highest recorded incidence of vessel-related mortality in Australia. This chapter explains the rationale behind my selection of two study sites within Moreton Bay and summarises my opportunistic observations of vessel traffic in each area and aims to provide additional background and context for Chapters 4 to 7.

Despite the increasing capacity and sophistication of telemetry devices deployed on turtles and other wild animals, their utility in behavioural studies is constrained by the need to infer behaviour from the physical and physiological data that these devices record. Richer detail about marine turtle behaviour underwater has only been revealed in fragmentary glimpses during opportunistic visual observations (e.g. encounters reported informally by scuba divers and snorkellers) and derived from automated video cameras attached for short periods to the carapaces of turtles (e.g. Heithaus et al., 2002; Seminoff et al., 2006). For my research I needed to expand the temporal scope of behavioural observation, and I needed to include coverage of turtle responses to vessels. I evaluated alternative ways to pursue this work and report here on the benefits and limitations of methods I trialled.

3.2 Study sites

3.2.1 Site selection

I sought study sites in Moreton Bay (Fig. 3.1) because it is the area where the majority of reported turtle carcasses showing evidence of vessel-related injuries have been found (Chapter 2). Within Moreton Bay the vicinity of Moreton Banks represents a scientifically valuable location. That area underpins current knowledge of Moreton Bay turtle populations thanks to long-term demographic monitoring by Queensland Environmental Protection Agency staff and diet studies integrated with mark-recapture sessions (e.g. Limpus et al., 1994; Read et al., 1996; Brand-Gardner et al., 1999; Read and Limpus, 2002). However, a research project of extended duration at Moreton Banks would have been logistically beyond my limited resources due the cost of travel to and from the mainland and lack of affordable accommodation nearby. Subsequent extensive exploration of greater Moreton Bay confirmed that no single location was suitable for the diverse components of my study, leading to the selection of two sites separated by approximately 40 km.

My first study site (MB1 in Fig. 3.1) was located on the north-western side of Moreton Island. Most of this large sand island (37 km long, 10 km wide) comprises relatively undisturbed natural vegetation communities interrupted only by four small residential settlements. Due to oceanic inflow the water clarity at this site was high and allowed daytime visual observation of submerged turtles during favourable weather (Chapter 4). My first fieldwork session at this remote location was conducted from a temporary base on Moreton Island very kindly provided by the Tangalooma Marine Research and Education Foundation, while the second was conducted from a campsite on the island. The absence of a boat harbour and long-term accommodation near MB1, and the 40 km distance from mainland supplies and services, made it impractical to use this site for the other components of my research that needed to cover all seasons of the year and would require many weeks of daily boat operations and intermittent night operations.

To meet the latter requirements I selected a second site (MB2 in Fig. 3.1) near a harbour and boat launching ramps on the mainland shore of Moreton Bay. In contrast to MB1, this site was surrounded by urban land. The shoreline was occupied by residential and commercial buildings, urban recreation parks, roads and car parking and featured two man-made boat harbours with dredged access channels. A narrow strip of mangrove forest surrounded a complex of un-dredged drainage channels at the mouth of Tingalpa Creek, which flowed into the study area. Visual observation of submerged turtles was impossible due to turbid water at MB2 (as is the case throughout western and southern Moreton Bay) so telemetry methods were obligatory (Chapters 5 to 7).

3.2.2 Vessel traffic

Both study sites and their surrounding waters were subject to light to moderate vessel traffic during study periods, while moderate to heavy traffic sometimes occurred adjacent to and within the northern part of MB2. Proximity or density of traffic occasionally required research activities to be suspended temporarily. My field research would not have been feasible in areas of regular heavy traffic, on grounds of personal safety and the potential for my activities to hamper the efficient travel of other vessels.

Time and budget constraints precluded formal traffic surveys and I therefore observed vessel activity on an opportunistic basis whenever possible during field sessions, ferry travel and recreational boat trips. I noted wide variation in numbers and types of vessels. The most intense vessel traffic typically occurred on sunny days with light winds. Very few vessels were observed to travel at night, even in favourable weather. Adverse weather (strong wind or rain or both) was invariably associated with reduced traffic but numbers were not consistently high on days of fine, calm weather.

As a possible source of vessel traffic data I inspected multiple series of high-resolution aerial survey images held by the Queensland Government’s Department of Natural Resources and Mines (Brisbane, Queensland). I found their coverage of Moreton Bay water areas to be incomplete because flight paths for the governmental aerial surveys were aligned for efficient gathering of terrestrial details and shoreline changes only. Furthermore, years elapsed between survey series, consistent with the objective of recording gradual processes. Finer temporal resolution and greater spatial coverage of water bodies might be obtained from commercial aerial imagery sources but the cost was beyond my resources.

In the governmental aerial images a few individual vessels could be detected but it was impossible to distinguish moving vessels from anchored or moored vessels. It was also impossible to infer travel routes before and after the instant that the image was recorded. Because individual identities of vessels could not be established from such images, inference about the tracks followed by individual vessels would be unreliable even if a rapid series of aerial images of the same location were available. The latter was unlikely since most aerial imagery is obtained from a moving plane or satellite.

I concluded that visual surveys of vessel traffic were the only feasible method to obtain traffic data relevant to mitigating the risk of wildlife collisions. (Observations at boat ramps, while logistically convenient, would not provide data representative of general vessel traffic in Moreton Bay because only relatively small vessels are transported on trailers and launched at public boat ramps.) The land surrounding Moreton Bay is generally low and lacks high viewpoints close to the shoreline and numerous islands within the bay prevent expansive views from single observation points at low elevation. Numerous observation sites would therefore be required, of which many would need to be boat-based. Adequate sampling to obtain robust quantitative measures would be challenging due to the spatial and temporal variation in vessel usage noted above. Even for a limited portion of Moreton Bay, a comprehensive traffic survey would be a substantial task; comprehensive coverage of the entire bay would require prodigious effort.

3.2.3 Vessel types at MB1

On most observation days several ocean-going ships passed <1 km to the west of MB1, constrained to beaconed deep water channels en route to and from the Port of Brisbane. Commercial craft of moderate draft, including fishing vessels, naval patrol boats, tugs, dredges, ferries and tour boats followed more diverse routes, at times passing <250 m from our experimental transits. Tour boats traversed the middle of this study site during several study sessions and I observed commercial fishing operations using gill nets or beach seines within MB1 on rare occasions.

The large majority of traffic within MB1 comprised recreational vessels. Small craft, including outboard-powered dinghies and runabouts, sailboats and kayaks were launched from the Moreton Island shore, particularly during holiday periods when many visitors occupied the island’s beach-side camping areas. Larger recreational craft using MB1 had evidently travelled from launching ramps and moorings close to Brisbane’s mainland suburbs and from residential townships on islands in the southern and northern sectors of Moreton Bay (inferred from approach trajectories). This category was dominated by fast planing motor boats of ~6 to 10 m, the balance comprising larger planing craft, displacement motor cruisers and occasional sailing vessels. Many vessels anchored for extended periods at popular fishing sites adjacent to MB1 while some passed without stopping, apparently bound for other destinations.

3.2.4 Vessel types at MB2

The absence of deep water close to MB2 entirely excluded large ships and other deep draft vessels. Small tugs and dredges passed occasionally and for two days during a study session I observed a tug and dredge operating within MB2 to conduct maintenance dredging of a boating channel. Small commercial fishing vessels conducted intermittent gill netting operations and regular deployments of crab traps within MB2. Within and beyond this study site numerous crab and fish traps were also deployed by recreational fishers, particularly during holiday periods. The northern part of MB2 was regularly used by numerous recreational craft and some ferries and tour boats. Central and southern parts of the site were used to a lesser extent, predominantly by very shallow draft vessels that could range widely and used intermittently by shallow to moderate draft vessels that traversed deeper channels at higher tidal levels.

Recreational vessels using waters in and adjacent to MB2 were diverse in type. Wind-powered vessels ranged from sailboards to yachts up to ~20 m but those of moderate to deep draft were constrained to the northern edge of MB2 when they travelled between Manly boat harbour (located close to the western side of MB2) and more distant deeper waters to the east and north-east. Sailing vessels were at times numerically dominant in the area, particularly during competitive events conducted separately for sailing dinghies and for cruising and racing yachts from ~6 to 10 m. Overall, however, the majority of vessels were motorised. Among these, planing motor boats of ~4 to 10 m predominated. The balance included motor cruisers up to ~20 m, and smaller craft such as jet-skis. Human powered craft (canoes, kayaks and rowing boats) represented a very small component of vessel traffic at MB2.

3.3 Methods for observing turtle behaviour

3.3.1 Underwater observation

Within the extensive scientific literature on marine turtles there are few studies entirely reliant on underwater observation of submerged turtles in their natural habitat. The time span between two notable examples (green turtles in tropical Australian waters - Booth and Peters, 1972; loggerhead turtles in the Mediterranean - Schofield et al., 2007) probably reflects the paucity of sites and opportunities for safe and efficient conduct of such observations.

Importantly the studies of Booth and Peters (1972) and Schofield et al (2007) both took place at mating and nesting areas where turtles in their reproductive phase apparently tolerated swimmers at close proximity. Such tolerance would be concordant with the reduced wariness of turtles engaged in reproductive activity, a situation that has long been exploited by hunters and land-based researchers at turtle nesting beaches. Outside of reproductive periods turtles show varying degrees of tolerance of swimmers at some locations (J Hazel personal observation) but turtles that I encountered during underwater investigations in Moreton Bay were wary and invariably moved away soon after I sighted them.

Deploying submerged observers among vessels operating in shallow water had been ruled out *a priori* on grounds of human safety, and Moreton Bay turtles' aversive responses to an underwater observer removed this method from consideration for a "vessels-absent" component of my study. I next considered alternative methods for above-water observation.

3.3.2 Observation from a stationary vessel

Given calm daylight conditions in Moreton Bay, an attentive boat-based observer could easily see green turtles within a radius of 60 m or more, whenever the animals exposed their heads above the sea surface to breathe. However, for an observer positioned close to water level, turtles were lost from view within seconds after they submerged in clear water at study site MB1. A turtle seen at the surface was instantaneously lost from view when it submerged in turbid water at MB2 and elsewhere.

Observation range was enhanced by an elevated platform on one of our research vessels that provided a height of eye approximately 3.2 m above sea level for a seated observer. Use of polarised sunglasses aided observation in bright light. While the vessel was anchored at study site MB1 in depths of 2 to 3 m, I used the elevated platform to observe turtles swimming in the water column and foraging or resting on the substrate at distances ≤30 m (Fig. 3.2). During trials of this method I observed focal animals for continuous periods up to 47 min but few focal follows exceeded 15 min and many failed within 5 minutes. These observations were interrupted not only when turtles moved beyond visibility range but also by temporary disruptions to visibility caused by wave action, cloud shadows and other animals.

Another limitation emerged, in that turtle behaviour was apparently influenced by the presence of the research vessel. Turtles often happened to move towards the vessel as they foraged but they changed their direction of movement to pass at distances of 10 to 15 m or more from it. Presumably turtles were able to detect the vessel visually, since the vessel was stationary and silent. Their avoidance response suggested that they perceived the vessel as a potential danger.

3.3.3 Observation via an aerial video camera

Tethered aerial video systems were first devised for marine mammal studies (e.g. Flamm et al., 2000; Nowacek et al., 2001). A modified version of those earlier designs was developed to investigate the behaviour of dugong (*Dugong dugon*) in eastern Moreton Bay (Hodgson, 2004). Hodgson's equipment, dubbed the blimp-cam, comprised a remote-controlled video camera (Panasonic WV-CS854) suspended from a large helium-filled balloon (approximately 2.5 m diameter) that was tethered to an anchored boat during observations sessions. Deployed only during calm weather under conditions of good visibility, the blimp-cam served well for its original purpose of observing dugong herds (Hodgson and Marsh, 2007).

I was given the opportunity to borrow the blimp-cam equipment and I conducted trial sessions at study site MB1 to evaluate its utility for turtle observations (Fig. 3.3). During these trials a second research vessel, a 4 m open boat powered by an outboard motor, was driven by my assistants. While I operated the blimp-cam from the primary research vessel, which remained at anchor, the second vessel made regular transits across the study area to provide controlled opportunities to observe turtle responses.

The blimp-cam proved unsatisfactory for continuous focal follows of turtle behaviour and for observing individual turtle responses to an approaching vessel. This was primarily due to the smaller size of my study subjects compared to dugongs. A green turtle at my study site was typically about 1/3 the overall length of a dugong and presented a much smaller and less distinctive shape within the video field of view. For example, when the blimp-cam was operated at its designed working height (40 to 50 m) and a potential study subject was identified on the substrate at 2 to 3 m below the sea surface, the differentiation between a near-stationary turtle and other objects of similar size and shape was often unreliable, and small movements made by a benthic turtle were indiscernible.

The relative size of a subject in the video image could be enlarged by flying the blimp on a shorter tether and thus reducing the distance between subject and camera. However, the overall field of view then became narrower, hampering behavioural study by restricting observation of a turtle's surroundings. Furthermore, reducing the field of view exacerbated the difficulty of maintaining camera orientation (via remote pan and tilt controls) in the face of wind- and sea-induced movements of boat and blimp.

Blimp-cam observations of turtle responses to a passing vessel (Fig. 3.4) highlighted further limitations. The turtle's response – or lack of response – could only be observed if the moving vessel passed on the far side of the turtle relative to the blimp. During a near-side pass the turtle was lost to view, either behind or under the vessel and its wake. Furthermore, the oblique angle of view from the blimp (which was never static) precluded accurate estimates of distance between the vessel and the turtle.

3.3.4 Observation from a moving vessel

None of the methods I trialled was suitable for recording turtle behaviour in the absence of vessels. However I established a satisfactory method for quantifying turtle responses to vessels, using a moving vessel that served a dual role as stimulus for potential turtle responses and as observation platform. This usage, fully described in Chapter 4, proved effective and efficient. Substantial time and costs were saved by using only one vessel and eliminating the complex transport, setup and storage requirements of the blimp-cam system.

Despite the apparent simplicity of this observation method, accurate and safe conduct of experiments depended on rigorous training for all personnel beyond the prerequisite skills of open water boat operation. I undertook extensive practice until I could consistently detect turtles, instantly estimate their distances and record the required data rapidly under variable operating conditions. All boat drivers undertook on-site training until they could accurately maintain the designated direction and speed throughout each experimental transit despite changing winds and tidal currents. All participants practiced emergency stops for last-minute collision avoidance.

Throughout the study, constant alertness was essential to avoid close encounters with other vessels and, much more difficult, to detect cryptic submerged animals. The intermittent presence of solitary dugongs constituted a particular hazard due to their erratic movement and apparent disregard for our vessel’s approach. On several occasions it was necessary for us to undertake last-minute evasive action or emergency stops to avoid collision with a dugong or a turtle in the water column. This method could not be used safely with a large or heavy vessel incapable of stopping abruptly.

3.4 Prospective validation experiments

To support necessary reliance on estimates of distance and turtle size made from a moving vessel (Chapter 4) it would have been valuable to undertake validation experiments at the study site MB1. I assessed the feasibility of testing observer estimates in a rigorous manner by deploying dummy turtles of various sizes, as has been done under different circumstances elsewhere, e.g. by Houghton et al. (2003).

During preliminary trials I determined that the need to operate from a moving vessel, a crucial component of my experimental design, greatly increased the complexity and logistical challenges involved in such an approach to validation. Because excessive additional time and funding would have been required to conduct satisfactory validation tests under the variable weather and sea conditions prevailing at MB1, I was obliged to adopt an alternative strategy. As described in Chapter 4, the method ultimately adopted used a single observer to promote consistency of estimates, recognised the approximate nature of distance estimates and classified turtle size in two broad categories that could readily be differentiated under the specific circumstances of this study.

3.5 Prospective comparison of noisy vs. near-silent vessel transits

I attempted to repeat my vessel transit experiments (Chapter 4) using a vessel of similar size that was able to operate alternately under sail or under motor power, in order to compare turtle responses to noisy (motorised) or near-silent (sailing) approaches. After obtaining a suitable vessel I commenced a new study at MB1 about six months after the first field expedition to that site. The substantial training effort required for motorised experiments (section 3.3.4) was greatly increased by the additional need to train research assistants to operate the vessel under sail. Precise speed control under sail was particularly difficult to achieve because winds and currents were always variable.

After a large investment in training, the intended experimental transits were repeatedly delayed by persistent strong winds and then further delayed by prolonged heavy rain. The latter caused an immediate and severe deterioration in water clarity that persisted for many days after the rain ceased. I conducted some experimental sessions during subsequent weeks but adverse conditions persisted until time and funds allocated for the study were exhausted. It was not possible to mount a third expedition to MB1 due to the high cost, both in dollars and time, of prolonged field research at this remote site.

During the few experimental sessions that we were able to conduct, I noted a broadly similar trend to the results of Chapter 4. However the data were inadequate for analysis, being confounded by the potential for unobserved encounters. Failure of this second study highlighted the absolute dependence of my observation method on reliable coincidence of water clarity and favourable wind and sea conditions.

Despite the frustration of months devoted to the unsuccessful second vessel study and extensive trial observations from a stationary vessel (direct viewing and via blimp-cam), all of which yielded insufficient data for analysis, these efforts provided me with many insights into turtle behaviour in Moreton Bay. These insights proved valuable in guiding the planning, conduct and data interpretation of telemetry studies I undertook in further components of my PhD research (Chapters 5, 6, 7).

3.6 Figures

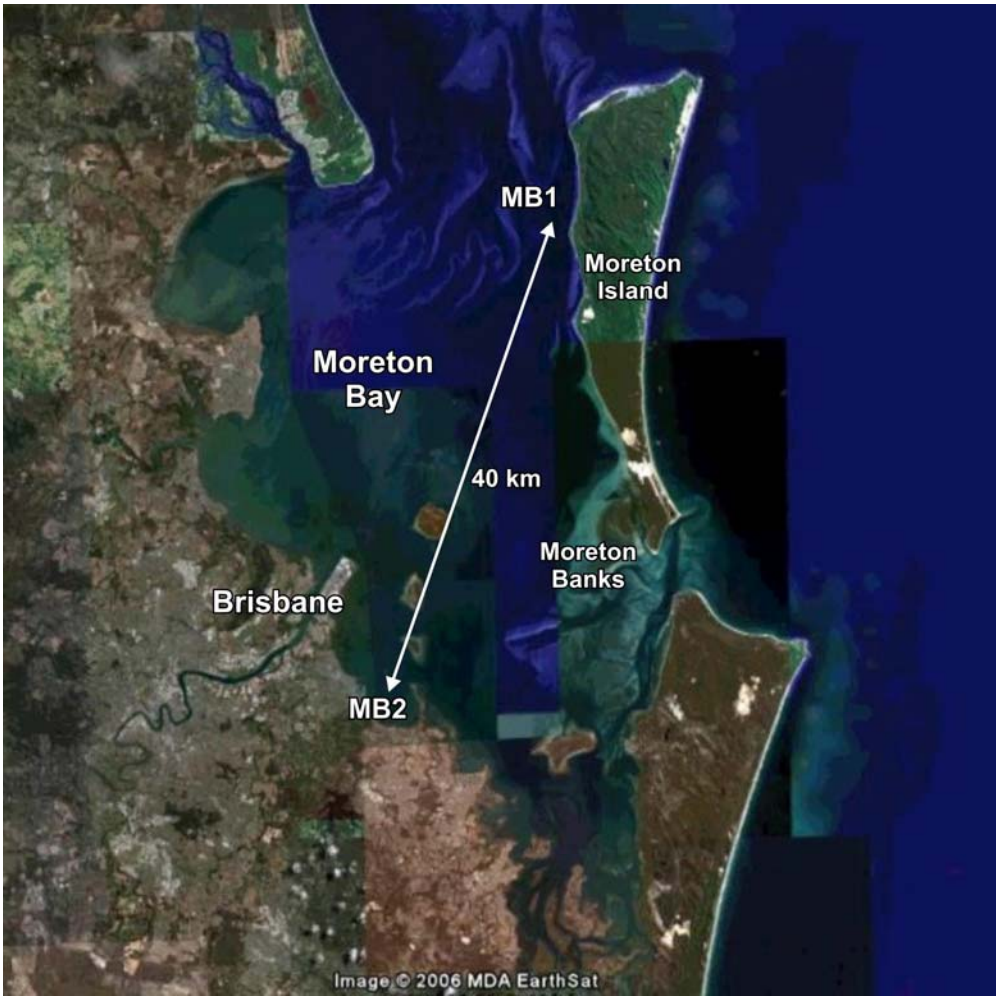

Figure 3.1. Moreton Bay lies adjacent to Brisbane, the state capital Queensland, Australia. It hosts a wide diversity of wildlife including green turtles that forage in areas of shallow, seagrass-dominated habitat such as my two study sites, MB1 and MB2, and the Moreton Banks where long-running demographic studies of turtles have been conducted by the Queensland Parks and Wildlife Service. Background image courtesy Google Earth.

Figure 3.2. *Chelonia mydas*. From an elevated platform on an anchored research vessel I conducted focal follow observations of individual turtles in open water at study site MB1 (Fig. 1). These images demonstrate the difficulty of discerning a turtle while it is resting or foraging on the substrate (centre left in panel a), whereas its distinctive shape becomes progressively clearer as the animal swims in the water column (b) and exposes its head at the sea surface (c). This turtle was approximately 25 m from the observation vessel, water depth ~2 m. The sequence of images (a to c) spans approximately 30 s.

Figure 3.3. At study site MB1 I evaluated the use of a remote-controlled aerial video system, supported by a helium-filled balloon. The equipment had originally been developed for studying herds of dugong (*Dugong dugon*) and had served well in that role (Hodgson, 2004). In contrast the equipment proved unsatisfactory for behavioural studies of green turtles. Photo courtesy K. Stockin.

Figure 3.4. *Chelonia mydas*. Blimp-cam video record of a 4 m vessel travelling at planing speed towards a submerged green turtle (panel a), over the turtle (b), and past the turtle (c). The turtle displayed no visible response. Water depth was ~1.5 m. The sequence of images (a to c) spans approximately 2 s.

3.7 References

BOOTH, J. & PETERS, J. A. (1972) Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Animal Behaviour,* 20**,** 808-812.

BRAND-GARDNER, S. J., LANYON, J. M. & LIMPUS, C. J. (1999) Diet selection by immature green turtles, *Chelonia mydas*, in subtropical Moreton Bay, south-east Queensland. *Australian Journal of Zoology,* 47**,** 181-191.

BURKHARDT, R. W. (2005) *Patterns of behaviour: Konrad Lorenz, Niko Tinbergen, and the founding of ethology,* Chicago, USA, University of Chicago Press.

DAWKINS, M. S. (2007) *Observing animal behaviour,* Oxford, UK, Oxford University Press.

FLAMM, R. O., OWEN, E. C. G., OWEN, C. F. W., WELLS, R. S. & NOWACEK, D. (2000) Aerial videogrammetry from a tethered airship to assess manatee life-stage structure. *Marine Mammal Science,* 16**,** 617-630.

HAMANN, M., LIMPUS, C. J. & OWENS, D. W. (2003) Reproductive cycles of males and females. In LUTZ, P. L., MUSICK, J. A. & WYNEKEN, J. (Eds.) *The Biology of Sea Turtles Volume II.* Boca Raton, CRC Press.

HEITHAUS, M. R., MCLASH, J. J., FRID, A., DILL, L. M. & MARSHALL, G. (2002) Novel insights into green sea turtle behaviour using animal-borne video cameras. *Journal of the Marine Biological Association of the United Kingdom* 82**,** 1049-1050.

HODGSON, A. (2004) Dugong behaviour and responses to human influences. *School of Tropical Environment Studies and Geography.* Townsville, James Cook University.

HODGSON, A. J. & MARSH, H. (2007) Response of dugongs to boat traffic: the risk of disturbance and displacement. *Journal of Experimental Marine Biology & Ecology,* 340**,** 50-61.

HOUGHTON, J. D. R., CALLOW, M. J. & HAYS, G. C. (2003) Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) around a shallow water coral reef. *Journal of Natural History,* 37**,** 1269-1280.

LIMPUS, C. J., COUPER, P. J. & READ, M. A. (1994) The green turtle, *Chelonia mydas*, in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum,* 35**,** 139-154.

MARTIN, P. & BATESON, P. (2007) *Measuring behaviour: An introductory guide,* Cambridge, UK, Cambridge University Press.

MUSICK, J. A. & LIMPUS, C. J. (1997) Habitat utilization and migration in juvenile sea turtles. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, CRC Press.

NOWACEK, D. P., TYACK, P. L. & WELLS, R. S. (2001) A platform for continuous behavioural and acoustic observations of free-ranging marine mammals: overhead video combined with underwater audio. *Marine Mammal Science,* 17**,** 191-199.

PLOTKIN, P. (2003) Adult migrations and habitat use. In LUTZ, P. L., MUSICK, J. A. & WYNEKEN, J. (Eds.) *Biology of Sea Turtles Volume II.* Boca Raton, CRC Press.

READ, M. A., GRIGG, G. C. & LIMPUS, C. J. (1996) Body temperatures and winter feeding in immature green turtles *Chelonia mydas* in Moreton Bay, south east Queensland. *Journal of Herpetology,* 30**,** 262-265.

READ, M. A. & LIMPUS, C. J. (2002) The green turtle, *Chelonia mydas*, in Queensland: feeding ecology of immature turtles in Moreton Bay, South Eastern Queensland. *Memoirs of the Queensland Museum,* 48**,** 207-214.

SCHOFIELD, G., KATSELIDIS, K. A., PANTIS, J. D., DIMOPOULOS, P. & HAYS, G. C. (2007) Female-female aggression: structure of interaction and outcome in loggerhead sea turtles. *Marine Ecology Progress Series,* 336**,** 267-274.

SEMINOFF, J. A., JONES, T. T. & MARSHALL, G. J. (2006) Underwater behaviour of green turtles monitored with video-time-depth recorders: what’s missing from dive profiles? *Marine Ecology Progress Series,* 322**,** 269–280.

WITHERINGTON, B. E. (1997) The problem of photopollution for sea turtles and other nocturnal animals. In CLEMMONS, J. R. & BUCHHOLZ, R. (Eds.) *Behavioural approaches to conservation in the wild.* Cambridge, UK, Cambridge University Press.

Chapter 4: Behavioural response of green turtles to an approaching vessel

---

Abstract

Vessel collisions contribute to the anthropogenic mortality of several threatened marine species including turtles, manatees, dugongs and whales, but scant data exist to inform the design of optimal mitigation measures. I conducted a field experiment to evaluate behavioural responses of green turtles *Chelonia mydas* to a research vessel approaching at slow, moderate or fast speed, respectively 4, 11 and 19 km h^{-1} (2, 6 and 10 knots). Data were recorded for 1890 encounters with turtles sighted within 10 m of the research vessel's track. The proportion of turtles that fled to avoid the vessel decreased significantly as vessel speed increased, and those turtles that fled from moderate and fast approaches did so at significantly shorter distances from the vessel than turtles that fled from slow approaches. These finding indicate that vessel operators cannot rely on turtles to actively avoid being struck by the vessel if it exceeds 4 km h^{-1}. As most vessels travel much faster than 4 km h^{-1}in open waters, I infer that mandatory speed restrictions will be necessary to reduce the cumulative risk of vessel strike to green turtles in key habitats subject to frequent vessel traffic.

4.1 Introduction

Vessel collisions contribute to the mortality and morbidity of several marine taxa, notably turtles (see Chapter 2 and references therein), sirenians (Ackerman et al., 1995; Greenland and Limpus, 2005; Laist and Shaw, 2006) and large cetaceans (Knowlton and Kraus, 2001; Laist et al., 2001; Jensen and Silber, 2003). Some affected species are of significant conservation concern in various jurisdictions, as a result of the cumulative effects of human-induced and natural mortality, habitat disturbance and low reproductive capacity, (e.g. U.S. Fish and Wildlife Service, 2001; Environment Australia Marine Species Section, 2003; National Marine Fisheries Service, 2005).

Vessel traffic has severely affected North Atlantic right whales *Eubalaena glacialis*, for which collisions have been identified as a major source of mortality (Knowlton and Kraus, 2001), and Florida manatees *Trichechus manatus latirostris* where 25% of all documented deaths have been caused by collisions (Haubold et al., 2006). Stranding records for Queensland, Australia indicate that 7% of dead dugongs (*Dugong dugon*) had been struck by vessels (Greenland and Limpus, 2006), as had 14% of dead sea turtles (Chapter 2). These records are largely from populated areas of the state and comprise an unknown proportion of total mortality.

Management authorities have sought to mitigate vessel-related injuries to wildlife by identifying locations of particular importance for vulnerable species. Vessel operators are urged to increase vigilance within these areas, where recommended or obligatory routes and speed restrictions may apply. Other protective measures such as acoustic warning devices have been proposed (e.g. Gerstein, 2002) but their utility in the wild remains uncertain. Proposed mandatory speed regulations for large vessels in some offshore areas have raised serious concerns about anticipated economic costs to shipping operators, who emphasize that speed regulation has not been confirmed as an effective measure for reducing ship-whale collisions (World Shipping Council, 2006). Furthermore, although speed restrictions in coastal waterways have been in place since the mid- or late 1990s at many locations in Florida and a few locations in Queensland, their intended role in reducing collisions between vessels and marine wildlife has not been clearly demonstrated.

There is, however, preliminary evidence from Merritt Island, Florida, that suggests speed restrictions can be effective in protecting manatees at some locations, provided the restrictions are refined to match site-specific conditions and provided compliance is assured by effective enforcement (Laist and Shaw, 2006). These provisos appear difficult to achieve: Variable levels of compliance with speed restrictions have been reported in many areas (e.g. Groom, 2003; Gorzelany, 2004; Hodgson, 2004) and only scant data exist to inform the optimal design of speed restrictions.

Speed reduction strategies apparently derive from the expectation that slower speed should afford greater opportunity for both vessel operators and animals to identify imminent collision risks and take avoidance action. However, even the most vigilant vessel crews are unable to see submerged animals (except at close range in very clear water) and are unlikely to see surface animals in rough seas or under low light conditions. Therefore, in practical terms, this rationale would imply a high degree of reliance on animals to avoid vessels. Yet the capacity of various species of marine wildlife to detect and evade approaching vessels remains poorly understood, hampering the determination of wildlife-safe maximum speeds for vessels travelling in critical habitats.

Researchers have investigated behavioural responses to vessels by manatees (Nowacek et al., 2004) and dugongs (Hodgson, 2004; Hodgson and Marsh, 2007) but systematic field data are lacking for other species susceptible to collisions. My study evaluated the ability of green turtles to avoid vessels and investigated behavioural characteristics of turtles that are potentially relevant to the reduction of collision risk.

4.2 Methods

4.2.1 Study site and species

The study was conducted during June to August 2004 at study site MB1 described in Chapter 3. The study site (Fig. 4.1) was selected because it provided favourable foraging habitat for green turtles, and the combination of clear water and a light-coloured sandy substrate made it possible for an attentive observer on a moving boat to detect benthic animals with a high level of reliability.

Most turtles observed in the study area were positively identified as green turtles (*Chelonia mydas*). A few loggerhead turtles (*Caretta caretta*) may have been present but undetected among submerged turtles sighted very briefly. Loggerhead turtles are known to share habitat with green turtles in some parts of Moreton Bay (Limpus et al., 1994) but no loggerhead turtles were actually identified during the entire study period. I assume that few loggerheads (if any) are included in the data presented in this chapter.

4.2.2 Experimental trials

I used a six-metre aluminium boat powered by a 40-horsepower outboard motor to simulate transits of recreational boats travelling across the study site. An assistant drove this research vessel while a second assistant kept a safety lookout. I acted as the observer, positioned at the bow, where I maintained a continuous watch directly ahead and recorded all encounters with turtles.

The driver steered by compass bearing and visual reference to land features, and kept the vessel on a steady course that was independent of the presence of turtles. Animals below the sea surface were not visible from the driver's position at the rear of the vessel. Emergency stopping procedures were practised in advance to ensure they could be employed immediately if I or the lookout person signalled danger. These measures proved effective; no collisions occurred. To avoid confounding effects, transits were temporarily suspended when other vessels approached.

Transits were conducted alternately north-bound and south-bound over a distance of approximately 5 km, roughly parallel to the shoreline. Distance from the shoreline (200-450 m) was varied from one transit to the next in order to distribute spatial coverage evenly, and to minimise the chance of sequential encounters with individual turtles. Each transit continued at least 300 m beyond the last turtle sighted and was followed by an interval (≥20 min) at anchor with the engine off.

All transits were conducted in water depths of 2 to 4 m. These limits were determined during preliminary trials to ensure the research vessel could pass safely over a grazing or resting turtle and the observer could see the substrate clearly. Water clarity was consistently good during the study period with vertical Secchi depths of 12 to 13 m measured in deeper water immediately adjacent to the study site. Experimental trials were restricted to 3 h before and after solar noon on days with good atmospheric visibility (no precipitation, predominantly clear sky) and calm or light wind (≤15 km h^{-1}). In addition, I re-evaluated visibility conditions before each transit and only allowed the trial to proceed if confident of detecting all turtles within 20 m of the vessel. When that criterion was not met, work was suspended temporarily (e.g. in the case of passing cloud or glare) or abandoned for the day (e.g. in the case of rising wind).

I defined three experimental speeds that reflected the operation of vessels ≤20 m length in Moreton Bay. 'Slow' speed, 4 km h^{-1} (2 knots) approximated a lower limit for maintaining steerage; 'moderate' speed, 11 km h^{-1} (6 knots), represented prudent operation near visible obstacles; ‘fast’ speed, 19 km h^{-1} (10 knots), represented the lower range of unrestricted travel in open water. Many vessels in Moreton Bay routinely exceed 19 km h^{-1} but safety and feasibility precluded experiments at higher speeds. My speed definitions were broadly generalised to cover the diverse types of recreational and commercial vessels using Moreton Bay, and derive from my unpublished data and long-term personal experience as well as published work (Maitland et al., 2006).

The speed of the research vessel was held constant for the duration of each transit by reference to a global positioning system receiver (GPS model Garmin 12, Garmin International Inc, Kansas, USA). Accuracy of the receiver’s velocity presentation was confirmed in separate time-distance trials. One of the three experimental speeds was assigned for each transit in an alternating pattern, subject to ambient conditions. It was sometimes necessary to substitute a slow or moderate transit in place of a fast transit, due to a minor increase in wind and sea state. I accepted the resulting imbalance in total encounters for the three speed categories as a necessary compromise in a field experiment subject to weather and time constraints.

While my main goal was to determine whether vessel speed influences collision risk for turtles, I also wanted to test an hypothesis (prompted by prior field observations) that turtles may rely on vision, rather than sound, to detect approaching vessels. For this purpose the alternating direction of transits served as a proxy for manipulating underwater visibility, in the following way. As the study was conducted during the austral mid winter, the sun maintained a northerly azimuth at relatively low elevation. Underwater objects were visible to a diver at a greater distance when looking south (sun behind) than when looking north (sun ahead). Thus turtles were expected to have greater opportunity for visually detecting a north-bound vessel (turtle looking south, sun behind) than a south-bound vessel (turtle looking north, sun ahead).

4.2.3 Data recording and analysis

During each transit I recorded all encounters with turtles sighted within 10 m of the vessel’s track. The 10 m limit was adopted to standardise sighting conditions. Preliminary trials had established that benthic turtles were detected by the observer at ≥20 m and that those beyond 10 m very rarely fled from the vessel. Distances were determined by visual estimates and must be regarded as approximate since calibration was not feasible. To promote consistency I made all observations myself and constantly referenced my estimates against the known dimensions of the research vessel. Shorthand notation was used to allow rapid data recording without compromising the continuity of observation.

For each encounter I recorded the turtle's vertical position (benthic, in the water column or at the sea surface) and estimated the lateral offset distance between the turtle and the vessel's track (1 in Fig. 4.2a). The outcome of the encounter was recorded as 'Flee' if the turtle abruptly commenced swimming before the bow of the vessel (or a perpendicular line projected from the bow) passed the turtle's initial position. If the turtle did not flee before the vessel passed, the outcome was recorded as 'No Response'.

Additional information was recorded for each 'Flee' observation, comprising the forward distance at the moment the turtle initiated its flight (2 in Fig. 4.2a) and the direction of the turtle's initial flight trajectory (Fig. 2.2b–d). Forward distance and lateral offset distance were subsequently used to calculate the flight initiation distance (FID), defined as the shortest distance between the turtle and the bow of the vessel at the moment the turtle responded (3 in Fig. 2.2a).

At each encounter the turtle was classified as 'large' (estimated size range 85 to 110 cm curved carapace length) or 'small' (estimated size range 65 to 75 cm curved carapace length). Under the experimental conditions, the two size categories could be differentiated readily by an observer familiar with the size range of the local green turtle population. I considered it appropriate to analyse data separately by size category because small turtles typically display greater agility in their movements (noted during my related studies that involve hand-capture of study turtles) and therefore might evade vessels more readily than large turtles.

Some turtles were probably encountered several times over the duration of the study. As there was no way to identify individuals I did not use repeated measures analyses. I used the Chi Square test to determine whether the frequency of flee responses was independent of the experimental speed categories. To determine whether flight initiation distances were independent of speed categories I used the Mann-Whitney test because the data did not meet underlying requirements of parametric tests (Zar, 1999). I report test results as significant at the 0.05 level.

4.3 Results

The experiment comprised 1890 encounters with turtles. The overwhelming majority (1876, 99%) were large turtles with estimated curved carapace length in the range 85 to 110 cm. In most encounters (1832, 97%) the turtle was foraging or resting on the substrate when sighted. These were dubbed 'benthic turtles'. My results refer to observations of large benthic turtles (n = 1819) except where explicitly noted otherwise.

4.3.1 Effect of vessel speed on frequency of flee responses

Turtles fled frequently in encounters with a slow vessel (60% of observations at 4 km h^{-1}) but infrequently in encounters with a moderate vessel (22% of observations at 11 km h^{-1}) and only rarely in encounters with a fast vessel (4% of observations at 19 km h^{-1}). At all offset distances the proportion of flee responses decreased as speed increased, most notably for close encounters (Fig. 4.3). The relationship between frequency of flee responses and vessel speed was statistically significant for all except the widest offset category where it approached significance (offset 0 m: $\chi^2 = 152.6$, df = 2, $P < 0.001$; offset 1-2 m: $\chi^2 = 177.4$, df = 2, $P < 0.001$, offset 3-4 m: $\chi^2 = 111.4$, df = 2, $P < 0.001$; offset 5-6 m: $\chi^2 = 69.5$, df = 2, $P < 0.001$; offset 7-10 m: $\chi^2 = 5.3$, df = 2, $P = 0.072$, Fig. 4.3).

4.3.2 Effect of vessel speed on flight initiation distance

Vessel speed influenced the distance at which turtles initiated their response, if they responded at all. Turtles that fled in encounters with a slow vessel did so at a significantly greater distance (median FID 4.1m, n = 416) than those that fled in encounters with moderate and fast vessels (median FID 2.2m, n = 157, Mann-Whitney U=18516.5, $P < 0.001$, Fig. 4.4a). Flee responses were pooled for fast and moderate speeds for this comparison as their flight initiation distances were not significantly different for these speeds (Mann-Whitney U= 1192, $P = 0.221$).

4.3.3 Effect of transit direction

During north-bound transits turtles tended to flee more frequently and at slightly greater distances than during south-bound transits. For all speed categories combined, on northbound transits 307 fled (35%) in 875 observations, with a median FID of 4.0 m, while on southbound transits 266 (28%) fled in 944 observations, with a median FID of 3.8 m. At slow speed, northbound, 220 (66%) fled in 333 observations with median FID 4.1 m, compared with slow speed southbound, 196 (54%) fled in 361 observations, median FID 4.5 m. At slow speed transit direction was associated with a significant difference in response frequency ($\chi^2 = 10.0$, df = 1, $P = 0.002$, Fig. 4.4b) and a marginally significant difference in flight initiation distance (Mann-Whitney U= 19149, $P = 0.049$). At moderate and fast speeds the differences were not statistically significant.

4.3.4 Non-benthic turtles

Encounters with non-benthic turtles (33 in the water column, 24 at the surface) followed the same general pattern as benthic turtles, showing reduced response frequency at faster vessel speed (Fig. 4.4c). The small sample sizes precluded statistical analysis.

4.3.5 Small turtles

Small turtle observations comprised 13 benthic turtles and 1 in the water column. Of the benthic turtles, 3 fled in 6 encounters at slow speed, 3 fled in 5 encounters at moderate speed, 1 fled in 2 encounters at fast speed. The small sample sizes precluded further analysis.

4.3.6 Response characteristics

All benthic turtles that responded to the vessel launched upwards at a shallow angle to the substrate and began swimming. Thereafter individual turtles followed diverse trajectories, with 426 (74%) of the 573 that fled immediately moving away from the vessel's track, a 'safe' flee response as defined in Fig. 4.2b. However 46 (8% of fleeing turtles) initially swam along the vessel's track ('in-track' response, Fig. 4.2c) and 101 (18% of fleeing turtles) crossed in front of the vessel before moving away ('cross-track' response, Fig. 4.2d).

In-track responses were slightly less frequent at slow speed (7%) than at moderate and fast speeds (10%, 10%). However, cross-track responses were more frequent at slow speed (20%) than moderate and fast speeds (11% and 10% respectively). The majority of cross track responses, 80 (79%) of 101, involved a turtle that was initially located on the landward side of the vessel moving towards deeper water.

4.4 Discussion

Greater vessel speed increased the probability that turtles would fail to flee from the approaching vessel. Failure to flee leaves a turtle vulnerable to collision risk, unless adequate vertical distance between the vessel and the turtle allows the vessel to pass safely above the animal. Importantly, overwhelming failure to flee occurred at speeds slower than typical travelling speeds of contemporary vessels (see 4.4.2) and, as my results indicate, the majority of turtles can not be relied upon to avoid vessels travelling faster than 4 km h^{-1}. My findings thus imply that changes in human activity will be necessary to mitigate collision risks in areas where vessels operate in important turtle habitat.

4.4.1 Constraints on turtles' avoidance responses

The opportunity for an animal to respond appropriately to an approaching source of danger is necessarily constrained by how soon the animal can detect the danger. Contemporary knowledge of the sensory biology of marine turtles (Moein Bartol and Musick, 2003) indicates that sound and light offer the only potential cues for detecting an approaching vessel. The ability of marine turtles to hear underwater sound has been confirmed by measuring their auditory brainstem responses (Ketten and Bartol, 2006) and by observations of their behavioural responses to sound (O'Hara and Wilcox, 1990; Moein et al., 1993). The relatively low frequency range of turtle hearing (Ketten and Bartol, 2006) lies well within the broad frequency spectrum of noise produced by vessels (Richardson et al., 1995). Yet despite turtles' known auditory capacity, several factors mitigate against primary reliance on sound cues.

The direction of an underwater sound source is difficult to identify precisely due to complex propagation characteristics of sound underwater (Richardson et al., 1995). In addition, marine areas heavily used by humans, such as Moreton Bay, are subject to noise from numerous vessels as well as other anthropogenic sources above and below the surface, which would tend to mask individual sounds. In such areas I infer that sound would have minimal utility for submerged turtles in escaping a mobile threat and suspect that turtles would tend to habituate to vessel sounds as background noise. My results were consistent with this proposition. If turtles relied primarily on sound cues then higher response rates would be predicted for faster approaches (louder engine noise at higher speed), the converse of my results.

There appears to be no precedent in chelonian evolutionary experience for fast-moving noisy predators in the water. However, marine turtles have co-existed for millennia with swift, silent underwater predators. Sharks remain important predators of turtles in near-pristine coastal areas (see Heithaus et al., 2005) and early visual detection of an attacking shark would enable a turtle to enhance its survival prospects. I suggest that turtles depend similarly on timely visual detection to evade approaching vessels.

Efficient turtle vision has been confirmed through physiological and behavioural studies in the laboratory and on nesting beaches. This research has established that turtles see with sufficient visual acuity to discern relatively small (prey-sized) objects, differentiate between colours, and rely on vision for returning to the sea after nesting (see Moein Bartol and Musick, 2003 and references therein). Retinal structures in turtles are considered likely to confer visual advantage in the marine environment (e.g. Oliver et al., 2000; Bartol and Musick, 2001; Mäthger et al., 2007). Anecdotal field observations also attest to the apparent ability of turtles to detect danger by sight while underwater. For example, when the research vessel was anchored (with engine off) in the study area, green turtles were frequently observed moving slowly towards the vessel as they grazed on the substrate but none passed close by or under the vessel. Instead approaching turtles altered course to maintain distances of ~15 m as they passed the silent vessel.

Underwater vision is limited in range because light transmission is attenuated by organic and inorganic matter in the water (Preisendorfer, 1986). Consequently a submerged turtle that relies on visual detection of an oncoming vessel must be constrained by the prevailing water clarity. For example, if turtles' underwater vision slightly exceeds that of humans, a maximum visual detection limit of about 20 m would be likely in the clearest parts of Moreton Bay, whereas a range of hundreds of metres would be expected for auditory detection of a vessel motor (as is routinely confirmed by scuba divers) given that low frequency sounds propagate efficiently underwater (Richardson et al., 1995). The flight initiation distances for turtles that responded to my experimental vessel did not exceed 12 m (Fig. 4.3 b), a finding consistent with dependence on visual cues rather than sound cues.

The difference in experimental response rates for north-bound vs. south-bound transits was also consistent with turtles' dependence on vision and water clarity. Response rates were higher and flight initiation distances were slightly greater for north-bound transits, when underwater visibility was expected to be enhanced by the direction of solar illumination (see 4.2.2). This differential response by transit direction cannot be explained in terms of sound detection since vessel heading did not alter engine noise.

The low rate of flee responses during moderate and fast experimental transits is consistent with physical limitations of visual detection. Simple calculation (time = distance/speed) shows that an optimistic scenario of a vessel approaching at 19 km h^{-1} in waters allowing 15 m visibility would provide only 3 s (Fig. 4.5) for a perpetually vigilant turtle to see the vessel, determine its trajectory and move out of its track. An even shorter response opportunity would apply if a turtle scans for danger only intermittently while it forages or rests, and if visibility is reduced by turbidity or darkness. I propose that the extreme brevity of response opportunity afforded to a vision-dependent turtle explains their inability to evade fast vessels.

4.4.2 The role of vessel operators in avoiding collisions

The moderate and fast speeds used in my experiment were lower than the speeds of many types of recreational and commercial vessels travelling across a large embayment like Moreton

Bay. In non-planing displacement mode, small open water boats typically maintain 8-12 km h^{-1} and larger craft can travel correspondingly faster without planing. Planing vessels often exceed 20 km h^{-1} and many travel at 30-45 km h^{-1}, some even faster (J. Hazel unpublished data, Maitland et al., 2006). Thus most vessels travelling in unrestricted coastal waters maintain speeds that preclude reliable avoidance responses by turtles and therefore collision avoidance must necessarily depend on vessel operators.

Stringent measures were employed during my experimental transits to ensure turtle safety: (1) a dedicated observer at the bow at all times, (2) travel restricted to high visibility conditions, (3) relatively low maximum speed, and (4) emergency stops when required. Comparable measures are seldom feasible for commercial and recreational vessels during normal operations. Choppy water and low light severely reduce the chance of sighting a turtle at the surface, while in turbid water even the most attentive observer cannot see submerged turtles. Turtles spend most of the time submerged – in my study 1866 out of 1890 encounters (99%) involved turtles below the surface – meaning that vessel operators will rarely be able to detect the close proximity of individual turtles. Even if a turtle is spotted at close range in front of a vessel, an immediate stop or abrupt course deviation will usually be impossible. Speed reduction appears to be the only way vessel operators can minimise collision risk when operating in turtle habitat.

4.4.3 Management considerations

My results strongly support the use of speed restrictions to prevent vessel injuries to turtles in shallow waters. Given the diverse types of vessels that use relatively shallow areas, a minimum safe depth cannot be defined exactly but as a guiding principle, deeper water can be expected to reduce – but not eliminate – the risk of collisions. As demonstrated in my study, a vessel can pass safely over a benthic turtle provided there is sufficient clearance between the animal and extremities of the vessel, with allowance for water turbulence generated by hull movement and propeller rotation. Additional clearance is essential for safety because a turtle that detects the vessel only at the last moment is likely to move upwards, in initiating a belated flee response, just as the vessel passes over it, behaviour often noted during the experimental transits.

My findings point to two situations where speed restrictions may be particularly valuable in protecting turtles: (1) where vessels travel across shallow turtle foraging habitat, and (2) where vessels use deeper channels between shoal banks that offer foraging opportunities for turtles. Deeper channels might be considered less risky on the criterion of depth alone. However, high volumes of vessel traffic adjacent to shallow foraging habitat may be particularly dangerous for turtles because they tend to (a) flee towards deeper water (see 4.3.6) and (b) use deeper water to rest between foraging bouts during the day as well as overnight (e.g. Bjorndal, 1980; Brill et al., 1995; Makowski et al., 2006). The collision risk for turtles in all areas is likely to be further exacerbated if water clarity is low and if vessel traffic continues at night, since both turbid water and darkness would impede turtles' visual detection of danger.

I note that optimal designation of speed restriction zones is a potentially complex task, especially for areas that host multiple vulnerable species. Some species may benefit from other mitigation measures (e.g. Gerstein (2002) advocates acoustic deterrents for manatees) and some sites may require a combination of speed and route restrictions (see recommendations of Maitland et al (2006) for dugongs at Burrum Heads, Queensland).

The trade-off between minimising potential inconvenience to vessel operators and optimal protection for marine wildlife presents a challenge to managers, particularly as my results indicate that a very slow speed (~4 km $h^{-1)}$ is necessary to assure a 'turtle-safe' transit across shallow foraging sites. Considering that vessel operators have long been accustomed to freedom of movement in coastal waters, it seems unlikely that the majority will voluntarily adopt substantially slower speeds. I believe that effective speed reduction will require mandatory measures backed by effective enforcement. Nevertheless, public education would be useful to raise awareness of the constraints on turtles' ability to evade vessels and increase vessel operators' understanding of collision mitigation measures.

If particular high-risk zones can be accurately identified, the most stringent enforceable speed constraint will maximise turtle safety. Enforcing stringent limits could provide further benefit by encouraging vessel operators to choose unrestricted alternate routes in deep water, where available. In addition to reducing collision risk, such choices should also reduce potential non-lethal disturbance of foraging and resting animals.

If vessels divert around speed-restricted zones, management measures should also address additional risks that arise from vessels travelling at high speed close to zone boundaries that follow the margins of a shallow area (for example, some Go-Slow zones in Moreton Bay are nominally defined by the 2-m depth contour). In close encounters near a shallow boundary, turtles are more likely to flee across the vessel's track towards adjacent deeper water. This risk could be alleviated by ensuring speed-restricted zones include broad safety margins around the shallow expanses they are designed to protect. Such safety margins could also benefit other species vulnerable to vessel collisions since deeper water probably represents safe refuge for dugongs (Hodgson and Marsh, 2007) and manatees have been observed to turn towards the nearest deep water when boats approach (Nowacek et al., 2004).

4.4.4 Long term risk mitigation

Individual green turtles are known to maintain long-term fidelity to their coastal foraging areas, with only brief absences during breeding migrations spaced several years apart (Limpus et al., 1992; Limpus et al., 1994). Thus for each individual turtle in a foraging area that receives vessel traffic, the risk of collision persists over decades. For turtles the cumulative risk of collision is high and the likely consequence, in the event of collision, is severe injury or death. With vessel numbers likely to increase over time, the risk for turtles must continue to escalate in future unless vessel speed can be effectively reduced.

My informal discussions with many local vessel operators have established that operators seldom assess cumulative risk and usually make operational decisions in terms of immediate risk. They quite reasonably assume a very low probability of collision with a turtle during a single voyage. Furthermore, they anticipate no harm to personnel and little or no damage to the vessel from a collision with a turtle. Therefore, from a vessel operator’s perspective, there is no self-interest in supporting voluntary speed reduction. Consequently I conclude that mitigation of risk for turtles must depend on management intervention. Compulsory speed limits, underpinned by effective enforcement measures, appear essential if turtles are to be protected in key habitats subject to vessel traffic.

4.5 Figures

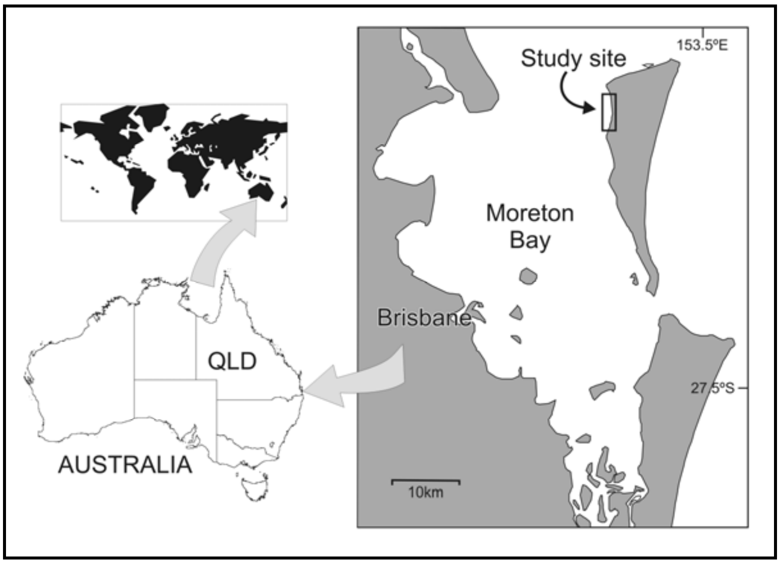

Figure 4.1. The study site comprised an area of clear shallow water (<5 m) on the north-eastern margin of Moreton Bay, Queensland, Australia.

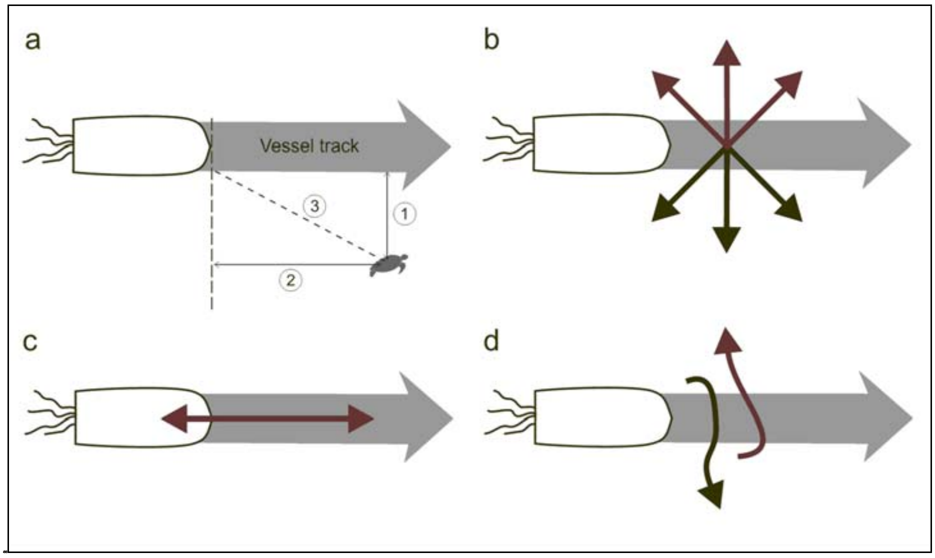

Figure 4.2. For each vessel-turtle encounter the observer estimated the lateral offset (a-1) of the turtle. If the turtle fled, the forward distance at the moment of response was also recorded (a-2). These two distances together allowed calculation of the flight initiation distance (a-3). For each flee response the turtle's initial flight trajectory was classified as safe (b), in-track (c) or cross-track (d).

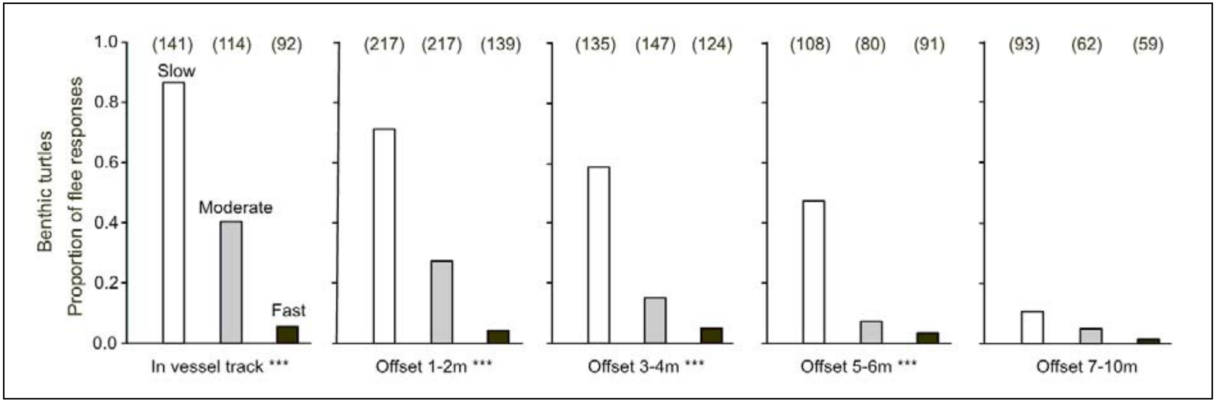

Figure 4.3. *Chelonia mydas*. The proportion of turtles that fled from the approaching research vessel diminished as vessel speed increased, significance denoted by *** $P < 0.001$. White bars denote vessel speed 4 km h^{-1}, grey bars denote vessel speed 11 km h^{-1}, black bars denote vessel speed 19 km h^{-1}. Number above each bar indicates total encounters (Flee + No Response, for definitions see section 4.2.3). Offset value indicates lateral distance between turtle and vessel. Statistical data: offset 0 m (in vessel track): $\chi^2 = 152.6$, df = 2, $P < 0.001$; offset 1-2 m: $\chi^2 = 177.4$, df = 2, $P < 0.001$, offset 3-4 m: $\chi^2 = 111.4$, df = 2, $P < 0.001$; offset 5-6 m: $\chi^2 = 69.5$, df = 2, $P < 0.001$; offset 7-10 m: $\chi^2 = 5.3$, df = 2, $P = 0.072$

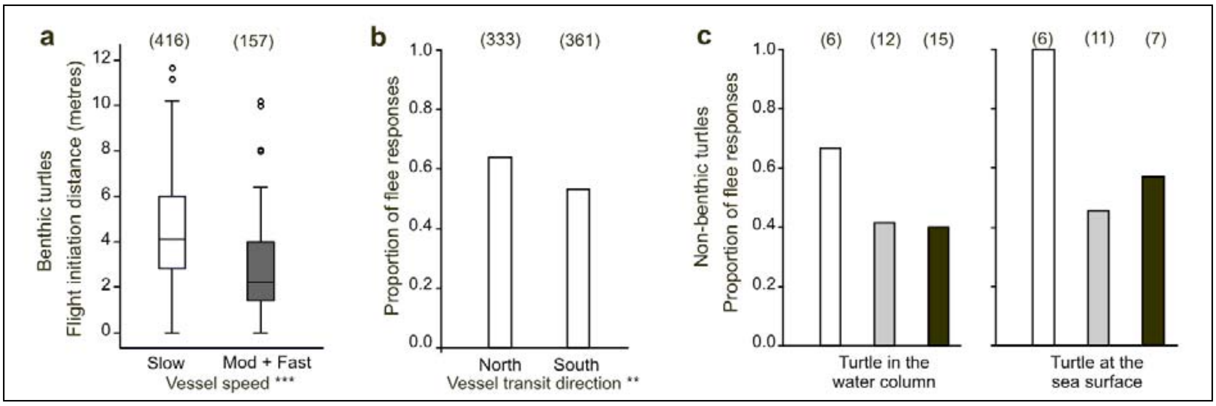

Figure 4.4. *Chelonia mydas* (a) Benthic turtles that fled in encounters with a slow vessel (4 km h^{-1}) had a significantly greater median flight initiation distance than those that fled in encounters with moderate (11 km h^{-1}) and fast (19 km h^{-1}) vessels, Mann-Whitney U=18516.5, P <0.001. Box plots show median, inter-quartile range, outliers and extreme cases. (b) Benthic turtles fled from a slow vessel more frequently when the vessel was heading North than when it was heading South ($\chi^2 = 10.0$, df = 1, $P = 0.002$). North-bound transits were expected to afford slightly enhanced underwater visibility – see text. (c) Turtles encountered at the sea surface fled more frequently than those in the water column, but small sample sizes precluded analysis by offset distances. White bars denote vessel speed 4 km h^{-1}, grey bars denote vessel speed 11 km h^{-1}, black bars denote vessel speed 19 km h^{-1}. In all panels the number above each bar indicates total encounters (Flee + No Response), significance denoted by ** $P < 0.01$; *** $P < 0.001$

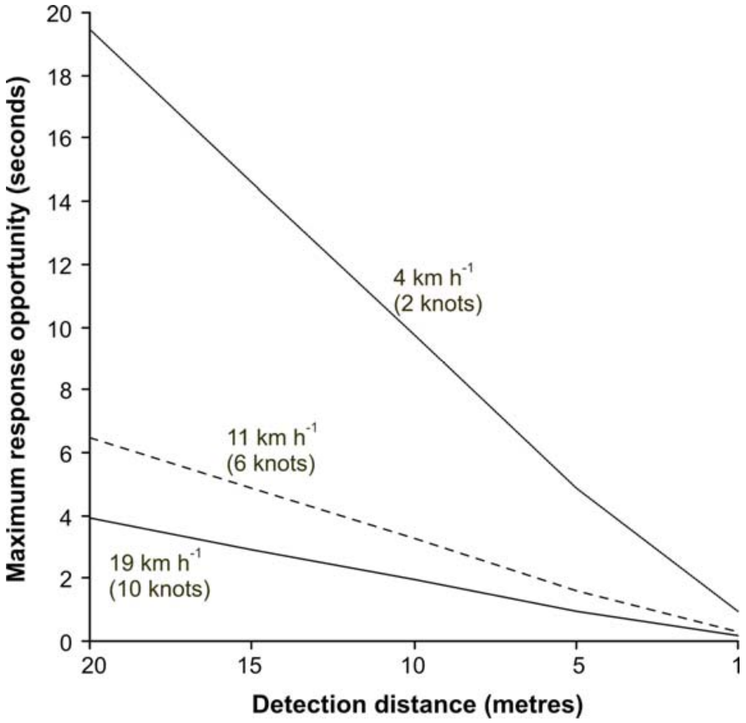

Figure 4.5. The theoretical maximum response opportunity time available to a perpetually vigilant turtle decreases with increasing vessel speed (plotted here for the three experimental speeds used in this study) and with decreasing detection distance.

4.6 References

ACKERMAN, B. B., WRIGHT, S. D., BONDE, R. K., O'DELL, D. K. & BANOWETZ, D. J. (1995) Trends and patterns in mortality of manatees in Florida, 1974–1992. In O'SHEA, T. J., ACKERMAN, B. B. & PERCIVAL, H. F. (Eds.) *Population biology of the Florida manatee.* Washington, DC, National Biological Service.

BARTOL, S. M. & MUSICK, J. A. (2001) Morphology and topographical organization of the retina of juvenile loggerhead sea turtles (*Caretta caretta*). *Copeia,* 2001**,** 718-725.

BJORNDAL, K. A. (1980) Nutrition and grazing behavior of the green turtle Chelonia mydas. *Marine Biology,* 56**,** 147-154.

BRILL, R. W., BALAZS, G. H., HOLLAND, K. N., CHANG, R. K. C., SULLIVAN, S. & GEORGE, J. C. (1995) Daily movements, habitat use and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L) within a foraging area in the Hawaiian islands. *Journal of Experimental Marine Biology & Ecology,* 185**,** 203-218.

ENVIRONMENT AUSTRALIA MARINE SPECIES SECTION (2003) Recovery plan for marine turtles in Australia. Canberra, Environment Australia.

GERSTEIN, E. R. (2002) Manatees, bioacoustics and boats. *American Scientist,* 90**,** 154-163.

GORZELANY, J. (2004) Evaluation of boater compliance with manatee speed zones along the Gulf Coast of Florida. *Coastal Management,* 32**,** 215-226.

GREENLAND, J. A. & LIMPUS, C. J. (2005) Marine wildlife stranding and mortality database annual report 2004: 1. Dugongs. Brisbane, Queensland Environmental Protection Agency.

GREENLAND, J. A. & LIMPUS, C. J. (2006) Marine wildlife stranding and mortality database annual report 2005: 1. Dugongs. Brisbane, Queensland Environmental Protection Agency.

GROOM, R. A. (2003) The efficacy of the voluntary vessel transit lanes in Missionary Bay, Hinchinbrook Island, for dugong conservation management. *School of Tropical Environment Studies and Geography.* Townsville, James Cook University.

HAUBOLD, E. M., DEUTSCH, C. & FONNESBECK, C. (2006) Final biological status review of the Florida manatee (*Trichechus manatus latirostris*). St Petersburg, Florida, Florida Fish and Wildlife Conservation Commission.

HEITHAUS, M. R., FRID, A., WIRSING, A. J., BEJDER, L. & DILL, L. M. (2005) Biology of sea turtles under risk from tiger sharks at a foraging ground. *Marine Ecology Progress Series,* 288**,** 285–294.

HODGSON, A. (2004) Dugong behaviour and responses to human influences. *School of Tropical Environment Studies and Geography.* Townsville, James Cook University.

HODGSON, A. J. & MARSH, H. (2007) Response of dugongs to boat traffic: the risk of disturbance and displacement. *Journal of Experimental Marine Biology & Ecology,* 340**,** 50-61.

JENSEN, A. S. & SILBER, G. K. (2003) Large whale ship strike database. US Department of Commerce.

KETTEN, D. R. & BARTOL, S. M. (2006) Functional measures of sea turtle hearing. Woods Hole, MA, Woods Hole Oceanographic Institution.

KNOWLTON, A. R. & KRAUS, S. D. (2001) Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean. *Journal of Cetacean Research and Management,* Special Issue 2**,** 193-208.

LAIST, D. W., KNOWLTON, A. R., MEAD, J. G., COLLET, A. S. & PODESTA, M. (2001) Collisions between ships and whales. *Marine Mammal Science,* 17**,** 35-75.

LAIST, D. W. & SHAW, C. (2006) Preliminary evidence that boat speed restrictions reduce deaths of Florida manatees. *Marine Mammal Science,* 22**,** 472-479.

LIMPUS, C. J., COUPER, P. J. & READ, M. A. (1994) The green turtle, *Chelonia mydas*, in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum,* 35**,** 139-154.

LIMPUS, C. J., MILLER, J. D., PARMENTER, C. J., REIMER, D., MCLACHLAN, N. & WEBB, R. (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildlife Research,* 19**,** 347-358.

MAITLAND, R., LAWLER, I. R. & SHEPPARD, J. K. (2006) Assessing the risk of boat strike on dugongs (*Dugong dugo*n) at Burrum Heads, Queensland, Australia. *Pacific Conservation Biology,* 12**,** 321-327.

MAKOWSKI, C., SEMINOFF, J. A. & SALMON, M. (2006) Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Marine Biology,* 148**,** 1167-1179.

MÄTHGER, L. M., LITHERLAND, L., FRITSCHES, K. A. & QUATTRO, J. M. (2007) An anatomical study of the visual capabilities of the green turtle, Chelonia mydas. *Copeia,* 2007**,** 169-179.

MOEIN BARTOL, S. & MUSICK, J. A. (2003) Sensory biology of sea turtles. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *Biology of Sea Turtles, Volume II.* Boca Raton, CRC Press.

MOEIN, S., LENHARDT, M., BARNARD, D., KEINATH, J. A. & MUSICK, J. (1993) Marine turtle auditory behavior. *Journal of the Acoustical Society of America,* 93**,** 2378.

NATIONAL MARINE FISHERIES SERVICE (2005) Recovery plan for the North Atlantic right whale (*Eubalaena glacialis*). Silver Spring, MD, National Marine Fisheries Service.

NOWACEK, S. M., WELLS, R. S., OWEN, E. C. G., SPEAKMAN, T. R., FLAMM, R. O. & NOWACEK, D. P. (2004) Florida manatees, *Trichechus manatus latirostris*, respond to approaching vessels. *Biological Conservation,* 119**,** 517-523.

O'HARA, J. & WILCOX, J. R. (1990) Avoidance responses of loggerhead turtles, *Caretta caretta*, to low frequency sound. *Copeia,* 1990**,** 564-567.

OLIVER, L. J., SALMON, M., WYNEKEN, J., HUETER, R. E. & CRONIN, T. (2000) Retinal anatomy of hatchling sea turtles: anatomical specializations and behavioral correlates. *Marine and Freshwater Behavavior and Physiology,* 33**,** 233-248.

PREISENDORFER, R. W. (1986) Secchi disk science: visual optics of natural waters. *Limnology & Oceanography,* 31**,** 909-926.

RICHARDSON, W. J., GREENE, C. R., JR, MALME, C. I. & THOMSON, D. H. (1995) *Marine mammals and noise,* London, Academic Press.

U.S. FISH AND WILDLIFE SERVICE (2001) Florida manatee recovery plan, (*Trichechus manatus latirostris*), Third revision. Atlanta, Georgia, U.S. Fish and Wildlife Service.

WORLD SHIPPING COUNCIL (2006) Comments of the World Shipping Council before the National Marine Fisheries Service In the matter of proposed rule to implement speed restrictions to reduce the threat of ship collisions with North Atlantic right whales. Washington, DC, World Shipping Council.

ZAR, J. H. (1999) *Biostatistical analysis,* Upper Saddle River, New Jersey, Prentice Hall.

Chapter 5: Sampling frequency and analysis of green turtle diving behaviour

Abstract

Animal-borne time-depth recorders (TDRs) are widely used to study the vertical movements of marine species. However sampling regimes and analytic methods for TDR data have been devised and evaluated predominantly for deep-diving predators in offshore waters, whereas this thesis addresses a contrasting situation, namely reptilian herbivores in shallow near-shore habitat. Furthermore, equipment and budget limitations may necessitate the use of a longer than optimal interval between depth measurements, as was the case for my study. I therefore evaluated different sampling regimes and alternative analytic approaches using a subset of my depth data before proceeding with comprehensive analysis. I used a subset of my field data, comprising 72 h in total, where depth was recorded at 2 s intervals. I resampled these data to derive additional data sets representing the same turtle behaviour sampled at intervals of 6 s, 10 s, 16 s, 20 s, 30 s and 60 s. I then compared metrics for resampled and original data. Results confirmed that longer sampling intervals caused negative bias in counts of discrete dives and near-surface events, and positive bias in their apparent duration. In contrast, measures of proportional time at depth remained consistent across the range of sampling frequencies tested. The classification of dives by their profiles (as depicted in a depth vs. time plot) proved unsatisfactory for my data. Poor performance of this classification technique could be ascribed to the shallow and diverse movement trajectories presented in my data. Close scrutiny of the data prompted me to test a method of manual correction of evident failures in detecting near-surface events between dives. The findings presented in this chapter supported my analytic methods for Chapter 6.

5.1 Introduction

Contemporary investigation of the behaviour and physiology of wide-ranging marine species relies extensively on animal-borne electronic sensors (Ropert-Coudert and Wilson, 2005; Ponganis, 2007). Time-depth recorders (TDRs) are conceptually among the simplest of such devices (they provide a time-series of depth values derived from the direct measurement of water-pressure) and they have a relatively long history in wildlife research. Early TDRs comprised entirely of mechanical components were introduced in studies of large pinnipeds during the early 1960s (Kooyman, 2004) and those instruments for the first time revealed dive trajectories of free-living animals that could not be observed visually. Technological advances over subsequent decades have enabled the production of electronic TDRs with progressively greater recording resolution, longer duration of operation and smaller physical dimensions, and enhanced equipment has promoted recent expansion in the scope of animal diving studies. This area of research now encompasses taxa as diverse as sperm whales (Aoki et al., 2007), dugong (Chilvers et al., 2004), platypus (Bethge et al., 2004) and marine turtles.

Diving studies published over the past decade include all extant marine turtle species (e.g. Hochscheid et al., 1999 - green turtle; Houghton et al., 2002 - loggerhead; Reina et al., 2005 - leatherback; Storch et al., 2005 - hawksbill; Sasso and Witzell, 2006 - Kemp's ridley; McMahon et al., 2007 - olive ridley; Sperling, 2008 - flatback). Collectively this body of work reveals wide diversity in the depth, duration and temporal patterns of turtle diving. The observed diversity may reflect behavioural differences between species that exploit diverse resources, between life-stages and between different habitats. However, potential study of such differences is hampered because it is difficult to make quantitative comparisons between diving studies, even when they concern the same species, due to the multiplicity of ways that turtle dives have been defined, measured and classified.

The intuitive notion that an air-breathing animal starts a dive when it leaves the sea surface and ends the dive on regaining the surface must be further qualified when diving behaviour is inferred from a series of discrete depth measures. TDRs are not designed to detect turtles' typically brief emergence at the sea-air interface. Therefore the usual practice is to infer a surfacing event when recorded depth is shallower than a nominated threshold depth. A dive is then defined as the period spent below the threshold depth. Threshold depth is study-specific and therefore dives reported in literature have been variously defined. Among examples from studies of green turtles, a ‘dive’ may mean a period spent below 1 m (Southwood et al., 2003), or below 2.5 m (Hochscheid et al., 1999), or below 3 m (Hays et al., 2000).

Further disparity in measuring dives arises from diverse TDR sampling intervals. Sampling intervals have varied widely between and within turtle diving studies, (e.g. Eckert et al., 1989 - 10 & 20 s; Hays et al., 2000 - 10 to 300 s; Hays et al., 2002 - 5 to 120 s; Southwood et al., 2003 - 5 & 10 s; Storch et al., 2005 - 30 s; Myers and Hays, 2006 - 10 & 60 s). Expanded memory capacity in recent equipment has alleviated the need to use very long sampling intervals but battery capacity remains an important constraint because size and weight of attached equipment must be minimised, in conjunction with other measures, to reduce deleterious effects on study animals (Wilson and McMahon, 2006). Economic constraints are also relevant because equipment with greater memory capacity is more costly. TDR studies therefore involve a trade-off between sampling frequency and overall duration of recording.

Disparity between diving studies is also evident in varied analytic methods and diverse schemes for classifying dive types and dive patterns. It is a common practice to base classifications on the two-dimensional dive profile depicted when data points are plotted (depth vs. time) but implementation of this practice varies. Some researchers have used visual assessment or computer algorithms to identify dives by shape analogies, e.g. U-, V-, S- and W-shapes variously adopted by Minamikawa et al. (1997), Houghton et al. (2002) and Seminoff et al. (2006). Others apply multivariate statistical techniques (e.g. Schreer and Testa, 1995) or calculate a numeric dive index based on mathematical constructs (Fedak et al., 2001).

In the literature there appears to be no consensus on an overall ‘best’ analytic technique for diving studies, nor any rules for selecting an optimal technique for particular circumstances. Furthermore, the critical evaluation of dive measurement and analysis techniques has occurred predominantly with reference to diving behaviour of endotherms that dive to pursue moving prey in deep, open waters (e.g. Gentry and Kooyman, 1986; Boyd, 1993; Boyd et al., 1995; Mori et al., 2005).

Given the contrasting context of my study of herbivorous turtles in a very shallow foraging area, I evaluated alternative approaches using a subset of my depth data before proceeding with comprehensive analysis. Specifically I wished to compare different sampling frequencies, apply dive profiles for classifying my data and assess a simple metric, proportional time at depth, for later application (Chapter 6) in summarising my study turtles’ occupation of vertical space and inferring potential for accidental contact with vessels.

5.2 Methods

5.2.1 Data preparation

I evaluated a subset of depth data from TDRs that I deployed on free-living green turtles *Chelonia mydas* in Moreton Bay, Queensland. My field procedures, equipment and data preparation are detailed in Chapter 6. For this chapter I used a data set comprising four periods of 6 h continuous duration from each of three turtles tracked during Sept 2006, Dec 2006 and April 2007 respectively, i.e. 72 h in total. The original data were recorded at 2 s intervals. I resampled the 2 s data by automatic selection of every 3rd record to create a data set with 6 s sampling intervals. Similarly, automatic selection of every 5th record created a resampled data set with 10 s sampling intervals, and so on. These resampled data sets were used to represent time-depth recordings that would have been obtained by hypothetical additional data loggers sampling the same behaviour at intervals of 6 s, 10 s, 16 s, 20 s, 30 s and 60 s respectively.

5.2.2 Definition of dives and near-surface events

After zero offset correction (see Chapter 6) the data were plotted with time on the x-axis and depth on the y-axis. From close visual scrutiny of the plotted 2 s data I determined that 1 m was the shallowest depth at which I could identify ascents towards the sea surface and descents towards deeper water. Consequently I defined dives numerically as trajectories below 1 m and considered intervals between consecutive dives, comprising a series of records ≤1 m, to be ‘near-surface’ events since the equipment was not designed to measure true surface emergence. I calculated descent and ascent speeds for dives that reached maximum depth >3 m after identifying trajectories with continuous vertical movement ≥0.015 m s^{-1}. Since multiple trajectories occurred within some dives, I based my evaluation on the longest uninterrupted trajectory in each direction and used the first long descent and last long ascent to resolve ties.

5.2.3 Dive profiles

For visual classification of dives according to their time-depth profiles I followed Hochscheid et al (1999). Thus U-dives were characterised by steady steep descent and ascent with extended intervening ‘bottom time’ at constant depth (hence a rectangular U-shaped time-depth profile), V-dives were characterised by steady steep descent and ascent with no bottom time (hence narrow V-shaped profiles) and S-dives were characterised by steady steep descent, no bottom time, steep initial ascent and subsequent gradual ascent, presenting distorted horizontal S-shaped profiles.

5.2.4 Proportional time at depth (PTaD)

I calculated the proportion of time spent in depth strata of 1 m increments below the sea surface. I then compared this measure, hereafter referred to as PTaD, for the original field data (2 s sampling) with the same measure for each resampled data set, i.e. 2 s vs. 6 s, 2 s vs. 10 s, etc. For these comparisons I used Lin's (1989) concordance correlation coefficient, calculated with equations provided by Zar (1999). Since some degree of pattern could be expected in diving behaviour, I repeated the tests of concordance using longer and shorter continuous time periods: 72 h duration (n = 1), 12 h duration (n = 6), 3 h duration (n = 24). 'Empty' categories, due to deeper zones being unused during some periods, were excluded from comparisons to avoid artificially inflating the concordance correlation coefficients.

5.3 Results

5.3.1 Sampling frequency

The original field data (72 h with 2 s sampling) contained 899 near-surface events and 899 dives. Distributions in both cases were strongly skewed toward brief events, near-surface events having median duration 10 s, range 2 s to 15.7 min and dives having median duration 2.1 min, range 2 s to 48.4 min. In the resampled data, as sampling interval increased, the number of near-surface events and dives decreased, the median durations increased and dive depths showed small changes (<0.5 m) with no clear trend (Table 5.1, Figure 5.1). All measures of vertical speed decreased as the sampling interval increased. Over the range from 2 s to 60 s the maximum descent rate decreased from 1.42 m s^{-1} to 0.86 m s^{-1} and maximum ascent rate decreased from 0.45 m s^{-1} to 0.08 m s^{-1}, mean descent rate (±SD) decreased from 0.12 (±0.055) to 0.05 (±0.013) m s^{-1} and mean ascent rate decreased from 0.11 (±0.034) to 0.04 (±0.016) m s^{-1} (Figure 5.1, panel d).

5.3.2 Concordance of proportional time at depth (PTaD) measures

The original data provided diverse patterns of time allocation (Figure 5.2 panels a-l) for testing the sensitivity of PTaD to sampling interval. PTaD values from 2 s data were almost perfectly reproduced by PTaD values determined from data sets with longer sampling intervals. The concordance correlation coefficient was > 0.999 in each case (Figure 5.2 panels m-q) with only very slight departure from the line of concordance evident for 60 s sampling (Figure 5.2 panel q). Concordance correlation coefficients were again ≥0.999 in all comparisons when the data were divided into periods of longer or shorter duration (72 h, 12 h, 3 h).

5.3.3 Profile classification

U-dives (n = 106) and V-dives (n = 9) were identified in the 2 s field data but close matches of the S-dive profile were not found. The combined total of U-dives and V-dives accounted for only 20.7 h (29%) of the 2 s field data, while the large majority of the data (71%) comprised irregular patterns. U-dives were highly variable in duration (range 2.9-48.4 min, median 8.7 min, mean 11.6 ± 9.1 min) while V-dives were generally of short duration (range 0.7-1.8 min, median 1.2 min, mean 1.3 ± 0.3 min). Distinctive dive profiles progressively degraded as the sampling frequency decreased, such that some V-dives became very short U-dives, some short U-dives became V-dives and in some instances two successive U-dives merged into one W-shaped dive (Figure 5.3).

5.4 Discussion

5.4.1 Sensitivity to bias

When discrete dives were evaluated, the detrimental effect of decreasing sampling frequency was demonstrated by a progressive negative bias in the total number of diving/surfacing events and positive bias in their duration. In contrast, proportional time at depth (PTaD) proved robust with respect to changes in sampling frequency across the range tested in my study. This finding supported the use of PTaD for reporting my field data sampled at 15 s intervals (Chapter 6). The consistent reliability that was demonstrated for periods as short as 3 h also suggested that PTaD might be used to investigate diel behavioural patterns with relatively fine temporal resolution as well as for broad comparisons between studies where disparate sampling regimes are used. For the latter purpose PTaD has an additional advantage in that it avoids confounding by disparate dive thresholds because it does not involve identification of discrete dives.

The propensity for longer sampling intervals to cause bias in the evaluation of discrete events was readily explained by dependence on chance for the detection of a near-surface event or dive event of shorter duration (t_d) than the sampling interval (t_s). The detection probability (t_d / t_s) necessarily declined as the sampling interval increased, and each failed detection caused preceding and succeeding events to be concatenated, with consequent decline in the number of events and increase in their duration. At any sampling frequency the probability of failed detection depended only on the duration of each event, but turtles typically surface very briefly and dive for relatively long periods, hence failed detection is more likely for near-surface events than for dives.

The same rationale explained why my turtle data showed greater bias at shorter sampling intervals than pinniped data subjected to similar analysis by Boyd (1993) (Figure 5.1 panel e). That is, failed detection was more likely for the very brief near-surface events of my study turtles than for longer surface events of species such as fur seals and elephant seals.

5.4.2 Limitations in profile classification

Profile classification had limited utility for my data since only 29% of 2 s data was amenable to this method and distinctive profiles degraded in data sampled at longer intervals (Figure 5.3). The low percentage of classification reflected diversity of movement trajectories by turtles in shallow water environments, prompting consideration of additional shape categories (e.g. profiles defined in studies by Minamikawa et al., 1997; Houghton et al., 2002; Seminoff et al., 2006). Re-analysis showed that extra categories offered little benefit because distinctive shapes were poorly represented in my data.

Dive profile classification has been used effectively in situations where turtles (and other animals) conduct deep dives with consistent profiles, and where research is focussed on a subset of dives meeting certain profile criteria (e.g. Hays et al., 2000) or where different dive functions can be inferred from distinctive profiles (e.g. van Dam and Diez, 1997). In contrast, my data reflected diverse trajectories of turtles in very shallow habitat, the research focus for my thesis included all dive behaviour around the clock, and my study circumstances offered no prospect for reliably inferring dive function from profiles, as discussed further in Chapter 6.

5.4.3 Constraints on the use of vertical speed for dive classification

The use of quantitative criteria to define discrete dives and different dive types or shapes is valuable to allow direct comparison between different studies. However, the typically study-specific nature of such criteria constrains potential comparisons to studies conducted under similar circumstances. For example, a threshold depth of 3 m and a least maximum depth of 6 m defined ‘resting’ dives for green turtles at Ascension Island (Hays et al., 2000). These criteria would clearly be inappropriate for turtles inhabiting much shallower habitat (e.g. Chapter 6) where resting dives must necessarily occur at lesser depths.

A less obvious constraint on sharing criteria between studies arises from the use of diverse time intervals for sampling depth. My finding that vertical speed tends to be negatively biased by longer sampling intervals (Figure 5.1 panel d) is particularly relevant to the use of vertical speed in dive classification criteria (e.g. Houghton et al., 2002). Close scrutiny of my 2 s data confirmed that the maximum ascent and descent rates reflected extremely brief spurts at speeds that were not sustained over the duration of longer sampling intervals, while the rarity of these brief spurts explained the large differences between maximum and mean rates. If short-term variation in vertical speed commonly occurs within turtles' dive trajectories, as seems likely, then inter-study comparisons involving vertical speed criteria may be confounded by use of different sampling frequencies. For example, if a hypothetical identical trajectory occurred in both cases, a study using a lower sampling frequency would report a slower vertical speed than a study using a higher sampling frequency.

In addition, dive depth can constrain the measurement of vertical speed. For example, if the TDR sampling interval is t_s s and the animal changes its depth by d m, the measured speed will not be greater than d / t_s m s^{-1} even if the animal actually moved at a faster rate. For this reason I based my evaluation of vertical speed on dives deeper than 3 m, ensuring movement up to 1.5 m s^{-1} could be measured with 2 s sampling. The issue is also relevant for slower ascent and descent rates. For example, if an animal dives at a sustained vertical speed of 0.3 m s^{-1} carrying a TDR that samples at 30 s intervals, the depth data would present negatively biased rates for dives < 9 m.

5.4.4 Alleviating sampling frequency bias

Given that TDR storage capacity is limited, particularly in smaller and less costly devices, it may be expedient, as it was for my study, to use a longer than optimal sampling interval to extend the duration of data recording and then interpret the data with due consideration for expected biases. Ideally one might wish to apply quantitative corrections for bias but my results suggest that potential correction factors could be considered only at a high level of data aggregation because the temporal distribution of bias within the data sets was uneven (Figure 5.1, panel f).

As discussed above, bias arises primarily from failure to detect near-surface events. Therefore I evaluated the potential for manual correction of 'missed' near-surface events to provide a partial remedy. I conducted this test using 16 s data, a sampling regime that represented a pragmatic trade-off for my study because 16 s intervals would allow 7 days of recording within the archival capacity of my data loggers instead of only 24 hours with 2 s sampling.

After close scrutiny of a large scale plot of the 16 s data I excluded three periods of very shallow depth records, in total 4 h 4 min, where I was unable to identify ascents and descents because depths fluctuated closely around 1 m. (Apparently the turtle was grazing or resting on the substrate at about 1 m, and from that depth it required minimal elevation to access the surface to breath.) In the balance of the data I identified steep ascent-descent sequences that peaked just below 1 m, indicative of failed detection of a near-surface event (see examples in Figure 5.3, panel b). A near-surface event was inserted at each of these points. Gradual ascent/descent sequences were ignored, to avoid the risk of creating spurious interruptions to dives.

For the period in which 654 near-surface events were detected in 2 s data (excluding 4 h 14 min as above) only 463 near-surface events (51%) had been detected in uncorrected 16 s data. After manual correction the count of near-surface event was 613 (94%). By reference to the 2 s data I determined that the 6% of near-surface events, which I had been unable to correct, occurred between dives to less than 2 m. Thus with 94% correction of all near-surface events and 100% correction of near-surface events defining dives >2 m I considered the time-intensive task of manual correction to be well justified for my purposes.

This manual correction method achieved good results for my data, although its efficacy for alleviating bias in different data sets at different sampling frequencies remains untested. Furthermore, bias could be alleviated more easily by sampling at high frequency if equipment with sufficient memory and battery capacity were available. However a modest research budget precluded more expensive equipment in my project and I relied on findings presented in this chapter to support the use of 15 s sampling (TDR option closest to 16 s used in evaluation) in my analysis of green turtle dive behaviour (Chapter 6).

5.5 Tables

Table 5.1. *Chelonia mydas.* The frequency at which turtle depth was sampled influenced the interpretation of diving behaviour. Longer sampling intervals caused notable bias in counts and durations of near-surface events (depth <=1 m) and dives (depth >1 m) with greatest influence on the shortest events. Dur Med (median), Min-Max, Mean ±SD indicate duration (seconds) of (a) near-surface events and (b) dives

	Sampling interval	**2 s**	**6 s**	**10 s**	**20 s**	**30 s**	**60 s**
a: Near-surface events							
Total	Count	899	754	680	468	351	203
	Dur Med (s)	10	12	10	20	30	60
	Min-Max	2-940	6-1626	10-1510	20-2000	30-1890	60-2220
	Mean ±SD	19 ± 42	23 ± 65	26 ± 64	38 ± 97	51 ± 106	88 ± 158
<=1min	Count	847	704	624	414	303	164
	Dur Med (s)	10	12	10	20	30	60
	Min-Max	2-60	6-60	10-60	20-60	30-60	60-60
	Mean ±SD	13 ± 11	16 ± 12	17 ± 11	25 ± 11	34 ± 10	60 ± 00
1-5 min	Count	49	48	54	52	46	37
	Dur Med (s)	82	84	80	80	90	120
	Min-Max	62-276	66-276	70-270	80-280	90-270	120-300
	Mean ±SD	92 ± 40	93 ± 37	96 ± 39	100 ± 37	117 ± 48	143 ± 41
5-10 min	Count	2	1	1	1	1	1
	Dur Med (s)	356	390	390	380	390	540
	Min-Max	318-394					
	Mean ±SD	356 ± 54					
10-30 min	Count	1	1	1	0	0	0
	Dur Med (s)	940	162	1510			
30-60 min	Count	0	0	0	1	1	1
	Dur Med (s)				2000	1890	2220

Table 5.1 continues on next page

Table 5.1 continued

	Sampling interval	**2 s**	**6 s**	**10 s**	**20 s**	**30 s**	**60 s**
b: Dives							
Total	Count	899	745	680	468	351	203
	Dur Med (s)	126	186	210	320	420	660
	Min-Max	2-2902	6-2898	10-3150	20-4880	30-6930	60-7920
	Mean ±SD	264 ± 363	315 ± 378	350 ± 432	507 ± 608	673 ± 870	1146 ± 1464
<=1min	Count	328	190	153	75	44	22
	Dur Med (s)	5	24	20	40	30	60
	Min-Max	2-60	6-60	10-60	20-60	30-60	60-60
	Mean ±SD	15 ± 17	25 ± 18	28 ± 17	34 ± 15	43 ± 15	60 ± 0
1-5min	Count	293	288	258	156	101	40
	Dur Med (s)	144	144	140	160	180	210
	Min-Max	62-298	66-300	70-300	80-300	90-300	120-300
	Mean ±SD	160 ± 69	162 ± 70	159 ± 68	164 ± 72	181 ± 68	206 ± 66
5-10min	Count	165	161	153	102	86	37
	Dur Med (s)	428	432	430	460	465	480
	Min-Max	302-598	306-594	310-600	320-600	330-600	360-600
	Mean ±SD	436 ± 89	438 ± 88	437 ± 91	461 ± 91	467 ± 94	485 ± 86
10-30min	Count	105	107	105	117	94	71
	Dur Med (s)	854	840	860	880	900	1020
	Min-Max	606-1750	606-1746	610-1750	620-1720	630-1770	660-1800
	Mean ±SD	904 ± 260	904 ± 260	929 ± 267	956 ± 274	1010 ± 303	1084 ± 337
30-60 min	Count	8	8	11	18	26	33
	Dur Med (s)	2411	2409	2590	2690	2790	3360
	Min-Max	1816-2902	1812-2898	1960-3150	1840-4880	1830-6930	1860-7920
	Mean ±SD	2390 ± 393	2388 ± 393	2545 ± 434	2791 ± 747	3118 ± 1316	3882 ± 1764

5.6 Figures

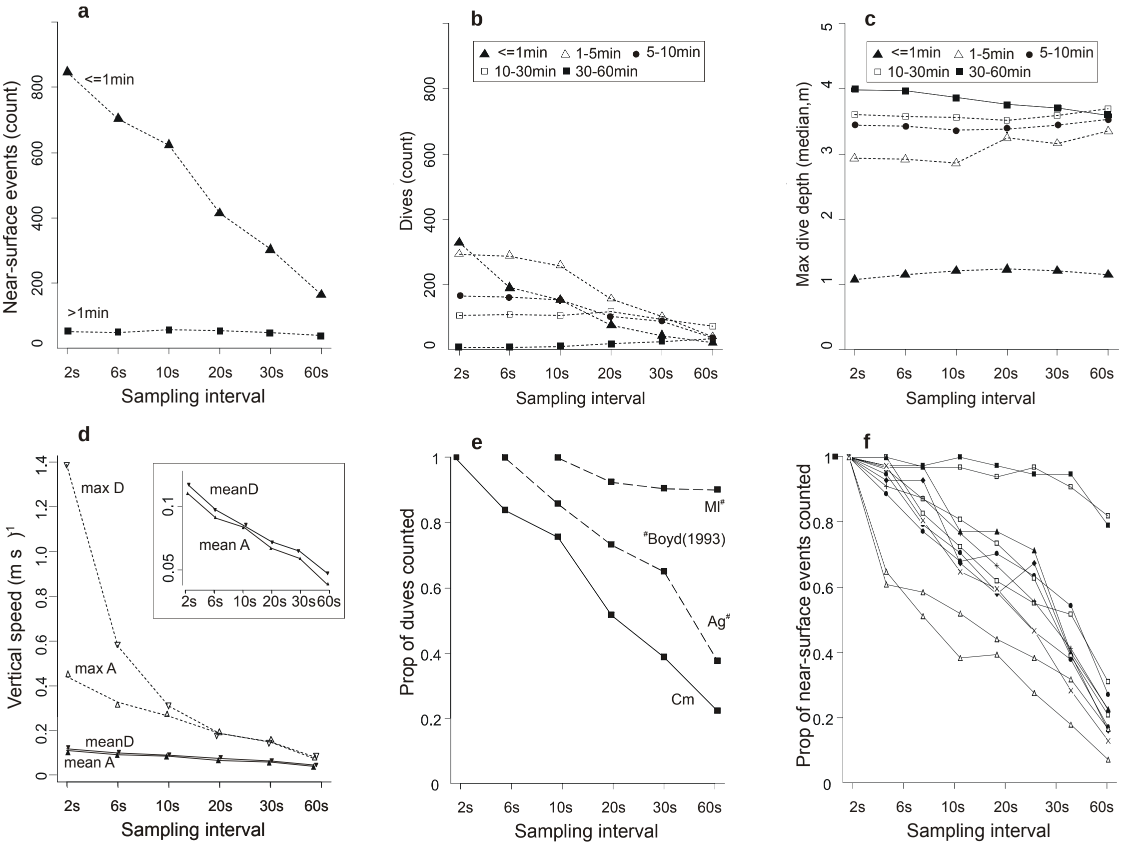

Figure 5.1. *Chelonia mydas* (Cm). Longer sampling intervals caused negative bias in counts of near-surface events (panel a) and dives (panel b) with greatest bias affecting brief events in both cases. Median maximum depth of dives (panel c) showed small changes (<0.5 m) with sampling interval and no consistent trend. Vertical speed in dives >3 m (panel d) was negatively biased at longer sampling intervals with most extreme bias affecting maximum descent and ascent rates (max D, max A). Inset with expanded y-axis shows detail of mean descent (mean D) and mean ascent (mean A). Panel e shows my data for green turtles (Cm) demonstrated bias at shorter sampling intervals than pinniped data (Ml = *Mirounga leonina*, Ag = *Arctocephalus gazella*) from Boyd (1993) included here for comparison. Panel f shows the uneven temporal distribution of negative bias arising from longer sampling intervals, as demonstrated here for my data divided into 12 periods, each of 12 h continuous duration.

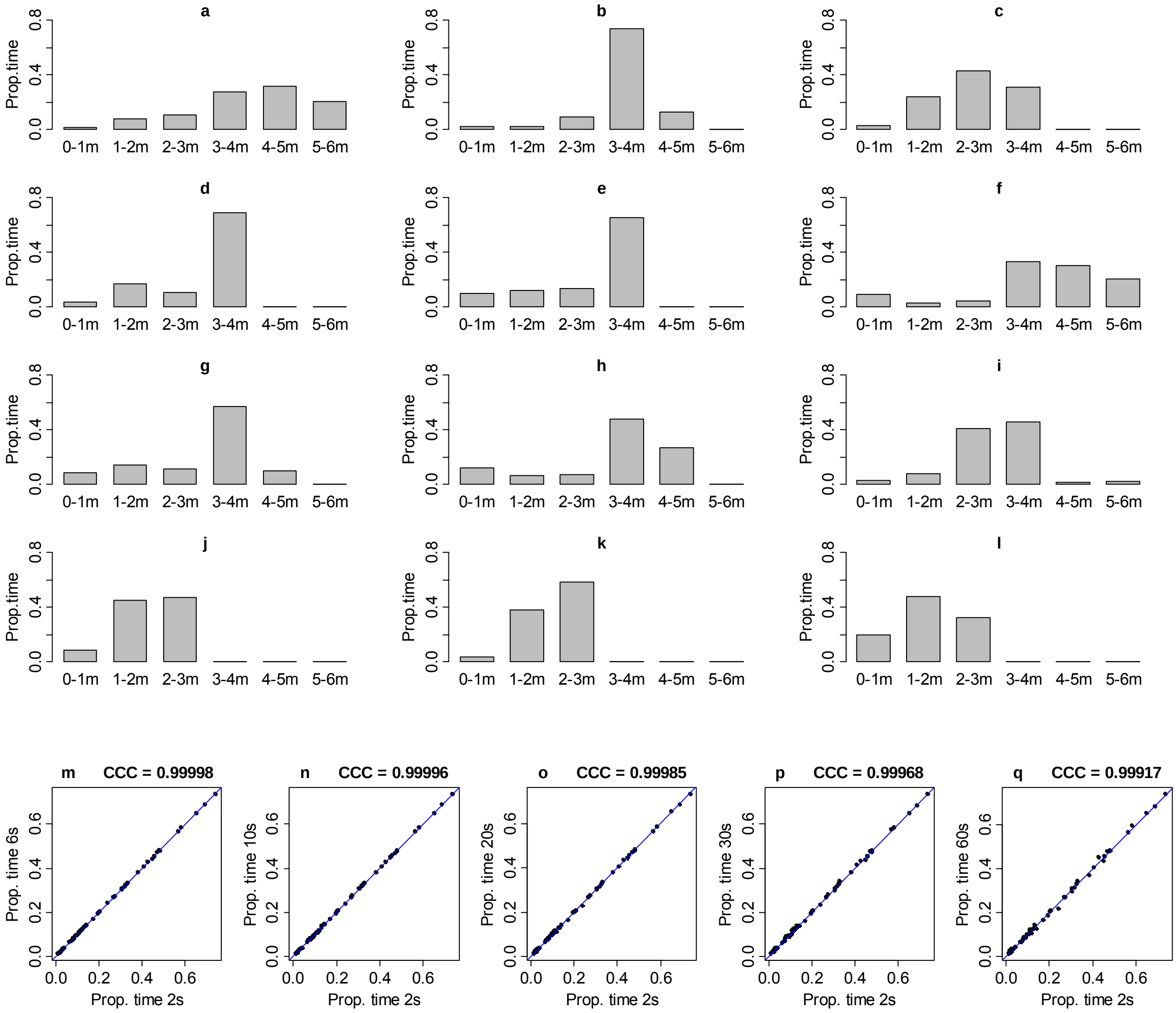

Figure 5.2. *Chelonia mydas*. Depth data for periods of 6 h continuous duration provided diverse activity in terms of depth usage (panels a-l) for testing the influence of longer sampling intervals on proportional time at depth, measured for 1-m depth strata. Values based on the original data (2 s intervals) were almost perfectly reproduced when depths were resampled at 6 s, 10 s, 30 s and 60 s (panels m-q) with all concordance correlation coefficients > 0.999

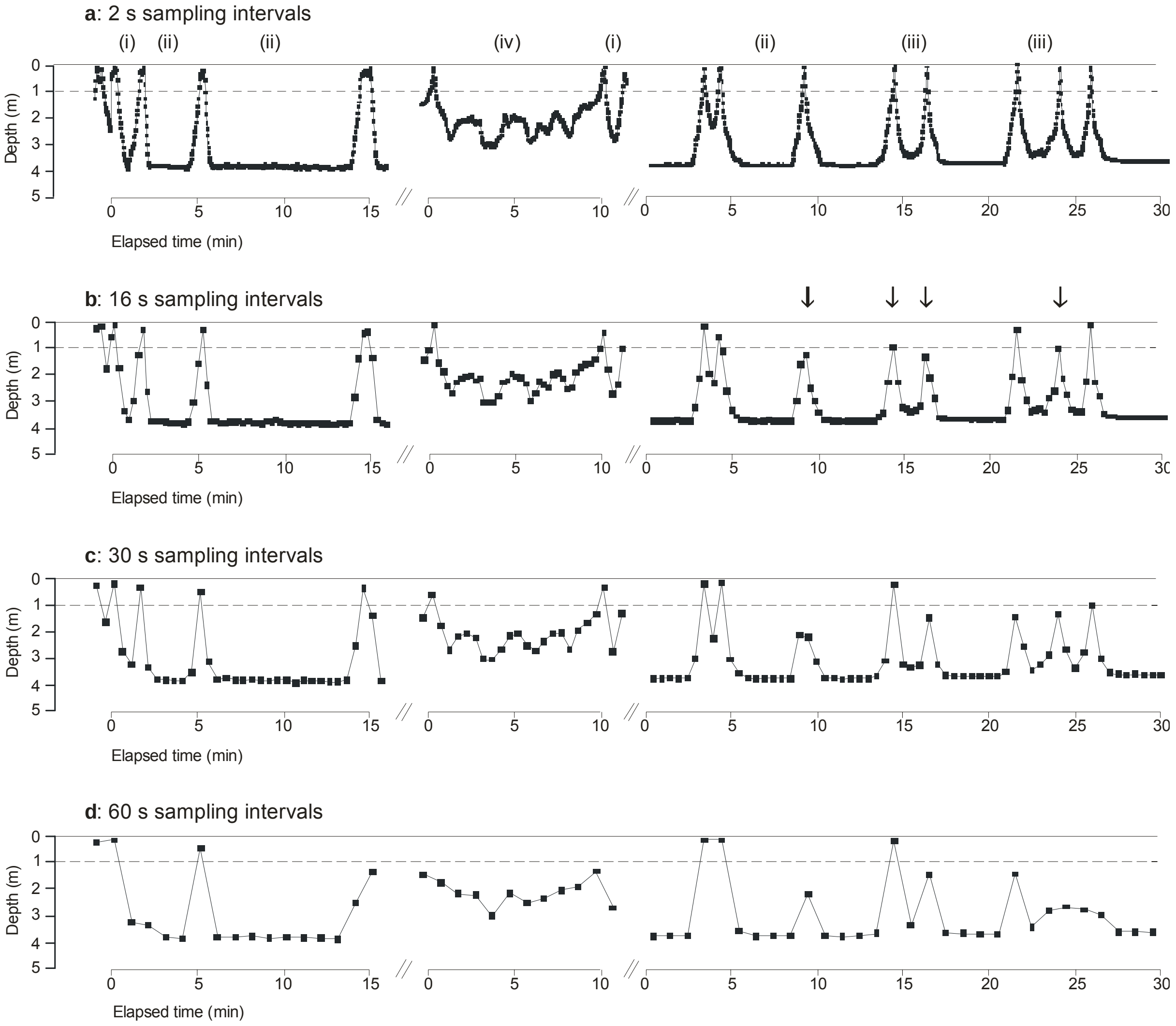

Figure 5.3. *Chelonia mydas.* Panel a: Dive profiles in depth data recorded at 2 s intervals included examples of V-dives (i) and U-dives (ii) as defined by Hochscheid et al (1999). There were also dives intermediate between V and U shapes (iii) and dives with irregular profiles (iv). The same data re-sampled at longer intervals (panels b, c, d) demonstrated progressive degradation of distinctive shapes and concatenation of successive dives when near-surface intervals <=1 m (broken line) were not recorded. Arrows in panel b mark examples of ‘missing’ near-surface events that can be identified visually, allowing for manual correction.

5.7 References

AOKI, K., AMANO, M., YOSHIOKA, M., MORI, K., TAKUDA, D. & MIYAZAKI, N. (2007) Diel diving behaviour of sperm whales off Japan. *Marine Ecology Progress Series*, 349**,** 277-287.

BETHGE, P., MUNKS, S., OTLEY, H. & NICOL, S. (2004) Diving behaviour, dive cycles and aerobic dive limit in the platypus *Ornithorhynchus anatinus*. *Comparative Biochemistry and Physiology Part A,* 136**,** 799-809.

BOYD, I. L. (1993) Selecting sampling frequency for measuring diving behaviour. *Marine Mammal Science,* 9**,** 424–430.

BOYD, I. L., REID, K. & BEVAN, R. (1995) Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behaviour,* 50**,** 769-784.

CHILVERS, B. L., DELEAN, S., GALES, N. J., HOLLEY, D. K., LAWLER, I. R., MARSH, H. & PREEN, A. R. (2004) Diving behaviour of dugongs, *Dugong dugon*. *Journal of Experimental Marine Biology and Ecology,* 304**,** 203-224.

ECKERT, S. A., ECKERT, K. L., PONGANIS, P. J. & KOOYMAN, G. L. (1989) Diving and foraging behaviour of leatherback sea turtles (*Dermochelys coriacea*). *Canadian Journal of Zoology,* 67**,** 2834-2840.

FEDAK, M. A., LOVELL, P. & GRANT, S. M. (2001) Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked recorders. *Marine Mammal Science,* 17**,** 94-110.

GENTRY, R. L. & KOOYMAN, G. L. (1986) Methods of dive analysis. In GENTRY, R. L. & KOOYMAN, G. L. (Eds.) *Fur seals: maternal strategies on land and at sea.* Princeton, NJ, USA, Princeton University Press.

HAYS, G. C., ADAMS, C. R., BRODERICK, A. C., GODLEY, B. J., LUCAS, D. J., METCALFE, J. D. & PRIOR, A. D. (2000) The diving behaviour of green turtles at Ascension Island. *Animal Behaviour,* 59**,** 577-586.

HAYS, G. C., GLEN, F., BRODERICK, A. C., GODLEY, B. J. & METCALFE, J. D. (2002) Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. *Marine Biology,* 141**,** 985-990.

HOCHSCHEID, S., GODLEY, B. J., BRODERICK, A. C. & WILSON, R. P. (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Marine Ecology Progress Series,* 185**,** 101-112.

HOUGHTON, J. D. R., BRODERICK, A. C., GODLEY, B. J., METCALFE, J. D. & HAYS, G. C. (2002) Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Marine Ecology Progress Series,* 227**,** 63-70.

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

LIN, L. I.-K. (1989) A Concordance Correlation Coefficient to Evaluate Reproducibility. *Biometrics,* 45**,** 255-268.

MCMAHON, C. R., BRADSHAW, C. J. A. & HAYS, G. C. (2007) Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea*. *Marine Ecology Progress Series,* 329**,** 239-252.

MINAMIKAWA, S., NAITO, Y. & UCHIDA, I. (1997) Buoyancy control in diving behaviour of the loggerhead turtle, *Caretta caretta*. *Journal of Ethology,* 15**,** 109-118.

MORI, Y., WATANABE, Y., MITANI, Y., SATO, K., CAMERON, M. F. & NAITO, Y. (2005) A comparison of prey richness estimates for Weddell seals using diving profiles and image data. *Marine Ecology Progress Series,* 295**,** 257-263.

MYERS, A. E. & HAYS, G. C. (2006) Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Marine Ecology Progress Series,* 322**,** 259-267.

PONGANIS, P. J. (2007) Bio-logging of physiological parameters in higher marine vertebrates. *Deep Sea Research II,* 54**,** 183-192.

REINA, R. D., ABERNATHY, K. J., MARSHALL, G. J. & SPOTILA, J. R. (2005) Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *Journal of Experimental Marine Biology & Ecology,* 316**,** 1-16.

ROPERT-COUDERT, Y. & WILSON, R. P. (2005) Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment,* 3**,** 437-44.

SASSO, C. R. & WITZELL, W. N. (2006) Diving behaviour of an immature Kemp's ridley turtle (*Lepidochelys kempii*) from Gullivan Bay, Ten Thousand Islands, south-west Florida. *Journal of the Marine Biological Association of the United Kingdom,* 86**,** 919-925.

SCHREER, J. F. & TESTA, J. W. (1995) Statistical classification of diving behaviour *Marine Mammal Science,* 11**,** 85-93.

SEMINOFF, J. A., JONES, T. T. & MARSHALL, G. J. (2006) Underwater behaviour of green turtles monitored with video-time-depth recorders: what’s missing from dive profiles? *Marine Ecology Progress Series,* 322**,** 269–280.

SOUTHWOOD, A. L., REINA, R. D., JONES, V. S. & JONES, D. R. (2003) Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. *Canadian Journal of Zoology,* 81**,** 1014-1024.

SPERLING, J. B. (2008) Two new dive types with a gradual ascent phase in flatback turtles (*Natator depressus*). *Marine Turtle Newsletter,* 120**,** 9-11.

STORCH, S., WILSON, R. P., HILLIS-STARR, Z.-M. & ADELUNG, D. (2005) Cold-blooded divers: temperature-dependent dive performance in the wild hawksbill turtle *Eretmochelys imbricata*. *Marine Ecology Progress Series,* 293**,** 263-271.

VAN DAM, R. P. & DIEZ, C. E. (1997) Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs,* 16**,** 133-138.

WILSON, R. P. & MCMAHON, C. R. (2006) Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment,* 4**,** 147-154.

ZAR, J. H. (1999) *Biostatistical analysis,* Upper Saddle River, New Jersey, Prentice Hall.

Chapter 6: Green turtle diving behaviour in near-shore foraging habitat

Abstract

Green turtles *Chelonia mydas* of immature and adult size (n = 19, curved carapace length 49 to 118 cm) were equipped with time-depth recorders for short periods (≤7 d) to investigate diel and seasonal variation in diving behaviour. Research sessions were distributed over 2 years to cover seasonal variation in sea temperature from 14ºC to 30ºC. Diurnal dives were shallower and shorter than nocturnal dives, with diel patterns also evident in dawn and dusk peaks in occupation of depths within 1 m of the surface, elevated diurnal occupation of depths 1 to 2 m below the surface and elevated nocturnal occupation of depths >2 m. Dive duration increased as sea temperature decreased, showing strong negative correlation by day and by night. Study turtles made resting dives that were 3 to 4 times longer in median duration, and six times longer in maximum duration, at cool temperatures than they were at warm temperatures, but there was no evidence of winter diapause or location shift to avoid cold water. The large majority of turtles spent 89 to 100% of their time at depths ≤5 m below the surface, three individuals did not exceed 3 m and the maximum depth recorded by any turtle was 7.9 m, although deeper water was available. Furthermore, the dive data indicated that study turtles collectively spent more than 80% of their time at charted (low tide) depths of 3 m or less, indicating that they consistently used the shallow margins of the bay where human activities tend to be concentrated, thereby potentially increasing their exposure to anthropogenic threats.

6.1 Introduction

The green turtle *Chelonia mydas* has long been regarded as a species of conservation concern, with declining stocks in all major ocean basins being ascribed primarily to harvesting of eggs, juveniles and adults (IUCN Marine Turtle Specialist Group, 2004). Harvest mortality is augmented by inadvertent human impacts (Lutcavage et al., 1997) whose accidental nature demands mitigation strategies informed by knowledge of turtle behaviour. For example, regulation of beach lighting in Florida followed studies that revealed the harmful effects of artificial lighting on the behaviour of both nesting turtles and turtle hatchlings (Witherington, 1992; Witherington, 1997), while research into dive-depth distributions of pelagic turtles may assist in reducing accidental capture of turtles by ocean long-line fisheries (Polovina et al., 2003).

Inadvertent impacts must also be addressed in near-shore foraging grounds because, among the diverse environments that the species occupies at different life-stages, the neritic is where individual green turtles spend the major part of their lives (Musick and Limpus, 1997; Plotkin, 2003). Threats recently recognised in the neritic environment include entanglement of turtles in near-shore fishing gear (nets, traps and discarded equipment) and mortality due to vessel strike (Greenland et al., 2004; Chapter 2; Chapter 4). These threats also affect other vulnerable species, including dugongs (Greenland and Limpus, 2005), manatees (Ackerman et al., 1995) and whales (Laist et al., 2001). However, mitigation is particularly challenging because the causative human activities are often too economically and socially important to permit their broad scale restriction. Hence narrowly-targeted mitigation measures must be devised. Their design requires detailed and location-specific information about the behaviour and fine-scale movement patterns of turtles in areas affected by accidental mortality.

Such fine-scale behavioural data remain scant, particularly for green turtles in foraging areas, since much field research on this species and other chelonians has been conducted at breeding sites. The relative paucity of studies in foraging habitat can probably be ascribed to the elusive habits of turtles in such areas, which severely constrain direct observation and hamper deployment and recovery of animal-attached telemetry devices. Furthermore, seawater blocks the transmission of radio signals and thereby limits the opportunities for obtaining satellite-tracking data to intermittent brief intervals when a turtle surfaces.

Technological advances have alleviated some difficulties in this field of research. For example, novel GPS devices have recently been used to record the locations of inter-nesting loggerhead turtles more frequently and more accurately than was possible with earlier equipment, allowing review of critical habitat in relation to protected area boundaries (Schofield et al., 2007a). In an alternative approach, time-depth recorders can provide a very high-resolution record of a turtle's vertical movements, thereby revealing diving behaviour and at the same time allowing inference about habitat utilisation, especially where water depth varies spatially in a predictable manner (e.g. depth increasing with distance from shore). I adopted this method to investigate the 'shallow end' of turtle diving behaviour.

Early research into turtle diving investigated physiological responses and recorded extremes in depth and duration of submergence (see Lutcavage and Lutz, 1997 and references therein). Subsequent advances in telemetry equipment have greatly expanded the scope of turtle diving studies. Many studies have addressed behaviour in inter-nesting habitats and during post-reproductive movement in offshore waters, but only a few present dive data for green turtles in near-shore foraging grounds (e.g. Seminoff et al., 2001; Southwood et al., 2003b; Makowski et al., 2006) and these represent reef habitats and deeper bathymetry dissimilar to areas where accidental turtle mortality in eastern Australian waters is of most concern. It would be inappropriate to assume similar behaviour in disparate foraging environments, given that green turtle diving behaviour has been shown to vary notably between different breeding sites (Hays et al., 2002).

Inference from stranding data suggests accidental turtle mortality in eastern Australian waters has occurred predominantly in shallow turbid water close to urban centres (Haines and Limpus, 2001; Greenland et al., 2004; Chapter 2). Accordingly, I chose a representative study site adjacent to an Australian capital city where significant marine wildlife populations, including green and loggerhead turtles, dugong and dolphins depend on shallow foraging habitat (Limpus et al., 1994; Chilvers et al., 2005). At this site I deployed time-depth recorders on green turtles during multiple short sessions spread over two years, to obtain sufficiently comprehensive data to investigate diel and seasonal variations in diving patterns and depth occupation.

6.2 Methods

6.2.1 Field research

The study was conducted in semi-sheltered waters within Moreton Bay, a large tidal embayment in Queensland, Australia, surrounded on its southern and western shores by residential suburbs of Brisbane, the state capital (Figure 6.1). My preliminary surveys at the intended study site (site MB2 described in Chapter 3) confirmed the presence of green turtles from large immature to adult-size. This range of size-classes was similar to long-term research sites in different habitat on the eastern side of the bay (Limpus et al., 1994). Since individual green turtles have demonstrated long-term associations with localised areas of the eastern bay and with other coastal foraging sites in Queensland (Limpus et al., 1994; Chaloupka et al., 2004), the green turtles I observed were considered likely to be resident at my study site.

Research was conducted in 10 separate sessions between July 2005 and April 2007. Each session commenced with a boat expedition to capture study turtles and attach tracking equipment. After deployment of the equipment, boat expeditions were undertaken on subsequent days when favourable wind and sea conditions permitted. The objective was to re-locate study turtles by means of ultrasonic signals because knowledge of recent locations could facilitate recovery of tracking tags after their automatic detachment (see 6.2.3). In addition I sought to conduct visual observations of turtles' emergence at the surface when possible.

6.2.2 Study turtles

Green turtles were captured individually in a net (stretched mesh 20 cm) using a method designed to minimise accidental capture of other species. Capture sessions were restricted to winds <18 km h^{-1} to facilitate visual searches for cryptic surface movements by turtles. When a suitable turtle was detected at close range the net was deployed over the stern of the boat (a 6 m net-fishing vessel operated by an experienced professional fisher) and rapidly laid out in a large circle (diam. ~50 to 100 m) around the location where the turtle had been seen. Thereafter the net was closely monitored for signs that the turtle had become entangled, usually revealed by sudden movement of small floats attached to the upper margins of the net. If no movement occurred over an extended period we concluded that the turtle had escaped and proceeded to retrieve the net before searching for another candidate. Once a turtle was entangled I promptly lifted it into the boat for inspection, measurement and attachment of tracking equipment. In all cases turtles were returned to the water at the same location within 5 to 15 minutes of capture.

6.2.3 Tracking equipment

I used custom-made tracking tags, each comprising electronic devices mounted in a streamlined housing with sufficient buoyancy to rise to the sea surface after detachment from the turtle. Each tag was fitted with a link made of fast-corroding metal (Galvanic Timed Release, International Fishing Devices Inc, Pompano Beach FL, USA) designed to release the tag within approximately 7 days of deployment. The corroding link was attached to the posterior margin of the turtle's carapace by a plastic cable tie (tie wrap) secured through a 2 mm diameter hole drilled in the extreme edge of the carapace. The cable tie, with breaking load 8 kg, served as a safety link to ensure the turtle could break free if the equipment snagged on an obstruction. I considered it important to ensure my equipment did not disturb the study turtles' natural buoyancy, since experimental manipulation of buoyancy has been shown to influence turtle behaviour (Minamikawa et al., 2000; Hays et al., 2004). Therefore, to achieve neutral buoyancy for each tag while attached to the turtle, small steel washers were connected to the attachment link to serve as counterweights, the size and number of washers being determined by individual testing.

My standard tags, used on the majority of turtles, were 120 mm long with maximum diameter 55 mm and contained a miniature time-depth recorder (TDR) (model DST Milli, Star-Oddi, Reykjavik, Iceland, depth accuracy ± 0.08 m, temperature accuracy ± 0.1°C) and an ultrasonic transmitter (model CHP-87-L, Sonotronics, Tucson AZ, USA). Three turtles (T22, T25, T28) received a larger tag (155 mm long, 105 mm max. diam.) containing the same items as a standard tag plus a second TDR and additional equipment for recording spatial movements as described in Chapter 7. On both types of tags the flexible attachment linkage allowed movement (±10 cm) of the TDR pressure transducer relative to the carapace margin and consequently I regarded the depth data as approximate representations of the turtle's body position. I programmed the TDRs to record depth every 15 s and temperature every 225 s, a schedule that allowed continuous recording for up to 7 days before filling the data storage capacity. The second TDR, present in the larger tag only, operated concurrently with the first TDR for two separate 12-hour periods during which it recorded depth every 2 s. High-frequency 2 s data were compared to 15 s data for periods of dual recording, as described in section 6.2.4. The ultrasonic transmitters emitted an individually coded signal, detectable at close range with a boat-mounted hydrophone and receiver (DH-4 and USR-96, Sonotronics Tucson, AZ, USA). These signals allowed intermittent identification of individual turtles and assisted in recovery of tracking tags after detachment.

6.2.4 Data analysis

Data were downloaded from each recovered tag using proprietary software (StarOddi, Reykjavik, Iceland). A zero offset correction (ZOC) was applied to the depth data following established practice to adjust for small baseline discrepancies typical of depth recorders. A single ZOC value was applied to each time-series of depth values, rather than separate corrections to each dive (e.g. Hays et al., 2007) or to each hour of data (e.g. Myers et al., 2006) because posterior attachment of tags in the present study meant that the data loggers reached zero depth only rarely, when a turtle elevated the posterior end of its carapace on commencing an exceptionally abrupt dive (confirmed by field observations). Preliminary field tests confirmed transducer accuracy of ±5 cm after ZOC. To allow for initial responses to capture and handling, the data from the first 12 h post-release were not used in analyses. The adequacy of this exclusion period was confirmed by scrutiny of plotted data that indicated some turtles appeared to dive more frequently during the first 6 hours while others showed no evident response.

Depth data were analysed both in terms of proportional time at depth and as discrete dives, based on my preparatory evaluation of methods described in Chapter 5. Dives were defined as trajectories below a threshold depth of 1 m with maximum depth ≥2 m. Intervals between consecutive dives were evaluated as 'near-surface' events, comprising a series of records ≤1 m, since my equipment was not designed to measure true surface emergence. Because the actual duration between dives could be shorter than the recording frequency of 15 s, it was necessary to scrutinise plotted data (time on the x-axis, depth on the y-axis) for each turtle to ensure that discrete dives were recognised correctly. A dive start/end was inserted where a distinctive steep ascent-descent trajectory peaked just below 1 m. As detailed in Chapter 5, comparison with high-frequency (2 s) data confirmed, for periods of dual recording (3 turtles, 2 x 12 h each), that each of these distinctive 'missed peaks' reliably indicated the turtle had followed a trajectory that actually peaked above 1 m, close to the surface.

I calculated the proportion of time spent in depth strata of 1 m increments below the sea surface and allocated data to three categories of depth-below-surface occupation (0 to 1 m, 1 to 2 m and >2 m). These categories reflect progressively reduced exposure to potential contact with vessels in areas where traffic comprises vessels of varied draft (maximum depth of vessel hull and appendages). Turtles occupying greater depths can potentially be struck only by deeper draft vessels, whereas turtles occupying lesser depths can potentially be struck by vessels of deep and shallow draft (i.e. a larger sub-set of available vessels). My categories make provision for future work to evaluate turtles' risk of contact with vessels, pending collection of data on vessel traffic that are not currently available.

I used time of sunrise and sunset to categorise data by day and night and to accommodate seasonal variation in day length. To estimate low-tide depths occupied by the study turtles, tide-adjusted depth data were derived by subtracting the current tidal height, measured at 10-minute intervals by Maritime Safety Queensland, Brisbane. Results reported include median, extreme range and mean ±SD. Non-parametric statistical tests were used where the assumption of normality was untenable. T-tests were used for mean temperatures and for diel patterns in depth occupation. For the latter, proportional times were arcsine transformed and tests were one-tailed. For all tests $p < 0.05$ was considered statistically significant.

6.3 Results

From a total of 25 deployments I obtained depth and temperature data for 19 green turtles of curved carapace length (CCL) 49 to 118 cm with individual recording periods from 30.3 to 165.5 h, excluding the first 12 h post-release (Table 6.1). One data logger yielded corrupted data due to an electronic fault and five tracking tags were not recovered. Sea temperature extremes over the entire study ranged from 13.8 ºC to 30.3 ºC (turtles T06 and T19 respectively) due to the seasonal spread of tracking sessions, but each individual turtle experienced a narrow range of sea temperatures during its tracking period (Table 6.1). Mean sea temperatures recorded in each turtle's data showed no statistically significant difference between day and night (paired t-test, $t = 0.896$, $df = 18$, $p = 0.382$).

6.3.1 Depth occupation

The large majority of turtles (17 out of 19 individuals) spent 89 to 100% of their time at depths ≤5 m below the surface, three turtles did not exceed 3 m and the maximum depth recorded by any turtle was 7.9 m (Table 6.1). The proportion of time spent within 1 m of the surface showed a slight positive association with mean water temperature, both by day (Spearman's $r_s = 0.53$, $p = 0.021$) and by night (Spearman's $r_s = 0.54$, $p = 0.019$). Proportional time in other depth zones was independent of temperature. Proportional time in all depth zones showed no consistent trend with respect to turtle size (CCL).

Diel variation in depth occupation presented three distinct patterns. (1) Small peaks were evident at dawn and dusk for occupation of depths 0 to 1 m below the surface (Figure 6.2a) with occupation of this depth zone significantly greater at dawn (sunrise ±1 h) and dusk (sunset ±1 h) than it was during 2 h periods at the middle of the solar day and night, $t = 4.8705$, $df = 18$, $p < 0.001$. (2) Elevated diurnal occupation of depths 1 to 2 m below the surface (Figure 6.2b) was statistically significant, $t = 6.734$, $df = 18$, $p < 0.001$. (3) Elevated nocturnal occupation of depths >2 m (Figure 6.2c) was also statistically significant, $t = -3.7526$, $df = 18$, $p < 0.001$. Statistical tests at different temperatures were precluded by small sample sizes. However, the three diel patterns were also evident in subsets of data for warmer and cooler temperatures, partitioned at 22.1 ºC, which was the grand mean for all tracking sessions.

6.3.2 Dives and near-surface events

Dives tended to be shorter and shallower by day for the large majority of study turtles, with median values showing longer nocturnal dives for 18 turtles, longer nocturnal near-surface events between dives for 18 turtles and deeper nocturnal dives for 17 turtles (Figure 6.3). Weak positive association between CCL and median dive depth for individual turtles suggested that smaller turtles tended to make shallower dives than larger turtles by day, but correlations were not statistically significant (day: Spearman's $r_s = 0.4$, $p = 0.09$, night: Spearman's $r_s = 0.22$, $p = 0.39$).

Dives became longer as sea temperature decreased. There was significant negative correlation between dive duration and mean temperature, both by day (Spearman's $r_s = -0.69$, $p = 0.001$) and by night (Spearman's $r_s = -0.77$, $p < 0.001$). The duration of nocturnal near-surface events was also inversely related to temperature (Spearman's $r_s = -0.54$, $p = 0.02$). A potentially similar trend in diurnal near-surface events (Spearman's $r_s = -0.22$, $p = 0.37$) might have been obscured in data recorded at 15 s intervals, since the majority of these events comprised a single record, representing duration ≤15 s. The depth of nocturnal dives tended to increase with temperature (Spearman's $r_s = 0.51$, $p = 0.03$) but dive depths during the day were independent of temperature (Spearman's $r_s = 0.06$, $p = 0.79$).

The influence of temperature was most notable for longer dives (Spearman's $r_s = -0.88$, $p = <0.001$ for dives ≥15 min). Dives exceeding 1 h (max depth 2 to 7.9 m) occurred only at sea temperatures below 22ºC, both by night (150 out of 214 dives, 70%) and by day (64 out of 214 dives, 30%), and involved 8 individuals (T05, T06, T07, T08, T11, T13, T22, T23) that spanned the entire size range of study turtles. The longest dives (2.5 to 2.9 h, max depth 3 to 7.5 m) occurred at 16 to 17 C. Near-surface events immediately following the longest dives did not exceed 4.25 min. Pooled data comprising the 10 longest dives for each turtle, inferred to represent resting behaviour by each individual, suggested a positive relationship between dive duration and depth as well as confirming the strong inverse relationship with temperature (Figure 6.4). Small samples and disparate distributions precluded statistical evaluation of these opposing influences.

Eight turtles recorded prolonged periods at depths ≤1 m with the maximum continuous duration for individuals ranging from 1.3 h (T27) to 5.7 h (T29). Close scrutiny of time-depth plots for each turtle indicated that these periods did not represent discrete events between two successive dives. Rather they appeared to be periods when turtles had occupied substrates ≤1 m below the surface and made extremely brief ascents and descents that could not be reliably detected by my data loggers. Therefore diving patterns during these periods could not be quantified.

6.3.3 Surface exposure

My visual observations encompassed study turtles, identified by signals from their ultrasonic transmitters, and many non-study green turtles at my site, all of which displayed similar behaviour. Turtles made only fleeting appearances at the sea surface with no turtle remaining visible for longer than 2 s. Turtles usually exposed only the dorsal-anterior part of the head but occasionally exposed the dorsal posterior surface of their carapace when diving very suddenly. Turbid water precluded visual observation of submerged turtles.

6.4 Discussion

Green turtles in this study maintained occupation of relatively shallow depths throughout their respective tracking periods. Yet within their narrow depth ranges they displayed significant day-night differences in depth occupation and diving patterns, while their dive durations demonstrated the strong influence of sea temperature.

6.4.1 Behavioural patterns

The predominant pattern of shorter, shallower dives during the day and longer, deeper dives during the night (Figure 6.3) suggested turtles were more active by day and rested by night. Short dives are consistent with heightened activity involved in seeking and consuming forage, since activity increases metabolic demand (Schmidt-Nielsen, 1997). An active submerged turtle would therefore be expected to ascend to the surface more frequently for respiration. Reduced metabolic demand while resting would allow correspondingly longer periods of submersion and on this basis prolonged dives by green turtles are widely considered to represent resting behaviour (e.g. Hays et al., 2000; Southwood et al., 2003b).

My behavioural inference was confined to differentiating active and resting periods because it was not possible to reliably identify the functions of individual dives. Under some circumstances the geometric shapes evident in plots of time-depth data can be informative, e.g. a turtle foraging on a reef makes small movements up- and down-slope that result in an irregular dive profile readily distinguishable from the square or U-shaped profile created when the turtle remains stationary on the substrate while resting (van Dam and Diez, 1997). However, in other habitat the correspondence between dive profile and dive function is uncertain. Studies using additional equipment together with depth recorders have shown that square or U-shaped dive profiles do not exclusively represent resting and can include movement activity (detected by a 3-D compass system, Hochscheid et al., 1999) as well as foraging behaviours (captured by carapace-mounted underwater cameras, Seminoff et al., 2006), and can encompass varying states of consciousness (inferred from jaw movements detected by a novel sensor, Houghton et al., 2008).

Slight gradients in bathymetry across much of my study site meant that the dive profile created by a turtle foraging across a near-level patch of seagrass could match that of a turtle resting immobile on the substrate for a similar duration, and such inherent ambiguity precluded functional interpretation of dive profiles in my depth data. Similarly, it was impossible to determine from the depth data exactly where a turtle had selected deeper water. A series of square or U-shaped dive profiles with progressively increasing or decreasing depth (after adjustment for tide height) clearly indicated when the turtle moved down or up a slope. However the micro-location of the slope remained uncertain because corresponding slopes in the substrate occurred in many parts of the site, as recorded in detailed bathymetry data from hydrographic surveys provided by Maritime Safety Queensland, Brisbane.

The finding that diurnal-biased activity prevailed across the range of study turtles (immature and adult-sized) supported generalisation of the pattern reported elsewhere, predominantly for immature green turtles. For example, diurnal activity has been visually observed (Bjorndal, 1980), inferred from movement between distinct feeding and resting sites (Mendonca, 1983; Taquet et al., 2006) and inferred from diving behaviour (Seminoff et al., 2001; Southwood et al., 2003b; Makowski et al., 2006). However, the selection of deeper water at night appears less amenable to generalisation. Deeper water was favoured at night in my study and in several other studies (e.g. Bjorndal, 1980; Makowski et al., 2006; Taquet et al., 2006) but the converse, nocturnal selection of shallower depths, has also been reported (Brill et al., 1995; Southwood et al., 2003b), as has individual variation in diurnal/nocturnal depth selection (Seminoff et al., 2001). Reasons for these divergent trends in depth selection remain unclear but may reflect disparate availability of forage resources and differences in foraging behaviour, variations in predatory pressures (Heithaus et al., 2007) and possible interactions with conspecifics (Schofield et al., 2007b).

6.4.2 Sea temperature effects

The significant negative correlation between dive duration and sea temperature was expected in its direction but novel in the strength of the relationship and the scope of resting dive duration demonstrated within a shallow depth range. Laboratory and field studies (Southwood et al., 2003a; Southwood et al., 2006) have shown reduced metabolic rates for green turtles occupying colder water. Consequently green turtles would be expected to replenish oxygen less frequently at lower temperatures. A slight trend towards longer dives in winter has been noted for juvenile green turtles in a coral reef environment (Southwood et al., 2003b) and researchers in the Mediterranean Sea have reported that post-nesting females in temperate coastal habitat demonstrated an abrupt increase in the proportion of dives >25 min when sea temperature dropped below 25ºC. The latter change in diving behaviour, accompanied by a location shift to deeper water, was interpreted as a mid-winter diapause (Godley et al., 2002; Broderick et al., 2007). In contrast, my results showed no evidence of diapause or location change. Study turtles remained at the study site (detected by acoustic signals) during the coldest tracking session and depth data showed that bouts of activity (frequent short dives) occurred intermittently despite the predominance of prolonged dives at low temperatures. Foraging was likely to have occurred during this activity, consistent with the observation that green turtles elsewhere in Moreton Bay continued to forage at water temperatures down to 15ºC (Read et al., 1996).

Prolonged dives at shallow depths (Figure 6.4) were notable in view of green turtles' reliance on their lungs to regulate their buoyancy. By diving with fully inflated lungs a turtle can rest passively at its maximum depth of neutral buoyancy, and by diving with lungs partially inflated (to varying degrees) it can rest passively at various lesser depths (Milsom, 1975; Hays et al., 2000; Minamikawa et al., 2000). However, partially inflated lungs provide a smaller volume of oxygen than fully inflated lungs, thereby reducing the duration of submergence. Consequently resting dives, when metabolism is assumed to be relatively stable, would tend to be shorter at shallower depths if turtles surface when oxygen reserves are depleted to approximately similar levels. The expected depth-duration relationship has been confirmed for mature female green turtles at Ascension Island, where they rested predominantly in deeper water within the range 5 to 20 m (Hays et al., 2004).

This buoyancy-related constraint must apply to all green turtles when they rest on open substrates, as at my study site where reefs and other structures were not available. Therefore the following aspects of my findings were notable. Firstly, study turtles selected shallow resting depths despite the availability of deeper water nearby that would have allowed them to dive with greater oxygen stores (due to greater lung inflation) and remain submerged for longer periods. Secondly, their resting dive durations were longer than expected from published data, although disparate life-stages, habitat and depth ranges require that this comparison be regarded with caution. As shown in Figure 6.4, my data for resting dives by study turtles at warm temperatures (26 to 29 deg) were 1.5 to 2.1 times longer, for depths 2 to 4 m and 4 to 6 m respectively, than values predicted by extrapolation of the duration-depth relationship reported for Ascension Island green turtles (Hays et al., 2004, p 1142). For lower temperatures no comparison with published data was feasible as sources could be not found with sufficient detail. However my data demonstrate that turtles made resting dives that were 3 to 4 times longer in median duration, and six times longer in maximum duration, at cool temperatures than they were at warm temperatures (Figure 6.4).

To my knowledge, dives of similar and even more prolonged duration by green turtles have been recorded only in deeper water (Broderick et al., 2007; Rice and Balazs, 2008). Thus in relation to their shallow depths the longest dives by my study turtles appear to have no precedents in the literature. However, I infer that my study turtles were diving within their aerobic limits, following the norm for voluntary dives (Lutcavage and Lutz, 1997). Near-surface events between dives remained relatively short (≤4.25 min) even after the longest dives (up to 2.9 h) and, as noted above, the turtles intermittently undertook short bouts of activity (potentially including foraging) and remained within the study area while making their longest dives. Therefore these prolonged dives do not appear to indicate a distinct physiological state such as diapause. Rather, I infer that they represent one end of a temperature-related continuum of behaviour by green turtles in shallow foraging areas.

6.4.3 Depth selection

The study turtles' preference for deeper water at night is consistent with the established understanding that lung-related buoyancy (discussed above) means deeper sites allow longer periods of continuous rest than shallower sites. Why then did their recorded depths remain so modest, despite unobstructed access to deeper water? Distance may have discouraged regular use of substantially deeper sites, since charted depths >10 m (high tide depths >12.6 m) were 3 to 6 km distant from shallow areas in the study site that appeared to be preferred foraging sites. (The latter were inferred from my visual observations of frequent surfacing behaviour by turtles.) Yet distance did not preclude use of intermediate depths greater than those actually selected. Depths of 4 to 8 m were available within 1 to 1.5 km of the assumed foraging areas, and I observed that study turtles travelled equal and greater distances (confirmed by intermittent detection of individuals by their ultrasonic signals). My extensive field observations, including substrate inspection by remote video, revealed no evident deterrents to the use of deeper areas in the study site. I therefore infer that other factors in addition to distance and depth must influence the choice of resting sites, but these remain to be elucidated.

6.4.4 Conservation implications

My data clearly demonstrated the study turtles' dependence on shallow habitat (Table 6.1). This is even more evident when tidal range (max 2.6 m during tracking sessions) is taken into account. Tide-adjusted depth data indicated that study turtles spent most of their time (mean

82% ±0.16) at charted depths (lowest astronomical tide) of 3 m or less. Since locally dominant seagrass species in south-western Moreton Bay (which includes my study site) are severely depth-limited by turbid water (Abal and Dennison, 1996) the use of shallow habitat was likely to enhance turtles' forage intake. However this habitat preference means turtles occupy the broad shallow margins of the bay and thereby have greater exposure to human activities that are typically more frequent near the shoreline than in waters more distant from shore. For example, the margins of Moreton Bay are favoured for some forms of recreational and commercial fishing, including the deployment of various types of nets and traps. Furthermore, bay margins include areas of vessel traffic concentration because vessels transit at least twice on each trip when leaving and returning to their points of origin at wharves, marinas, moorings and launching ramps.

Temporal patterns in turtle behaviour also appear to exacerbate risk. Diurnal and dawn/dusk biases in turtles' occupation of shallow depth strata (Figure 6.2) coincide with a diurnal bias in vessel traffic (concomitant with human preferences for conducting outdoor activities by day) and thereby would be expected to increase turtles' risk of vessel strike. It appears that broadly similar levels of exposure to vessels persist year-round, as shallow water occupation and diel patterns were maintained at colder and warmer temperatures. However there may be a slight increase in exposure during the warmer months, since the proportion of time that turtles spent at 0 to 1 m below the surface showed a small positive association with mean water temperature, and this is the depth zone where turtles are potentially within vertical range of a large proportion of passing vessels (i.e. shallow and deeper draft vessels).

My detailed data on green turtles' vertical movements might in principle be complemented by geographically-referenced data on their horizontal movements. Novel variants of GPS technology enable researchers to track turtles at a relatively fine scale (e.g. Schofield et al., 2007a) albeit not matching simple TDRs in spatial (<10 cm) and temporal resolution (<1 min). However, tracking turtles is a costly and logistically challenging task. In contrast, human activities associated with accidental turtle mortality can be directly monitored. Effort might therefore more usefully be applied to determine the spatial and temporal distributions of vessel traffic and various types of fishing activity within near-shore turtle habitat. Such data could be used in conjunction with the findings of my study, to accurately identify time- and location-specific risks, and hence enable mitigation through narrowly targeted strategies that could offer a dual benefit by maximising protection for green turtles and other vulnerable species while minimising constraints on human activities.

6.5 Tables

Table 6.1 *Chelonia mydas.* Summary of proportional time spent in depth-below-surface categories (upper limits inclusive) by 19 green turtles of diverse curved carapace lengths (CCL). Dur = duration of depth records excluding 12 h post-release. Sex was inferred by reference to the sexual dimorphism of adult turtles in eastern Moreton Bay (Limpus et al., 1994) as males (M - long tail), likely females (LF - short tail & CCL > 95cm) or undetermined (U). # indicates <1% of proportional time at max. depth.

Turtle	CCL (cm)	Sex	Date (MM/YY)	Dur (h)	Max Dep (m)	Sea Temp (ºC) Mean [Min-Max]	Proportional time at depth below surface							
							0 - 1m	1 - 2m	2 - 3m	3 - 4m	4 – 5m	5 - 6m	6 - 7m	7 - 8m
T05	105.0	M	07/05	165.5	7.9	17.3 [15.8-19.0]	4%	8%	18%	24%	21%	5%	9%	11%
T06	57.5	U	07/05	163.6	2.7	16.1 [13.8-19.3]	10%	63%	27%					
T07	49.3	U	07/05	142.2	5.1	16.7 [15.0-18.6]	3%	5%	29%	39%	24%	#		
T08	55.6	U	07/05	163.0	3.0	16.5 [14.6-19.3]	7%	56%	37%					
T10	69.5	U	09/05	98.4	4.6	21.1 [19.4-23.0]	5%	25%	38%	20%	12%			
T11	81.6	U	09/05	85.6	7.7	20.1 [19.3-21.5]	6%	17%	13%	16%	17%	18%	12%	1%
T13	117.9	LF	09/05	137.8	6.4	20.7 [19.1-23.0]	4%	16%	26%	21%	25%	7%	1%	
T14	82.8	U	10/05	109.6	5.0	23.6 [21.8-25.5]	8%	20%	32%	25%	15%			
T15	78.9	U	10/05	108.2	5.6	23.7 [21.7-25.6]	8%	22%	35%	22%	9%	4%		
T16	94.2	U	11/05	78.2	7.8	23.6 [22.8-25.5]	8%	38%	20%	26%	8%			#
T18	88.0	U	02/06	30.3	5.7	27.8 [27.1-30.2]	13%	22%	14%	21%	19%	11%		

T19	84.5	U	02/06	31.5	6.9	28.6 [27.8-30.3]	8%	25%	23%	21%	13%	10%	#
T22	113.2	LF	09/06	161.3	6.5	21.1 [18.9-23.7]	13%	38%	21%	13%	10%	4%	1%
T23	107.0	LF	10/06	161.3	5.7	21.9 [19.5-24.2]	16%	31%	26%	14%	11%	2%	
T25	108.8	LF	12/06	94.7	5.7	25.0 [24.3-25.8]	13%	14%	18%	27%	21%	7%	
T26	56.6	U	12/06	63.8	2.8	24.8 [22.4-27.6]	44%	39%	17%				
T27	92.6	M	12/06	150.2	5.9	25.1 [23.1-27.1]	20%	30%	20%	8%	15%	7%	
T28	96.0	LF	04/07	133.5	5.3	23.5 [22.1-26.4]	9%	27%	25%	21%	16%	2%	
T29	71.0	U	04/07	135.2	5.4	23.4 [22.0-25.4]	19%	27%	24%	17%	10%	3%	

6.6 Figures

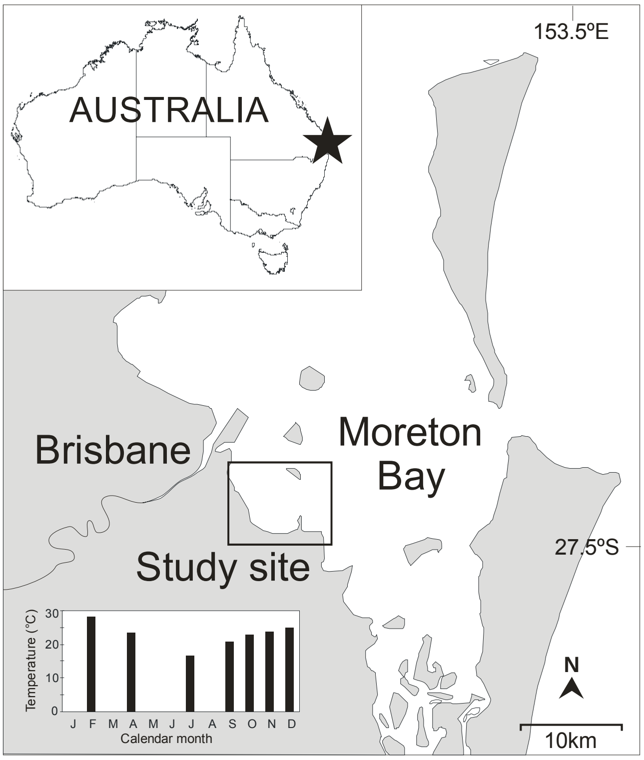

Figure 6.1. The study site was located within Moreton Bay on the east coast of Australia. The city and suburbs of Brisbane, state capital of Queensland, surround the western and southern shores of the bay. Inset lower left shows mean sea temperature experienced by study turtles, for detail see Table 6.1.

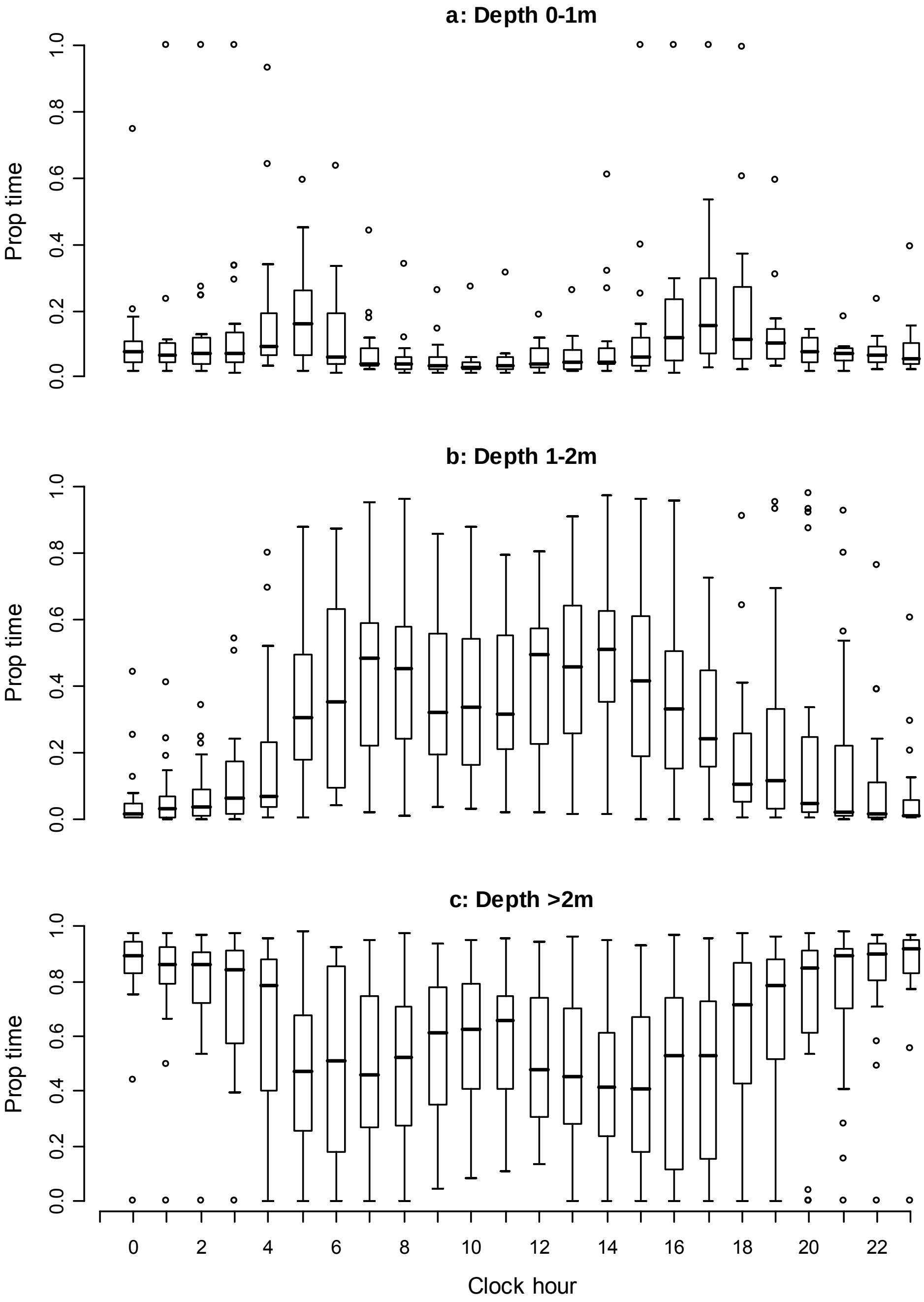

Figure 6.2: *Chelonia mydas*. Diel patterns in depth occupation for 19 study turtles showed peaks at dawn and dusk for depths 0 to 1 m below the surface (panel a), elevated occupation of depths 1 to 2 m during the day (panel b) and elevated occupation of depths >2 m at night (panel c). Differences were statistically significant in all three instances. Box plots show the median (horizontal bar), inter-quartile range (box length), largest values within 1.5 x inter-quartile range (whiskers) and all data points beyond the whiskers (open circles).

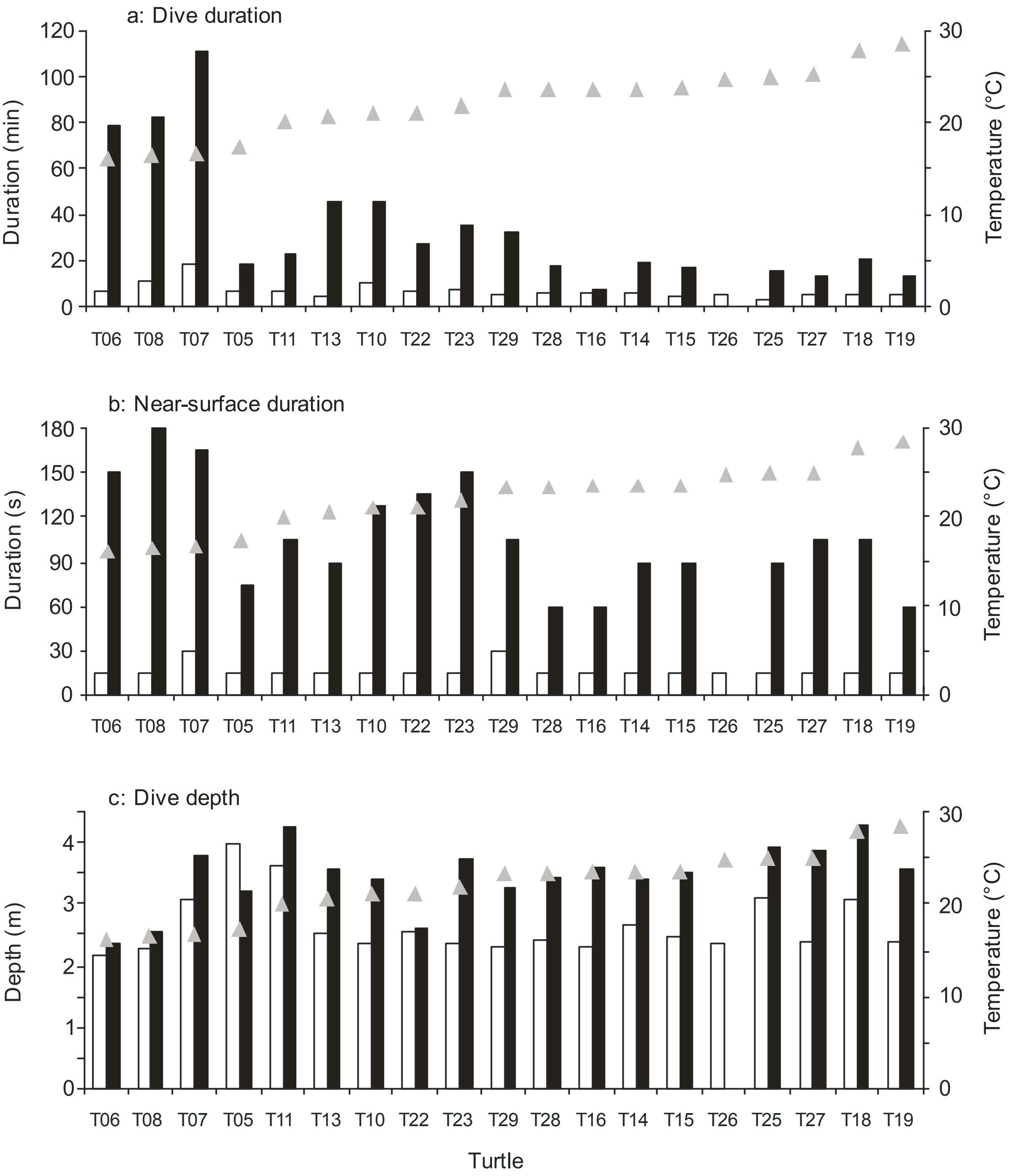

Figure 6.3. *Chelonia mydas*. Median duration of dives (panel a) and near-surface events between dives (panel b) was shorter by day (white bars) and longer by night (black bars) for all turtles except T26. The latter made no qualifying dives at night as it remained at depths <2m. With increasing sea temperature (grey triangles) durations tended to decrease, with the exception of diurnal near-surface events. Note left-hand Y-axes of panels a and b use different units. Dive depth (panel c) was greater by night, and night depth tended to increase with temperature.

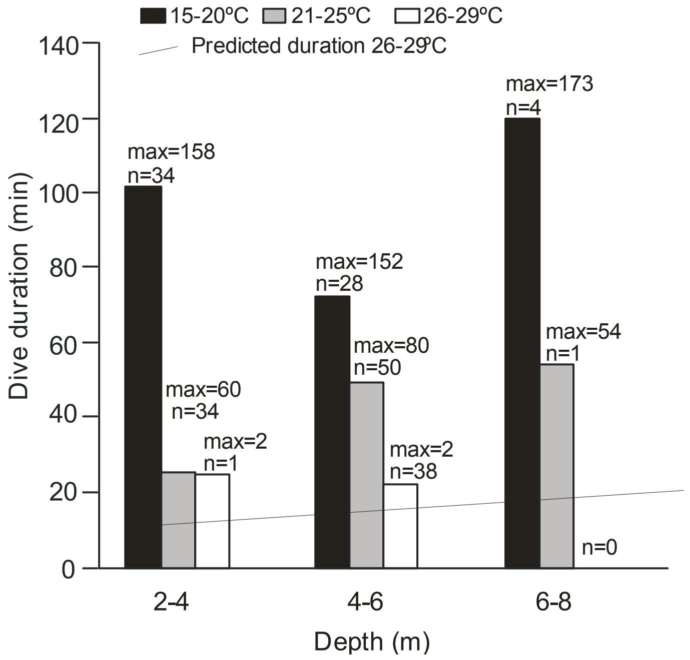

Figure 6.4. *Chelonia mydas*. Median duration of resting dives by green turtles showed both depth and temperature dependence. Pooled data for the 10 longest dives (inferred resting) by each of 19 study turtles were classified by depth and sea temperature (white bars 15-20ºC, grey bars 20-25ºC, black bars, 25-29ºC). Maximum duration (min) and number of dives in each category are indicated above bars. Line represents predicted dive duration for warm sea temperature derived from equation provided by Hays et al (2004) extrapolated beyond the original depth range and life-stage, hence this comparison must be regarded with caution.

6.7 References

ABAL, E. G. & DENNISON, W. C. (1996) Seagrass depth range and water quality in Southern Moreton Bay, Queensland, Australia. *Marine and Freshwater Research,* 47**,** 763-771.

ACKERMAN, B. B., WRIGHT, S. D., BONDE, R. K., O'DELL, D. K. & BANOWETZ, D. J. (1995) Trends and patterns in mortality of manatees in Florida, 1974–1992. In O'SHEA, T. J., ACKERMAN, B. B. & PERCIVAL, H. F. (Eds.) *Population biology of the Florida manatee.* Washington, DC, National Biological Service.

BJORNDAL, K. A. (1980) Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Marine Biology,* 56**,** 147-154.

BRILL, R. W., BALAZS, G. H., HOLLAND, K. N., CHANG, R. K. C., SULLIVAN, S. & GEORGE, J. C. (1995) Daily movements, habitat use and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L) within a foraging area in the Hawaiian islands. *Journal of Experimental Marine Biology and Ecology,* 185**,** 203-218.

BRODERICK, A. C., COYNE, M. S., FULLER, W. J., GLEN, F. & GODLEY, B. J. (2007) Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society of London B, Biological sciences,* 274**,** 1533-1538.

CHALOUPKA, M., LIMPUS, C. & MILLER, J. (2004) Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. *Coral Reefs,* 23**,** 325-335.

CHILVERS, B. L., LAWLER, I. R., MACKNIGHT, F., MARSH, H., NOAD, M. & PATERSON, R. (2005) Moreton Bay, Queensland, Australia: An example of the co-existence of significant marine mammal populations and large-scale coastal development. *Biological Conservation,* 122**,** 559-571.

GODLEY, B. J., RICHARDSON, S., BRODERICK, A. C., COYNE, M. S., GLEN, F. & HAYS, G. C. (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography,* 25**,** 352-362.

GREENLAND, J. A. & LIMPUS, C. J. (2005) Marine wildlife stranding and mortality database annual report 2004: 1. Dugongs. Brisbane, Queensland Environmental Protection Agency.

GREENLAND, J. A., LIMPUS, C. J. & CURRIE, K. J. (2004) Marine wildlife stranding and mortality database annual report, 2001-2 - III Marine turtles. Brisbane, Queensland Parks and Wildlife Service.

HAINES, J. A. & LIMPUS, C. J. (2001) Marine wildlife stranding and mortality database annual report, 2000 - III Marine turtles. Brisbane, Queensland Parks and Wildlife Service.

HAYS, G. C., ADAMS, C. R., BRODERICK, A. C., GODLEY, B. J., LUCAS, D. J., METCALFE, J. D. & PRIOR, A. D. (2000) The diving behaviour of green turtles at Ascension Island. *Animal Behaviour,* 59**,** 577-586.

HAYS, G. C., FORMAN, D. W., HARRINGTON, L. A., HARRINGTON, A. L., MACDONALD, D. W. & RIGHTON, D. (2007) Recording the free-living behaviour of small-bodied, shallow-diving animals with data loggers. *Journal of Animal Ecology,* 76**,** 183-190.

HAYS, G. C., GLEN, F., BRODERICK, A. C., GODLEY, B. J. & METCALFE, J. D. (2002) Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. *Marine Biology,* 141**,** 985-990.

HAYS, G. C., METCALFE, J. D. & WALNE, A. W. (2004) The implications of lung-related buoyancy control for dive depth and duration. *Ecology,* 85**,** 1137-1145.

HEITHAUS, M. R., FRID, A., WIRSING, A. J., DILL, L., FOURQUREAN, J. W., BURKHOLDER, D., THOMSON, J. & BEJDER, L. (2007) State-dependent risk-taking by green turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology,* 76**,** 837-844.

HOCHSCHEID, S., GODLEY, B. J., BRODERICK, A. C. & WILSON, R. P. (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Marine Ecology Progress Series,* 185**,** 101-112.

HOUGHTON, J. D. R., CEDRAS, A., MYERS, A. E., LIEBSCH, N., METCALFE, J. D., MORTIMER, J. A. & HAYS, G. C. (2008) Measuring the state of consciousness in a free-living diving sea turtle. *Journal of Experimental Marine Biology and Ecology,* 356**,** 115-120.

IUCN MARINE TURTLE SPECIALIST GROUP (2004) 2004 Global Status Assessment: Green Turtle (*Chelonia mydas*). The World Conservation Union (IUCN).

LAIST, D. W., KNOWLTON, A. R., MEAD, J. G., COLLET, A. S. & PODESTA, M. (2001) Collisions between ships and whales. *Marine Mammal Science,* 17**,** 35-75.

LIMPUS, C. J., COUPER, P. J. & READ, M. A. (1994) The green turtle, *Chelonia mydas*, in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum,* 35**,** 139-154.

LUTCAVAGE, M. E. & LUTZ, P. L. (1997) Diving physiology. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, Fla, CRC Press.

LUTCAVAGE, M. E., PLOTKIN, P., WITHERINGTON, B. & LUTZ, P. L. (1997) Human impacts on sea turtle survival. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, Fla, CRC Press.

MAKOWSKI, C., SEMINOFF, J. A. & SALMON, M. (2006) Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Marine Biology,* 148**,** 1167-1179.

MENDONCA, M. T. (1983) Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia,* 4**,** 1013-1023.

MILSOM, W. K. (1975) Development of buoyancy control in juvenile Atlantic loggerhead turtles, *Caretta caretta*. *Copeia,* Vol 1975**,** 758–762.

MINAMIKAWA, S., NAITO, Y., SATO, K., MATSUZAWA, Y., BANDO, T. & SAKAMOTO, W. (2000) Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *Journal of Experimental Biology,* 203**,** 2967-2975.

MUSICK, J. A. & LIMPUS, C. J. (1997) Habitat utilization and migration in juvenile sea turtles. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, CRC Press.

MYERS, A. E., LOVELL, P. & HAYS, G. C. (2006) Tools for studying animal behaviour: validation of dive profiles relayed via the Argos satellite system. *Animal Behaviour,* 71**,** 989-993.

PLOTKIN, P. (2003) Adult migrations and habitat use. In LUTZ, P. L., MUSICK, J. A. & WYNEKEN, J. (Eds.) *Biology of Sea Turtles Volume II.* Boca Raton, CRC Press.

POLOVINA, J. J., HOWELL, E., PARKER, D. M. & BALAZS, G. H. (2003) Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: Might deep longline sets catch fewer turtles? *Fisheries Bulletin,* 101**,** 189–193.

READ, M. A., GRIGG, G. C. & LIMPUS, C. J. (1996) Body temperatures and winter feeding in immature green turtles *Chelonia mydas* in Moreton Bay, south east Queensland. *Journal of Herpetology,* 30**,** 262-265.

RICE, M. R. & BALAZS, G. H. (2008) Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *Journal of Experimental Marine Biology and Ecology,* 356**,** 121-127.

SCHMIDT-NIELSEN, K. (1997) *Animal physiology: adaptation and environment,* Cambridge, Cambridge University Press.

SCHOFIELD, G., BISHOP, C. N., MACLEAN, G., BROWN, P., BAKER, M., KATSELIDIS, K. A., DIMOPOULOS, P., PANTIS, J. D. & HAYS, G. C. (2007a) Novel GPS tracking of sea turtles as a tool for conservation management. *Journal of Experimental Marine Biology and Ecology,* 347**,** 58-68.

SCHOFIELD, G., KATSELIDIS, K. A., PANTIS, J. D., DIMOPOULOS, P. & HAYS, G. C. (2007b) Female-female aggression: structure of interaction and outcome in loggerhead sea turtles. *Marine Ecology Progress Series,* 336**,** 267-274.

SEMINOFF, J. A., JONES, T. T. & MARSHALL, G. J. (2006) Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? *Marine Ecology Progress Series,* 322**,** 269–280.

SEMINOFF, J. A., RESENDIZ, A., SMITH, T. W. & YARNELL, L. (2001) Diving patterns of green turtles (*Chelonia mydas agassizii*) in the Gulf of California. In COYNE, M. S. & CLARK, R. D. (Eds.) *Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation.* Philadelphia, NOAA.

SOUTHWOOD, A. L., DARVEAU, C. A. & JONES, D. R. (2003a) Metabolic and cardiovascular adjustments of juvenile green turtles to seasonal changes in temperature and photoperiod. *Journal of Experimental Biology,* 206**,** 4521-4531.

SOUTHWOOD, A. L., REINA, R. D., JONES, V. S. & JONES, D. R. (2003b) Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. *Canadian Journal of Zoology,* 81**,** 1014-1024.

SOUTHWOOD, A. L., REINA, R. R., JONES, V. S., SPEAKMAN, J. R. & JONES, D. R. (2006) Seasonal metabolism of juvenile green turtles (*Chelonia mydas*) at Heron Island, Australia. *Canadian Journal of Zoology,* 84**,** 125-135.

TAQUET, C., TAQUET, M., DEMPSTER, T., SORIA, M., CICCIONE, S., ROOS, D. & DAGORN, L. (2006) Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Marine Ecology Progress Series,* 306**,** 295-302.

VAN DAM, R. P. & DIEZ, C. E. (1997) Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs,* 16**,** 133-138.

WITHERINGTON, B. (1992) Behavioural responses of nesting sea turtles to artificial lighting. *Herpetologica,* 48**,** 31-39.

WITHERINGTON, B. E. (1997) The problem of photopollution for sea turtles and other nocturnal animals. In CLEMMONS, J. R. & BUCHHOLZ, R. (Eds.) *Behavioural approaches to conservation in the wild.* Cambridge, UK, Cambridge University Press.

Chapter 7: Fine-scale tracking of green turtles

Abstract

Fastloc GPS (FGPS) is a variant of Global Positioning System (GPS) technology that offers important new utility for investigating fine-scale movements of marine animals like green turtles that surface too briefly for effective use of standard GPS. I report here on the accuracy and efficiency of this novel technology, compare it with two alternative methods, namely boat-based ultrasonic tracking and Argos Platform Transmitter Terminals (PTTs), and provide new data on the vagility and habitat selection of green turtles in shallow coastal foraging habitat. I used a combined FGPS receiver and PTT transmitter (Sirtrack, Havelock North, New Zealand) mounted together with an ultrasonic transmitter and time-depth recorder in a tether-attached housing that allowed automatic detachment and subsequent retrieval of the equipment without the requirement to recapture turtles. With this equipment I conducted short deployments (4.5 to 16.8 d) on 3 free-living adult-size green turtles in coastal foraging habitat in Queensland, Australia. In addition, stationary tests in air and afloat were conducted at the same site. FGPS location error (mean ±SD) increased as the number of satellites used in each computation decreased, from 26 m ±19.2 (8 satellites) to 172 m ±317.5 (4 satellites). During live tracking the frequency of FGPS locations greatly exceeded Argos PTT, such that screened data comprised about 50 times more FGPS locations despite a much tighter screening threshold for FGPS (250 m) than for Argos PTT (1000 m). FGPS locations showed the three study turtles used modest short-term activity ranges with Minimum Convex Polygon area mean ±SD 662 ha ±293.9. They all remained within <4.7 km of their capture-release locations and favoured shallow water, with 86% of locations at charted depths ≤3 m and the deepest location at 5.9 m. Fine-scale movements of each turtle varied from day to day with respect to tortuosity and areas traversed. Statistically significant day-night differences were evident in average rates of movement (greater by day) and in habitat selection, where diurnal locations had greater seagrass density while nocturnal locations featured deeper bathymetry. Individual turtles revisited some of their centres of activity (identified from 50% fixed kernel utilisation distributions) on multiple occasions but none of the study turtles travelled consistently between the same day-night pair of sites as has been reported elsewhere. Such disparity and the day-to-day variation in movements revealed by these short-term findings highlight the need for detailed tracking over longer periods at multiple locations. Fastloc GPS technology proved an effective new tool for this area of research.

7.1 Introduction

Topics of broad spatial and temporal scope receive much attention in current research on turtles and other large marine vertebrates, e.g. the use of oceanic hotspots, energy budgets over large timescales and potential impacts of climate change (for a recent review see Hays, 2008). For the green turtle *Chelonia mydas*, scientific understanding of its geographic range, spatial movement and habitat use is most advanced at the big-picture level, with data provided by techniques as diverse as recapturing marked individuals (Limpus et al., 2009), electronic tracking (Broderick et al., 2007) and molecular studies (Dethmers et al., 2006). Yet data remain sparse for the small end of the scale.

There are compelling grounds for researching the detail of green turtle behaviour, particularly in neritic areas as this is where individuals are known to spend the major part of their lives (Musick and Limpus, 1997; Plotkin, 2003), where the importance of the species' ecological role is well recognised (Bjorndal and Jackson, 2003), and where turtles suffer multiple anthropogenic impacts (e.g. see Lutcavage et al., 1997; Chapter 2). However, even fundamental data such as activity ranges have been reported for only a few sites among the wide diversity of coastal foraging areas occupied by green turtles (e.g. Mendonca, 1983; Whiting and Miller, 1998; Makowski et al., 2006; Seminoff and Jones, 2006) and continuous fine-scale tracking of green turtles has rarely been achieved (Mendonca, 1983; Seminoff and Jones, 2006). A major constraint for such research has been the intensive hands-on effort necessary for tracking individual turtles equipped with acoustic or Very High Frequency (VHF) transmitters and the lack of more suitable technology for this purpose.

In contrast, the convenience of automated satellite-linked technology has facilitated numerous studies of large-scale turtle movements (for comprehensive references see Godley et al., 2008). Most broad scale studies have used Platform Transmitter Terminals (PTTs) operating in conjunction with the Argos data service (CLS Service Argos, 1996) but this technology provides insufficient spatial and temporal resolution for fine-scale tracking. Global Positioning System (GPS) technology, an alternative satellite-linked system with much higher resolution, is extensively used in human navigation and underpins visual surveys of wildlife distribution (e.g. Rowat et al., 2009). Yet while it serves well in tracking terrestrial animals and birds (Steiner et al., 2000), standard GPS has limited utility for tracking turtles and other marine species that typically surface too briefly to permit acquisition of the full complement of GPS satellite data. As soon as the animal dives, data reception is blocked by seawater. If this occurs before the unit has downloaded a substantial volume of orbital data from the GPS satellites, a position will not be recorded because updated orbital data is essential for GPS calculations.

Novel variants of standard GPS have been developed to minimise the time required for data acquisition in the field. These systems defer data processing until a later time when orbital data, acquired separately, are provided. Current examples include TrackTag (Navsys, Colorado Springs, USA) and Fastloc (Wildtrack Telemetry Systems Ltd, Leeds, UK). The latter was specifically designed to accommodate the very brief surface intervals of diving animals. The utility of both systems has been confirmed in a study with important conservation implications regarding loggerhead turtles (Schofield et al., 2007; Schofield et al., 2009b). Rapid uptake of Fastloc technology for tracking a range of marine species is evident in recent conference presentations (Third International Biologging Science Symposium, California, September 2008, abstract booklet available online at http://biologging.wordpress.com/abstracts/) and fast-acquisition GPS has been identified as one of the major advances in biologging science (Rutz and Hays, 2009).

Given the strong interest in scientific use of fast-acquisition GPS it is important to evaluate its performance in the field. In the present study my objective was to test Fastloc GPS (FGPS) at fixed locations, in air and afloat, and during short-term deployments on free-living green turtles at the same study site. I report here on the accuracy and efficiency of this novel technology, compare it to alternative methods (boat-based ultrasonic tracking and Argos PTT) and provide new data on the vagility and habitat selection of green turtles in shallow coastal foraging habitat.

7.2 Methods

7.2.1 Study site and habitat survey

I conducted live tracking and stationary tests at the same location in Moreton Bay, Queensland (Figure 7.1), using study site MB2 described in Chapter 3. I defined survey points covering the study area on a 200 m x 200 m grid. At each survey point, found with a hand-held standard GPS (GPS 12, Garmin Ltd, Olathe, Kansas, USA), I inspected approximately 1 m^2 of the substrate with a cable-connected remote underwater video camera (Model-10, Applied Microvideo, Inc, Sunnyvale CA, USA) and recorded a qualitative assessment of seagrass coverage using 5 categories: none, trace, sparse, moderate, dense. I also measured water depth with an echo-sounder (Model Cuda, Eagle Electronics, Tulsa, OK, USA) calibrated before and after surveys against a steel tape measure. Depth values were subsequently adjusted to Lowest Astronomical Tide (LAT) by subtracting tidal height measured at 10-minute intervals by Maritime Safety Queensland, Brisbane and then merged in a Geographic Information System (GIS) database (Arcview 3.3, ESRI, Redlands, California, USA) with Maritime Safety Queensland bathymetry that covered all of Moreton Bay area at lower spatial resolution.

7.2.2 Tracking equipment

To investigate the fine-scale detail of green turtle movements I sought to record turtle locations as often as possible. This objective prompted a different approach to the usual practice of carapace-mounted satellite-tracking equipment because green turtles at the study site typically surfaced extremely briefly without exposing the carapace (Chapter 7). I therefore mounted a combined Fastloc receiver and PTT transmitter (Sirtrack, Havelock North, New Zealand) in a tether-attached housing (155 mm long, 105 mm max. diam.) with buoyancy at the top and weight concentrated at the bottom. This configuration facilitated surface exposure and optimal orientation of the Fastloc antenna (see inset Figure 7.1). It also allowed automatic detachment and subsequent retrieval of the equipment without recapturing the turtle.

To conserve battery capacity the Fastloc-PTT device was turned off by a saltwater switch when submerged and its operation at the sea surface was pre-programmed as follows: For live tracking (see section 7.2.3) the minimum interval between attempts to acquire FGPS data was 30 min for the first tracking session and 5 min for subsequent tracking sessions. For stationary tests the minimum interval was also 5 min. In all situations an unsuccessful acquisition attempt could be repeated after 1 min (provided the device was not submerged) with a maximum of 4 re-tries. The PTT repetition rate was 90 s for the first live tracking session and 60 s for subsequent sessions. PTT operation was turned off for stationary tests to reduce Argos costs.

The complete equipment package, hereafter called a tracking tag, included an ultrasonic transmitter and two time-depth recorders (TDRs). The ultrasonic transmitter (model CHP-87-L, Sonotronics, Tucson AZ, USA) emitted a coded signal that was inaudible to humans and animals but detectable at close range with a boat-mounted hydrophone and receiver (DH-4 and USR-96, Sonotronics Tucson, AZ, USA). The TDRs (DST Milli, Star-Oddi, Reykjavik, Iceland) contributed data for a separate study of diving behaviour, reported in detail in Chapter 6. TDR data were applied in the present study for screening FGPS locations as described below in section 7.2.5.

The tracking tag was connected to the posterior margin of the turtle's carapace by a 60 cm tether and a fast-corroding metal link (Galvanic Timed Release, International Fishing Devices Inc, Pompano Beach FL, USA). The metal link was secured by a plastic cable tie through a 2 mm diameter hole drilled in the extreme edge of the carapace. The cable tie (breaking load 8 kg) served as a safety link to ensure the turtle could break free if the equipment snagged on an obstruction. Steel washers were attached to the galvanic link, their size and number determined by field testing to achieve neutral buoyancy of the equipment package and thereby avoid disturbing the study turtle's natural buoyancy control, since experimental manipulation of buoyancy has been shown to influence turtle behaviour (Minamikawa et al., 2000; Hays et al., 2004).

7.2.3 Live tracking

Three green turtles were tracked in separate sessions: Sept 2006, T22, curved carapace length (CCL) 113.2 cm; Dec 2006, T25, CCL 108.8 cm; April 2007, T28, CCL 96.0 cm. These turtles were likely adult or near-adult females, inferred from the combination of short tails and CCL >95 cm (Limpus et al., 1994). All were in 'very good' body condition as evaluated by the criteria of Heithaus et al (2007). After each study subject was captured individually in a net (as described in Chapter 7) it was lifted into the boat at the capture site. In order to minimise stress and possible aberrant movement after release we maintained a quiet environment on the boat, reduced turtle handling to a minimum and returned each animal to the water at the same location within 15 minutes. These precautionary measures were deemed effective as one turtle returned to the capture site on the day of capture, all turtles re-visited their capture-release vicinity on multiple days, and maximum displacement from the capture-release sites was modest with similar distances travelled on diverse days within tracking sessions.

Each tracking session included additional boat expeditions when favourable weather allowed. The objective was to re-locate the study turtle intermittently by the acoustic signal from its ultrasonic transmitter and use that signal to determine the turtle's geographic location, for later comparison with FGPS data. After identifying an acoustic signal with the hydrophone we moved the tracking boat closer until the distance to the transmitter was estimated to be <100 m, based on the strength of the received signal. We then stopped to observe successive compass bearings of the signal and check that the turtle was near-stationary (indicated by minimal change in bearings) or wait for the animal to become near-stationary, before recording its location. The latter was accomplished by taking bearings on the signal from two observation positions (recorded using standard GPS) such that approximately perpendicular bearings were obtained in quick succession. The point of intersection of each pair of bearings was accepted as representing the turtle's location provided the time lapse was <5 min and the angle of intersection was within the range 45 to 135º.

7.2.4 Equipment tests

For 'dry' tests the Fastloc-PTT tracking tag was mounted in a fixed position in the boat harbour adjacent to the study area. For 'wet' tests it was secured by a line to an anchor and deployed afloat at diverse positions within the study area. Acoustic tracking tests used six ultrasonic transmitters identical to that in the tracking tag. These were secured to lead weights by short tethers that positioned each transmitter ~15 cm above the substrate when submerged, simulating their deployment on benthic foraging or resting turtles. The transmitters were successively placed at different positions within the study area and each location was determined from pairs of compass bearings as described above in section 7.2.3..

Linear error was calculated as the great circle distance (using standard spherical trigonometry formulas) between each location recorded in test sessions and the corresponding reference co-ordinates. Great circle distance was also used for North-, South-, East- and West-components of linear error. Dry tests used reference co-ordinates obtained by averaging latitudes and longitudes of 2000 records from a prior period of standard GPS recording at the same position, validated against a large-scale harbour plan. Wet tests used reference coordinates obtained by averaging 25 standard GPS locations for each test position. Prior stationary tests had shown the location error (mean ±SD) of our standard GPS receiver at the study site was 3 m ±2.1 (n=13036) with 95% of errors ≤ 6.7 m, max 42 m. Finally Argos PTT accuracy during live tracking was estimated by comparing PTT locations with concurrent FGPS locations screened as described immediately below.

7.2.5 Data processing, screening and analysis

Standard GPS data (downloaded from the handheld unit) and Argos PTT data (downloaded via internet) provided time, latitude and longitude of each location. In contrast the raw FGPS data, downloaded from the device after the tag was recovered, required subsequent processing that was accomplished with proprietary software (Sirtrack Ltd, Havelock North, New Zealand) and satellite ephemeris data obtained from electronic archives maintained by NASA (http://cddis.gsfc.nasa.gov/). FGPS output comprised a time-series of successful and failed acquisition attempts. The former provided latitude and longitude, reported together with the number of satellites used in computation, whereas failed attempts indicated the acquired data were insufficient to compute a location.

Data for live tracking were entered in the GIS database and screened to remove locations with large errors. This is normal practice in satellite tracking studies but the usual strategy of discarding locations implying a biologically unrealistic speed of travel (e.g. Luschi et al., 1998; Hays et al., 2001) was unsuitable for turtles in foraging habitat because they did not maintain directed travel as is the case for animals making long-distance migrations. Instead I screened Argos PTT data by location class (LC) and retained only LC 3, LC 2 and LC 1. I inspected FGPS locations sequentially in the GIS to remove those with apparent error >250 m. Apparent error was assessed by comparing individual locations to near-concurrent acoustic tracking locations and concurrent depth data from the TDR. Extra scrutiny was applied to locations indicating abrupt changes in direction and locations derived from <6 satellites because lower accuracy is expected when Fastloc calculations are based on fewer satellites (Bryant, 2007). Only the screened data were subsequently used for evaluation of turtle behaviour.

Diurnal and nocturnal centres of activity were identified using 50% fixed kernel utilisation distributions with smoothing parameters determined by least squares cross validation, as implemented in the Animal Movement Extension to Arcview (Hooge and Eichenlaub, 2000). The same software served to compute Minimum Convex Polygon (MCP) ranges for each turtle and linear distances between their successive FGPS locations. Vagility was assessed using each turtle's average rate of movement (m h^{-1}) by day and by night, where days comprised the period from the first FGPS location after sunrise to the last before sunset, nights from the first location after sunset to the last before sunrise. The initial 4.5 d of each tracking session provided periods of equal duration for comparisons of areas and movement distances. GIS spatial joins were used to associate the nearest depth and seagrass density values with each tracking location.

Results are reported as mean ±SD. Paired t-tests (one-sided) were applied to day vs. night comparisons of FGPS acquisition attempts per hour, proportions (arcsine transformed) of acquisition attempts that provided computed locations, and rates of movement (means for each turtle). To evaluate the study turtles' habitat selection collectively, their FGPS locations were pooled for day vs. night comparisons of depth and seagrass density and the Wilcoxon rank sum test was applied because the assumption of normality was untenable. For the same reason, Spearman's correlation (r_s) was used to evaluate linear error in equipment tests and the relationship between water depth and seagrass density in the habitat survey. Statistical significance was inferred for $p < 0.05$.

7.3 Results

7.3.1 Location error

FGPS location error (mean ±SD) for all stationary tests (n = 9910) was 40 m ±80.5 with 95% of errors ≤ 101 m. The number of satellites used ranged from 4, the minimum necessary for computation, to 8, the maximum acquired throughout this study. Error increased as the number of satellites decreased, from 26 m ±19.2, 95% of errors ≤ 56 m (8 satellites) to 172 m ±317.5, 95% of errors ≤ 646 m (4 satellites). Errors were similar in wet tests and dry tests (Table 7.1), with a superficial anomaly of higher mean error for 4 satellite locations during wet tests arising from one location with large error in a very small sample. Wet tests and dry tests, evaluated separately, showed the same negative correlation between linear error and number of satellites used (Spearman's $r_s = -0.31$, $p < 0.001$). The distribution of linear error was strongly skewed left, i.e. large errors were relatively infrequent (Figure 7.2a). There was no appreciable directional bias in error with means (all tests pooled) for North-, South-, East- and West-components of linear error differing by <1 m, and no statistical significance in a two-sided test comparing latitudinal and longitudinal components of linear error ($t = 1.3781$, $df = 9909$, $p = 0.1682$).

Acoustic tracking error was 7 m ±4.5 ($n = 1723$) for observation distances 25 to 100 m and 10 m ±5.4 ($n = 919$) for observation distances 100 to 200 m. Positive correlation between linear error and observation distance was significant: Spearman's $r_s = 0.36$, $p < 0.001$. Figure 7.2a provides error comparisons between FGPS, acoustic tracking and standard GPS. Estimates of Argos PTT error during live tracking are presented in Table 7.2.

7.3.2 Location frequency

During live tracking the frequency of FGPS locations greatly exceeded Argos PTT locations, with a 3- to 9-fold increase in total locations and a 45- to 53-fold increase in locations retained after screening (Table 7.3). Enhanced Fastloc performance was evident in the second and third sessions when the average hourly rate of successful locations was 3.5 to 4.3 by day and 1.9 to 3.3 by night with 96 to 98% of all locations retained after screening (Table 7.3). The hourly rate of FGPS acquisition attempts was higher by day ($t = 3.2799$, $df = 2$, $p = 0.04$) but the proportion of successful locations was lower by day ($t = 7.8805$, $df = 2$, $p = 0.008$).

Given that locations computed from higher numbers of satellites had lower error (Table 7.1), a large proportion of such locations would provide more efficient tracking than a small proportion. In these terms the proportions of 4- to 8-satellite locations actually obtained (Figure 7.2) showed FGPS operation to be less efficient during live tracking than during stationary tests, while the difference in efficiency between dry and wet tests was slight. FGPS operation was also notably more efficient at night during tests and slightly more efficient at night during live tracking (Figure 7.2). The three tracking methods produced wide disparity in the area of activity ranges for individual turtles, as depicted in Figure 7.3, with the FGPS activity ranges construed as the most informative due to relatively high accuracy and comprehensive sampling. Although acoustic tracking provided greater location accuracy, sampling was less comprehensive for that method because manual tracking could only be maintained for limited periods, see section 7.4.3.

7.3.3 Short term activity range and diel vagility

FGPS locations showed the three study turtles used the same geographic area (Figure 7.3) and occupied modest MCP activity ranges (662 ha ±293.9). All remained within <4.7 km of their release locations and all re-visited the capture-release vicinity on multiple days during their respective tracking periods (4.5 to 16.8 d, Table 7.3). The average rate of movement was considerably greater by day (679 ±209.5 m h^{-1}) than by night (297 ±126.1 m h^{-1}) for all data pooled. In a comparison using periods of equal duration (4.5 d) for each turtle, the day-night difference was statistically significant (t = 9.031, df = 2, $p = 0.006$). Despite clear disparity in diurnal and nocturnal distances (Figure 7.4) the fine-scale movements of each turtle varied from one day to the next, with respect to tortuosity and areas traversed (Figure 7.5).

7.3.4 Habitat use

Collectively the study turtles demonstrated significant day-night differences in habitat selection. Diurnal FGPS locations, pooled for all turtles, had greater seagrass density than nocturnal locations (W = 171896, $p < 0.001$), while nocturnal locations had deeper bathymetry (LAT depths) than diurnal locations (W = 103509.5, $p < 0.001$). However, the difference in depth was modest (median LAT depth: day 1.4 m, night 2.2 m) and 86% of all locations were at charted (LAT) depths ≤3 m with the deepest location at 5.9 m. Diurnal and nocturnal centres of activity, identified from 50% fixed kernel utilisation distributions, were usually spatially disjunct but sometimes overlapped (Figure 7.6). Individual turtles revisited some of their centres of activity on multiple occasions but none of the study turtles travelled consistently between the same day-night pair of sites.

7.4 Discussion

7.4.1 Fastloc GPS performance

FGPS provided greatly enhanced accuracy relative to Argos PTT, which is arguably the de facto standard for tracking marine vertebrates. My field tests showed linear error for the three best categories of FGPS locations (pooled data for 6-, 7- and 8-sat locations) was 32 m ±36.9, compared to error of 150 to 1000 m for the best Argos PTT categories (LC 3, 2, 1) estimated by the service provider (CLS Service Argos, 1996) at the time of this study, noting that estimates have subsequently been revised upwards (CLS, 2008). Considerably higher PTT errors have been reported for field tests (Table 7.2). Similarly, FGPS errors in my tests exceeded the system developer's data (Bryant, 2007) with a median increase in error from 33% (50th percentile) to 47% (95th percentile). Unknown factors evidently tend to increase error under field conditions, implying that researchers should conduct on-site tests rather than rely on error values obtained under different circumstances.

FGPS also greatly exceeded Argos PTT in the frequency of locations obtained during live tracking (Table 7.3) where screened data comprised about 50 times more FGPS locations despite a much tighter screening threshold for FGPS (250 m) than for Argos PTT (1000 m). FGPS performance was even better in the second and third sessions than in the first, with a higher proportion of successful acquisition attempts and a higher proportion of locations retained after screening (Table 7.3). This performance enhancement could in part be ascribed to technical changes when our Fastloc unit was upgraded after the first session, as well as to the reduction in minimum interval between acquisition attempts (initially 30 min; for subsequent sessions 5 min).

Only a modest proportion of FGPS attempts produced high quality locations, e.g. in the second and third sessions, 32% of attempts resulted in locations using 6 to 8 satellites. Therefore, when the objective is to record fine detail in turtle movements, it is important to maximise Fastloc acquisition attempts by setting the shortest feasible minimum interval. However, one must be mindful of relatively high battery consumption when FGPS and PTT systems operate concurrently. Conserving battery capacity was vital in this study where the equipment was powered by a single C-cell in order to minimise weight and bulk of the tag. Tag recovery depended crucially on continued Fastloc and PTT operation well beyond the duration of turtle attachment (potentially considerably longer than actually achieved) because open-water searches could be greatly delayed by bad weather and rough sea conditions. New programming features introduced after the first tracking session allowed multiple duty cycles (e.g. I could define a minimum interval of 5 min for the first 20 days, thereafter changing to 30 min) and thereby greatly facilitated battery management.

Fastloc acquisition attempts were limited not only by the programmed minimum interval, but also by each turtle's surfacing behaviour, because transmissions to and from satellites are blocked by seawater when the turtle is submerged. The tendency for green turtles to surface more often and extremely briefly during the day, and less often but for longer intervals during the night (Chapter 6) was reflected in day-night differences in FGPS data (Table 7.3). Here the higher diurnal rate of Fastloc acquisition attempts could clearly be ascribed to the tag reaching the surface more frequently than at night. The lower proportion of successful locations during the day may have resulted in part from diurnal surface intervals that were often too brief to permit acquisition of sufficient data. However, relatively greater success at night was not exclusively due to longer exposure at the sea surface. As Figure 7.2 shows, Fastloc operation was also more efficient at night during stationary tests when the tag was never submerged. The performance difference probably arose from a greater number of GPS satellites being available (i.e. in 'line-of-sight' for receivers at our geographic location) during nocturnal hours. The current constellation of GPS satellites provides global around-the-clock availability of at least 6 satellites (United States Coast Guard, 2009) but availability of additional satellites varies geographically and temporally, while local topography and structures may obstruct line-of-sight visibility of low altitude satellites. When planning Fastloc tracking studies researchers can consider predicted GPS satellite passes, e.g. using Satscape, www.satscape.co.uk, or similar software tools, but other constraints might have greater weight in deciding the study site and timing.

7.4.2 Fastloc GPS data processing

FGPS clearly out-performed Argos PTT in location accuracy and temporal resolution but lacked the convenience of processed location data, remotely delivered in near-real time, as is provided by CLS Service Argos. Raw Fastloc data require post-processing to derive geographic locations. The task is an essential component of FGPS usage because Fastloc computation depends crucially on the input of accurate start time and deployment location, informed adjustment of processing parameters (e.g. to accommodate irregularities in time-keeping or gaps in data that may occur if animal behaviour or severe weather prevents regular data acquisition) and provision of GPS ephemeris data. Ephemeris data become publicly available from governmental archives after a time delay (typically ≥24 h). This delay is of no consequence when processing FGPS data after recovering a tag but it precludes immediate processing of Fastloc data received via near-real time Argos PTT transmissions. Instead one can directly acquire ephemeris data by continuous operation of a computer-connected GPS receiver at or near the study site. This extra task was important in my study because I relied on near-real time FGPS locations to narrow down the search area for a drifting tag after its detachment from a turtle. In some situations tag recovery might be accomplished purely by using a radio receiver and directional Yagi antenna to detect UHF or VHF signals from a supplementary transmitter, if fitted. Preliminary trials of that method had shown it offered limited utility for my study circumstances.

In this study the process of screening FGPS locations was based on supplementary fine-scale data (acoustic tracking and high-resolution bathymetry). Frequent FGPS locations, as obtained in the second and third sessions when the FGPS operating schedule was optimised, coupled with the study turtles' modest spatial range, also facilitated the detection of erroneous locations. For example, an error greater than 1000 m is possible in 4-satellite locations albeit rare (Figure 7.2a) but such large errors create anomalies clearly noticeable in the plotted data when there are 3 or 4 locations per hour (Table 7.3) and the turtle typically moves less than 1000 m in an hour (Figure 7.4).

In most satellite tracking situations, however, supplementary location data suitable to guide FGPS screening are unlikely to be available. FGPS locations are also likely to be acquired less frequently when tracking animals over large distances because, in order to extend battery life, devices must be programmed for longer intervals between acquisition attempts. When many hours elapse between FGPS locations, errors of the magnitude possible (Figure 7.2a) will tend to be masked, especially for animals capable of fast travel. The simple expedient of screening out locations with fewer than 6 satellites would greatly reduce the probability of large errors (Figure 7.2a) and might be an acceptable strategy if the proportion of discarded data were low. Indeed under different circumstances, particularly when tracking animals that spend longer periods at the surface, FGPS may provide a greater proportion of locations with high numbers of satellites than in my study. Nevertheless, since location error can impede detection of biological signals at multiple scales (Bradshaw et al., 2007), there is a clear need to develop more refined methods of screening FGPS data.

7.4.3 Acoustic tracking

Acoustic tracking locations exceeded FGPS in accuracy (Figure 7.2b) and potentially this method could also provide higher temporal resolution than FGPS since acoustic tracking is not limited by turtle surfacing behaviour as is the case for all satellite-linked systems. In practicality, however, acoustic tracking fell far short of FGPS because the necessary boat operations are weather dependent and labour intensive so it was seldom feasible to maintain continuous acoustic tracking over extended periods. The study turtles' variable movements were impossible to predict and we faced long delays (from several hours to several days) in re-locating an individual study animal after any interruption in tracking. Benthic habits of the study turtles meant that ultrasonic transmitters were often positioned close to silty and vegetated substrates, which severely attenuated signal propagation, while scattered shoals within the study site tended to block signals entirely. Signal detection was also hampered by underwater noise from wave action, vessel traffic and other animals.

7.4.4 Activity ranges and rates of movement

FGPS locations showed the study turtles had short-term activity ranges of moderate extent (662 ±294 ha) relative to other studies reporting MCP areas for green turtles in open water foraging areas, e.g. 238±178 ha (Makowski et al., 2006), 1662 ±324 ha (Seminoff et al., 2002).

The comparison must be qualified because disparate methods and periods of tracking were used, and because the geography of my study site meant that convex polygons around recorded turtle locations also encompassed space unavailable to turtles such as a small island and adjacent rubble banks. Short term range reduced to 459 ±112.1 ha when determined from irregular polygons that excluded the above-mentioned inaccessible areas. Based on the modest spatial areas they occupied, my study subjects might be considered homebodies of the green turtle world but they were surprisingly active within their small areas. For example, in mean diurnal movement rates (679 ±209.5 m h^{-1}) they clearly exceeded green turtles in Mexico (392 ±287.3 m h^{-1}) tracked acoustically by Seminoff & Jones (2006) and those authors in turn identified substantially greater vagility in their subjects than inferred for earlier studies reliant on intermittent tracking. In part my study subjects' movements might be ascribed to their exploitation of tidal currents (they often travelled with the current and were never observed to travel against the current). However, I was unable to test this tentative hypothesis due to the short duration of tracking and lack of quantitative data on tidal flows at the study site.

7.4.5 Habitat selection

Although tracked in separate sessions, all three study turtles displayed notable consistency in habitat selection. Areas occupied by each turtle during their first 4.5 d (Figure 7.3b) overlapped substantially, and the area occupied by T28 was matched almost exactly by that of T22 over the full duration of its session (16.8 d). Active habitat selection was implied by the significant day-night difference in movement rates (Figure 7.4), predominantly separate diurnal and nocturnal centres of activity (Figure 7.6) and significant day-night differences in seagrass and depth associations. It could be argued that selections on the basis of seagrass density and water depth were not quantitatively independent, because across the study site these attributes were negatively correlated (Spearman's $r_s = -0.41$, $p < 0.001$). That is the norm for south-western areas of Moreton Bay where turbid water restricts light penetration and thereby constrains seagrass distribution (Abal and Dennison, 1996). However, it seems implausible that the study turtles selected deeper night locations with the objective of avoiding seagrass, or chose daytime locations for shallowness rather than for forage resources so the interpretation that the turtles sought greater seagrass density by day and preferred greater water depth by night remains compelling. This pattern of habitat selection reinforces current understanding that green turtles prefer to travel and forage by day and then rest much of the night, a behavioural dichotomy previously inferred from intermittent observation (visual - Bjorndal, 1980; or acoustic - Mendonca, 1983; Taquet et al., 2006) and from short-term records of diving behaviour (Seminoff et al., 2001; Makowski et al., 2006; Chapter 6)).

Habitat avoidance was only tentatively inferred but also appeared consistent in that (1) none of study turtles used the south-eastern part of the study site although they frequently travelled past it, and (2) all of them invariably deviated around well-submerged shoals at times when tidal height was more than sufficient to allow a direct route. Observation (1) likely reflected the absence of attractive locations in that part of the study site where my habitat survey confirmed a dearth of forage resources and lack of deeper bathymetry evidently preferred for resting sites. Observation (2) suggested the turtles might have perceived negative attributes of well-submerged shoals, of sufficient importance to outweigh potentially attractive seagrass on these shoals and the shorter travel distance offered by a direct route across them. Their behaviour contrasts with observations elsewhere of green turtles exploiting inter-tidal areas by moving in when tidal height allows and retreating at low tide (Limpus et al., 1994). Although inter-tidal foraging is more commonly observed among smaller juveniles (Limpus et al., 1994) explanatory factors remain to be elucidated. Tentatively, these might reflect age-class differences in forage selection and risk avoidance, analogous to condition-dependent use of space identified by Heithaus et al (2007).

7.4.6 Patterns of movement

As Figure 7.5 and Figure 7.6 show, each study turtle visited a suite of activity centres in irregular sequences, rather than consistently shuttling between the same foraging and resting sites (e.g. Bjorndal, 1980; Ogden et al., 1983; Makowski et al., 2006). In part the difference may reflect the capacity of continuous FGPS tracking to detect more diverse activity centres than might be inferred from intermittent observations. It is also likely that green turtles adopt different behavioural patterns in different habitats. For example, shuttling behaviour seems to be associated with environments providing structured resting places (e.g. reefs) with favourable forage patches nearby. However, both features were lacking at my study site.

In the absence of benthic structure, the study turtles evidently did not select resting sites for maximum depth even though they used slightly deeper locations at night. Rather they seemed to choose resting sites in or beside slight depressions in the substrate and on moderate slopes. These criteria could be met at many places in the study area, and sparse forage resources were also widely dispersed. It was presumably beneficial for a turtle in this situation to exploit multiple locations rather than shuttle back and forth between only two centres of activity.

The reasons why study turtles adopted their particular activity ranges remain unclear. Behavioural thermoregulation was an unlikely explanation given their warm subtropical location. Indeed temperature-related movement was not detected during the study of turtle diving behaviour at the same site (Chapter 6) that covered the full range of seasonal variation in water temperature. However temperature-related movement has been reported for pre-breeding loggerhead turtles under cooler Mediterranean conditions (Schofield et al., 2009a). Boat-based investigation of adjacent areas confirmed additional locations with broadly similar habitat features. A number of additional foraging and resting places would therefore have been available to the study turtles, at similar and shorter distances than their recorded diel movements, if they had travelled to the north or south-east (eastward of the shoals) beyond the edge of their recorded ranges. Although density-dependant effects might be proposed, few turtles were sighted in these adjacent areas during my study. Perhaps the study turtles maintain a high degree of familiarity with their habitat by concentrating their activities within a modest area, and thereby achieve more efficient exploitation of scattered resources than would be the case if they ranged more widely.

The apparent irregularity of movement routes depicted during brief tracking sessions might resolve to more consistent patterns over longer periods of study, if green turtle behaviour is influenced by factors operating over weeks or months. For example, I suspect that green turtles’ fine-scale movements are influenced by tidal currents in places like my study site where these currents vary in speed between neap and spring tides and flow in different directions during ebb and flood tides. By travelling with tidal currents rather than against them, turtles could reach their destination more quickly and reduce energy expenditure. Seasonal factors may also influence their movement patterns as changes in water temperature have been shown to influence diving behaviour (Chapter 6). Investigation of such questions will need larger samples than the present study and longer tracking sessions. These are now entirely feasible with the new capability of Fastloc GPS for fine-scale tracking. This novel technology also offers benefit at oceanic scales. In that arena advanced quantitative techniques are starting to extract more information out of low quality Argos data sets (e.g. state-space models applied to leatherback turtle movements, Bailey et al., 2008) and could have even greater utility when applied to high resolution Fastloc data.

7.5 Tables

Table 7.1. Linear error in metres (Mean ±SD and Max) of Fastloc GPS locations recorded at a fixed position (Dry tests) adjacent to the bay where live tracking was conducted and at fixed positions floating on the sea surface within the study site (Wet tests). Categories indicate number of satellites used to compute locations.

Number of satellites	8	7	6	5	4	Pooled ≥6 sats
Dry tests						
Mean ±SD	26 ±19.2	33 ±42	42 ±53.2	64 ±79.4	167 ±311.2	32 ±37.1
Max	386	924	846	857	3172	924
n	4016	2257	1927	1069	373	8200
Wet tests						
Mean ±SD	27 ±18.5	31 ±40.1	38 ±37.9	59 ±42.8	489 ±543.5	30 ±30.5
Max	104	337	211	128	1505	337
n	127	68	52	15	6	247
All tests						
Mean ±SD	26 ±19.2	33 ±41.9	42 ±52.9	54 ±79.0	172 ±317.5	32 ±36.9

Table 7.2. Argos PTT error (m) determined in field tests (mean ±SD) exceeded error estimates by CLS Service Argos (1996). This study provided a rare opportunity to evaluate PTT accuracy during live tracking, by comparing PTT locations with concurrent Fastloc GPS locations (screened as described in text section 7.2.5). Data from stationary tests by Hays et al (2001) and Boyd et al (1998) are reproduced here to facilitate comparison.

Argos location class	LC 3	LC 2	LC 1	LC 0	LC A	LC B
Deployment on green turtles, this study	482 ±153 (n = 3)	785 ±583 (n = 5)	1430 ±1156 (n = 13)	5179 ±3677 (n = 14)	8072 ±15448 (n = 38)	11484 ±19679 (n = 95)
Field tests on land, Hays et al (2001)	270 ±200 (n = 38)	540 ±400 (n = 28)	1330 ±1350 (n = 19)	10100 ±12310 (n = 9)	990 ±1360 (n = 18)	7000 ±6920 (n = 22)
Field tests on land, Boyd et al (1998)	1228 ± 957 (n = 15)	1115 ±362 (n= 21)	1566 ± 1082 (n = 29)	3779 ± 2587 (n = 7)	18843 ± 42604 (n = 14)	22841 ± 43926 (n = 8)
Estimates by CLS Service Argos (1996)	150	350	1000	>1000	n/a	n/a

Table 7.3. *Chelonia mydas*. Summary of data obtained concurrently by Argos PTT and Fastloc GPS systems during live tracking of three green turtles. Total locations were screened to exclude Argos PTT data with predicted errors >1000 m and Fastloc data with apparent errors >250 m, as described in text section 7.2.5. FGPS acquisition attempts and recorded locations show hourly rates as mean ±SD by day (D) and by night (N).

Turtle	Deployment start and duration	Argos PTT locations total | screened	FGPS locations total | screened	FGPS acquisition attempts h^{-1}	FGPS recorded locations h^{-1}
T22	18/09/06 (16.8 d)	89 | 6 (7%)	337 | 305 (91%)	D: 4.9 ±0.60 N: 3.8 ±0.74	D: 0.7 ±0.43 N: 0.9 ±0.20
T25	19.12.06 (4.5 d)	41 | 7 (17%)	386 | 371 (96%)	D: 7.9 ±2.28 N: 4.7 ±1.71	D: 4.3 ±0.90 N: 3.3 ±1.04
T28	5.04.07 (6.1 d)	39 | 8 (21%)	368 | 360 (98%)	D: 6.6 ±1.50 N: 2.7 ±0.99	D: 3.5 ±0.43 N: 1.9 ±0.49

7.6 Figures

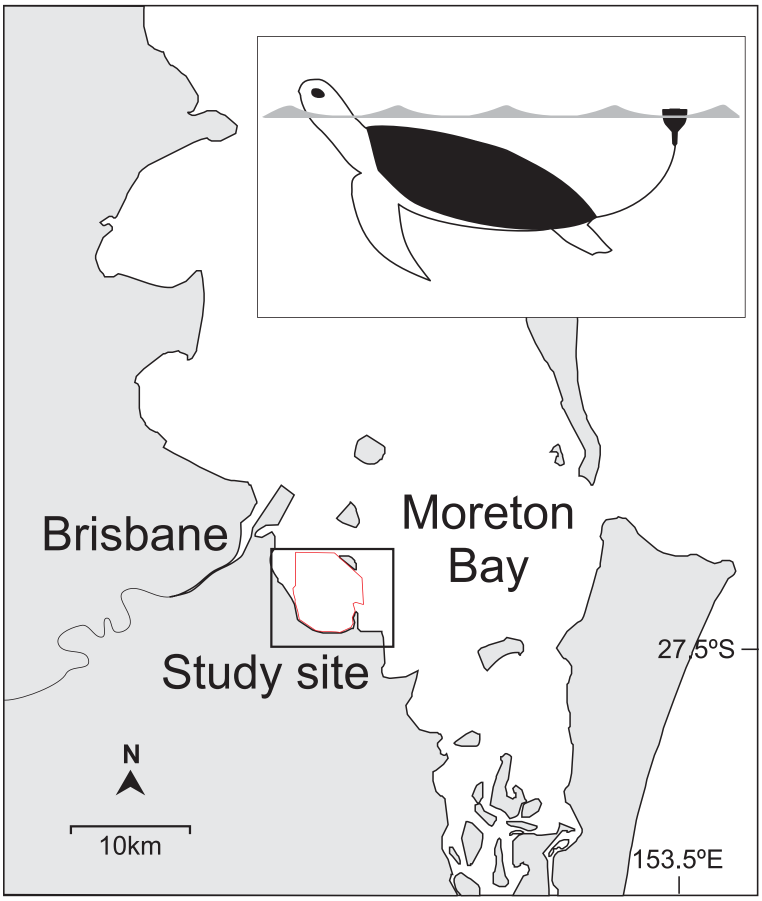

Figure 7.1: The study site was located in Moreton Bay, adjacent to the city and suburbs of Brisbane, the state capital of Queensland, Australia. Underwater habitat was surveyed within the red outline. Inset top right depicts deployment of a tether-attached Fastloc GPS tracking tag. This configuration facilitated optimal orientation of the Fastloc antenna while at the surface and enabled automatic detachment and subsequent retrieval of the equipment without recapturing the turtle.

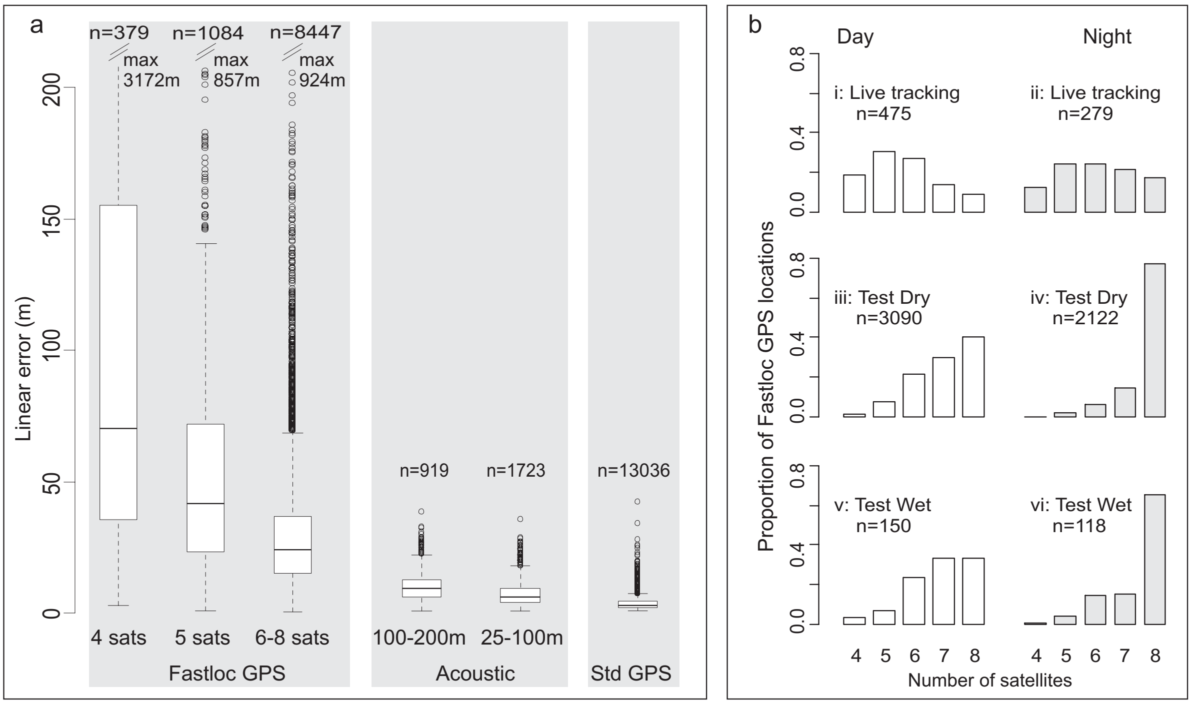

Figure 7.2. Evaluation of Fastloc GPS (FGPS) and boat-based acoustic tracking. (a) Linear error determined in field tests, FGPS data categorised by number of satellites (sats) used to compute each location, acoustic tracking data categorised by observer-to-transmitter distance. Standard GPS error was also determined at the study site. Box plots show median (horizontal bar), inter-quartile range (box length), largest values within 1.5 x inter-quartile range (whiskers) and all data points beyond (circles) except for truncation of extreme FGPS errors. (b) For FGPS the proportional distribution of 4- to 8-satellite locations reflects relative efficiency of this system under different conditions, given that location accuracy is enhanced when higher numbers of satellites are used (Table 7.1). By this measure FGPS operation proved less efficient during live tracking (panels i & ii, comprising all locations for T25 & T28) than during stationary tests (panels iii to vi) while the difference between dry and wet tests was slight. FGPS operation was notably more efficient at night (grey bars) during tests and slightly more efficient at night during live tracking.

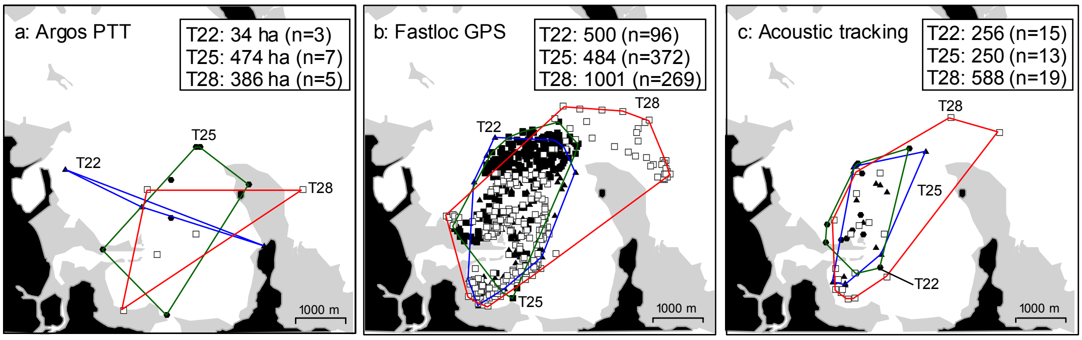

Figure 7.3. *Chelonia mydas*. Short term activity ranges for the first 4.5 days of each tracking session varied with the different tracking methods, panels a, b, c. Screened locations and Minimum Convex Polygons are shown for each study turtle: T22 – triangles, blue lines; T25 - filled squares, green lines; T28 - open squares, red lines. Black areas depict land, grey areas depict drying shoals i.e. water depth ≤0 m at Lowest Astronomical Tide.

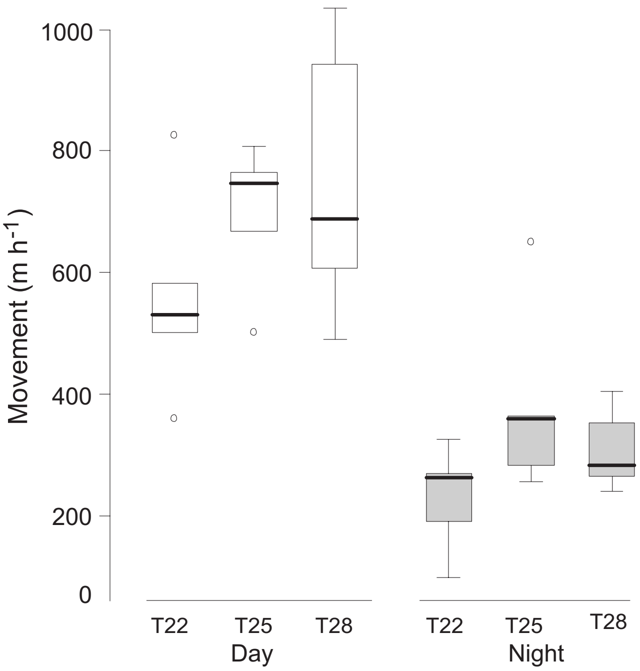

Figure 7.4: *Chelonia mydas*. Diurnal movement significantly exceeded nocturnal movement for all study turtles. The comparison was based on average rates of movement depicted by screened Fastloc GPS locations (for details see text 7.2.5 Data processing, screening and analysis) and covered the first 4.5 d of each turtle's tracking session. Box plots show median (horizontal bar), inter-quartile range (box length), largest values within 1.5 x inter-quartile range (whiskers) and all data points beyond (open circles).

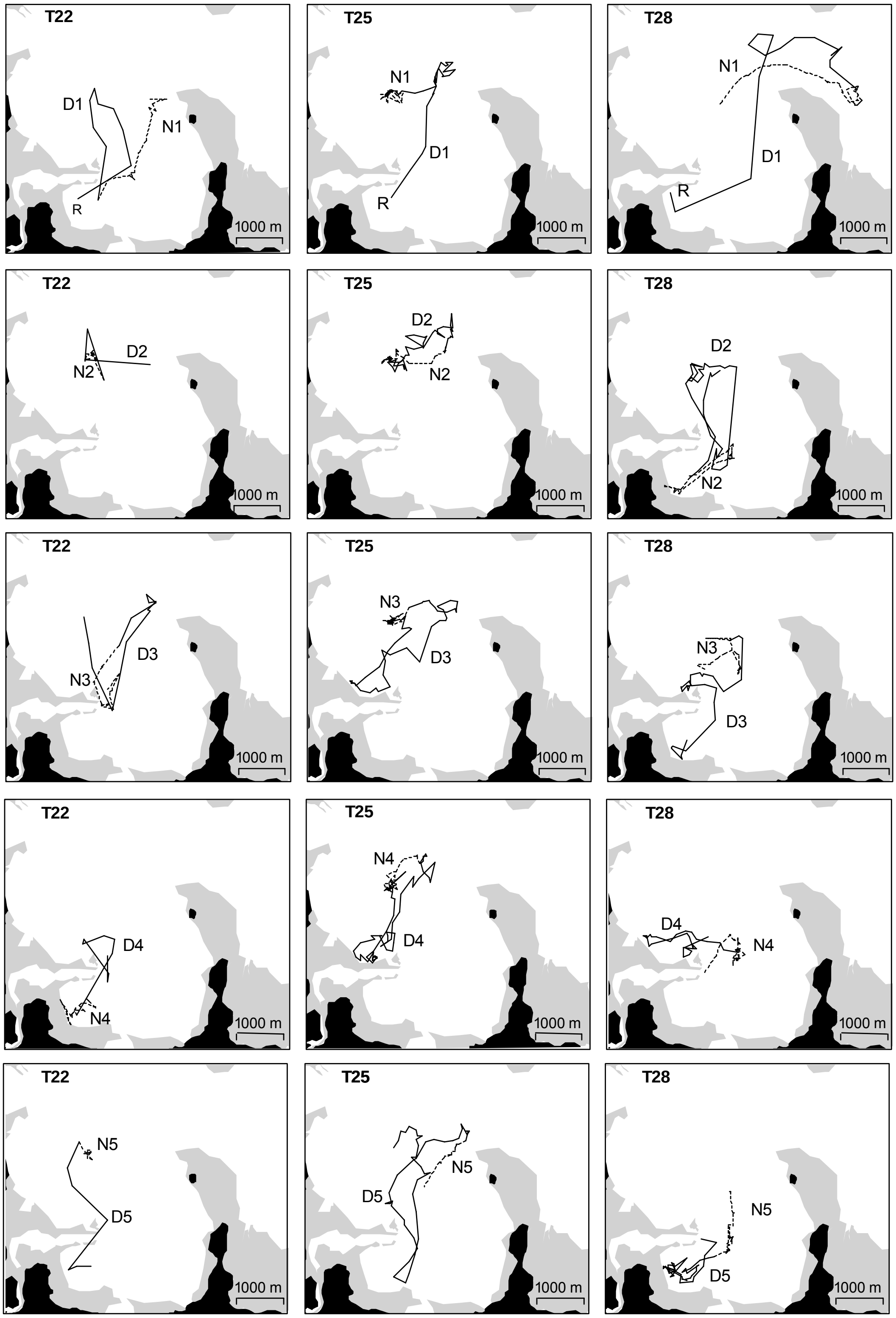

Figure 7.5: *Chelonia mydas*. Vagility of study turtles T22, T25, T28 recorded by Fastloc GPS showed significantly greater movement by day than by night. Tracks begin at release location R for each animal and show diversity of movements on subsequent days (D1 to D5, solid lines) and nights (N1 to N5, broken lines).

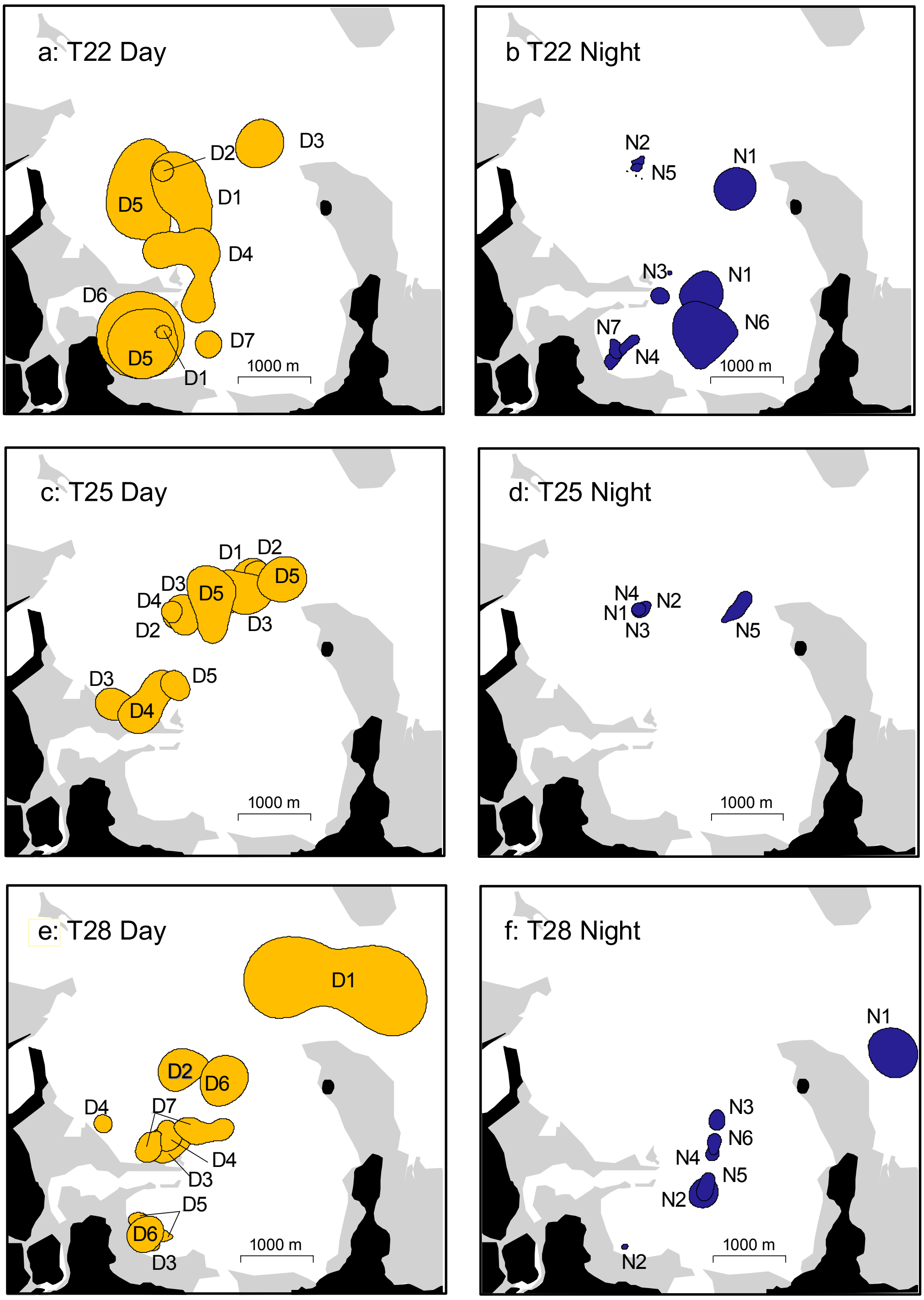

Figure 7.6. *Chelonia mydas*. Activity centres recorded by Fastloc GPS locations were identified using 50% fixed kernel utilisation distributions with smoothing parameters determined by least squares cross validation. Activity centres at night (N) were less diverse and generally smaller than those by day (D). None of the study turtles repeatedly used the same pair of day and night areas although one individual used the same area on 4 successive nights (panel d).

7.7 References

ABAL, E. G. & DENNISON, W. C. (1996) Seagrass depth range and water quality in Southern Moreton Bay, Queensland, Australia. *Marine and Freshwater Research,* 47**,** 763-771.

BAILEY, H., SHILLINGER, G., PALACIOS, D., BOGRAD, S., SPOTILA, J., PALADINO, F. & BLOCK, B. (2008) Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology,* 356**,** 128-135.

BJORNDAL, K. A. (1980) Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Marine Biology,* 56**,** 147-154.

BJORNDAL, K. A. & JACKSON, J. B. C. (2003) Roles of sea turtles in marine ecosystems: reconstructing the past. In LUTZ, P. L., MUSICK, J. A. & WYNEKEN, J. (Eds.) *The Biology of Sea Turtles Volume II.* Boca Raton, CRC Press.

BOYD, I. L., MCCAFFERTY, D. J., REID, K., TAYLOR, R. & WALKER, T. R. (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Fisheries and Aquatic Sciences,* 55**,** 845-852.

BRADSHAW, C. J. A., SIMS, D. W. & HAYS, G. C. (2007) Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data. *Ecological Applications,* 17**,** 628-638.

BRODERICK, A. C., COYNE, M. S., FULLER, W. J., GLEN, F. & GODLEY, B. J. (2007) Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society of London B, Biological sciences,* 274**,** 1533-1538.

BRYANT, E. (2007) 2D Location Accuracy Statistics for Fastloc® Cores Running Firmware Versions 2.2 & 2.3, Technical Report Fastloc/TR01. Leeds, UK, Wildtrack Telemetry Systems Ltd.

CLS (2008) *Argos User's Manual,* Ramonville Saint-Agne, France, CLS.

CLS SERVICE ARGOS (1996) User’s Manual. Toulouse, France, CLS Service Argos.

DETHMERS, K. M., BRODERICK, D., MORITZ, C., FITZSIMMONS, N. N., LIMPUS, C. J., LAVERY, S., WHITING, S., GUINEA, M., PRINCE, R. I. T. & KENNETT, R. (2006) The genetic structure of Australasian green turtles (*Chelonia mydas*): exploring the geographical scale of genetic exchange. *Molecular Ecology,* 15**,** 3931-3946.

GODLEY, B. J., BLUMENTHAL, J. M., BRODERICK, A. C., COYNE, M. S., GODFREY, M. H., HAWKES, L. A. & WITT, M. J. (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endangered Species Research,* 4**,** 3-22.

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

HAYS, G. C., AKESSON, S., GODLEY, B. J., LUSCHI, P. & SANTIDRIAN, P. (2001) The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour,* 61**,** 1035-1040.

HAYS, G. C., METCALFE, J. D. & WALNE, A. W. (2004) The implications of lung-related buoyancy control for dive depth and duration. *Ecology,* 85**,** 1137-1145.

HEITHAUS, M. R., FRID, A., WIRSING, A. J., DILL, L., FOURQUREAN, J. W., BURKHOLDER, D., THOMSON, J. & BEJDER, L. (2007) State-dependent risk-taking by green turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology,* 76**,** 837-844.

HOOGE, P. N. & EICHENLAUB, B. (2000) Animal movement extension to Arcview. Anchorage, AK, USA, Alaska Science Center Biological Science Office, U.S. Geological Survey

LIMPUS, C. J., BELL, I. & MILLER, J. D. (2009) Mixed stocks of green turtles foraging on Clack Reef, Northern Great Barrier Reef identified from long term tagging studies *Marine Turtle Newsletter,* 123**,** 3-5.

LIMPUS, C. J., COUPER, P. J. & READ, M. A. (1994) The green turtle, *Chelonia mydas*, in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum,* 35**,** 139-154.

LUSCHI, P., HAYS, G. C., DEL SEPPIA, C., MARSH, R. & PAPI, F. (1998) The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proceedings of the Royal Society of London - Series B: Biological Sciences,* 265**,** 2279-2284.

LUTCAVAGE, M. E., PLOTKIN, P., WITHERINGTON, B. & LUTZ, P. L. (1997) Human impacts on sea turtle survival. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, Fla, CRC Press.

MAKOWSKI, C., SEMINOFF, J. A. & SALMON, M. (2006) Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Marine Biology,* 148**,** 1167-1179.

MENDONCA, M. T. (1983) Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia,* 4**,** 1013-1023.

MINAMIKAWA, S., NAITO, Y., SATO, K., MATSUZAWA, Y., BANDO, T. & SAKAMOTO, W. (2000) Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *Journal of Experimental Biology,* 203**,** 2967-2975.

MUSICK, J. A. & LIMPUS, C. J. (1997) Habitat utilization and migration in juvenile sea turtles. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *The Biology of Sea Turtles Volume 1.* Boca Raton, CRC Press.

OGDEN, J. C., ROBINSON, L., WHITLOCK, K., DAGANHARDT, H. & CEBULA, R. (1983) Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. *Journal of Experimental Marine Biology and Ecology,* 66**,** 199-205.

PLOTKIN, P. (2003) Adult migrations and habitat use. In LUTZ, P. L., MUSICK, J. A. & WYNEKEN, J. (Eds.) *Biology of Sea Turtles Volume II.* Boca Raton, CRC Press.

ROWAT, D., GORE, M., MEEKAN, M. G., LAWLER, I. R. & BRADSHAW, C. J. A. (2009) Aerial survey as a tool to estimate whale shark abundance trends. *Journal of Experimental Marine Biology and Ecology,* 368**,** 1-8.

RUTZ, C. & HAYS, G. C. (2009) New frontiers in biologging science. *Biology Letters,* Preprint published online March 2009.

SCHOFIELD, G., BISHOP, C. M., KATSELIDIS, K. A., DIMOPOULOS, P., PANTIS, J. D. & HAYS, G. C. (2009a) Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology* 78**,** 14-21.

SCHOFIELD, G., BISHOP, C. N., MACLEAN, G., BROWN, P., BAKER, M., KATSELIDIS, K. A., DIMOPOULOS, P., PANTIS, J. D. & HAYS, G. C. (2007) Novel GPS tracking of sea turtles as a tool for conservation management. *Journal of Experimental Marine Biology and Ecology,* 347**,** 58-68.

SCHOFIELD, G., LILLEY, M. K. S., BISHOP, C. M., BROWN, P., KATSELIDIS, K. A., DIMOPOULOS, P., PANTIS, J. D. & HAYS, G. C. (2009b) Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. . *Endangered Species Research,* Preprint published online Jan 2009.

SEMINOFF, J. A. & JONES, T. T. (2006) Diel movements and activity ranges of green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, Mexico. *Herpetological Conservation and Biology,* 1**,** 81-86.

SEMINOFF, J. A., RESENDIZ, A. & NICHOLS, W. J. (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series,* 242**,** 253-265.

SEMINOFF, J. A., RESENDIZ, A., SMITH, T. W. & YARNELL, L. (2001) Diving patterns of green turtles (*Chelonia mydas agassizii*) in the Gulf of California. In COYNE, M. S. & CLARK, R. D. (Eds.) *Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation.* Philadelphia, NOAA.

STEINER, I., BUERGI, C., WERFFELI, S., DELL'OMO, G., VALENTI, P., TROESTER, G., WOLFER, D. P. & LIPP, H.-P. (2000) A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiology & Behavior,* 71**,** 589-596.

TAQUET, C., TAQUET, M., DEMPSTER, T., SORIA, M., CICCIONE, S., ROOS, D. & DAGORN, L. (2006) Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Marine Ecology Progress Series,* 306**,** 295-302.

UNITED STATES COAST GUARD (2009) GPS Frequently asked questions. U.S. Coast Guard Navigation Center.

WHITING, S. D. & MILLER, J. D. (1998) Short term foraging ranges of adult green turtles (*Chelonia mydas*). *Journal of Herpetology,* 32**,** 330-337.

Chapter 8: General discussion

The threat of vessel strike for marine turtles had received scant coverage in the scientific literature at the commencement of my study, which makes a contribution towards filling the evident knowledge gap. In this chapter I summarise the results of my project with respect to each research objective originally set out in Chapter 1. I then synthesise insights into turtle behaviour that my data provided and discuss implications of my findings for conservation management. Finally I identify data needs and suggest directions for further research.

8.1 Major findings of this study

8.1.1 Objective 1

To evaluate vessel strike as a threat to marine turtles in Queensland

In fulfilment of this objective I reviewed records of stranded wildlife held by the Queensland Environment Protection Authority to identify all instances containing evidence of vessel-related mortality of turtles (Chapter 2). Based on a conservative interpretation of the available data, I found adequate evidence that during the period 1999-2002 an annual average 65 recorded turtle deaths were ascribed to collisions with vessels on the Queensland east coast. Sparse data for earlier periods precluded assessment of long-term trends.

Green turtles *Chelonia mydas* comprised the majority of vessel-related mortality evident in stranding data, followed by loggerhead turtles *Caretta caretta*. Adult and sub-adult turtles constituted 72% of cases. The majority of vessel-related records came from the greater Moreton Bay area, followed by the Hervey Bay and Cleveland Bay areas. Results confirmed collision risk for turtles in these three broad localities, all subject to variable levels of commercial and recreational vessel traffic. However, recorded locations indicated where carcases were found, not collision sites. Inferring the latter from the former was impossible due to unknown elapsed time between each assumed collision and the subsequent carcass discovery. Inferences about potential “hot-spots” for collision risk were further constrained by the coarse geographic resolution of stranding records.

The finding of an average of 65 annual deaths from vessel collisions constituted an unknown proportion of true mortality from this cause. This must be construed as an extremely conservative indication of the actual mortality level because no systematic surveys for stranded animals were conducted and records were contingent on chance discoveries and on motivation of members of the public to report findings. In addition, potential discovery of turtle carcasses was constrained by dense vegetation that impeded access to substantial portions of the shoreline in all areas where notable vessel-related mortality was recorded. Consequently the true level of vessel-related mortality is likely to substantially exceed the recorded level.

8.1.2 Objective 2

To investigate the immediate behavioural responses of free-living green turtles to vessel traffic

Despite green turtles' continuous occupation of shallow coastal waters, these animals are particularly challenging subjects for behavioural research. My study required an extensive search for a suitable study site and the development of an effective observation method (Chapter 3) in order to achieve my second objective.

My experimental transits (Chapter 4) at nominally slow, moderate and fast speed, respectively 4, 11 and 19 km h^{-1} showed that the proportion of turtles that fled to avoid the vessel decreased significantly as vessel speed increased, and turtles that fled from moderate and fast approaches did so at significantly shorter distances from the vessel than turtles that fled from slow approaches. Transit direction also influenced the proportion of turtles that fled. Response rates were higher and flight initiation distances were slightly greater for north-bound transits, when the direction of solar illumination enhanced underwater visibility. The latter finding, as well as the speed-related response rate and response distance, supported the inference that turtles relied on visual detection of approaching vessels, with the corollary that their ability to evade vessels would likely be reduced by turbid water and at night.

My results confirmed the crucial importance of slow travel to minimise the risk of turtle-vessel collisions and directly contradicted the popular belief of vessel operators that turtles routinely evade vessels. The slow experimental speed of 4 km h^{-1} appeared to represent an approximate upper limit of 'turtle-safe' travel for shallow foraging grounds, but this is much slower than typical operating speeds of vessels in open waters.

8.1.3 Objective 3

To study diving behaviour and vertical space use by green turtles in foraging grounds adjacent to vessel traffic

I deployed time-depth recorders on green turtles during 10 research sessions distributed over 2 years to cover seasonal variation in sea temperature. I used a sub-set of the depth data in a detailed evaluation of sampling bias and tested alternative methods of dive analysis (Chapter 5) in support of the methods I adopted for my full analysis (Chapter 6).

Diurnal dives were shallower and shorter than nocturnal dives. Diel patterning was also apparent in dawn and dusk peaks in occupation of depths within 1 m of the surface, elevated daytime occupation of depths 1 to 2 m below the surface and elevated nocturnal occupation of depths >2 m. Dive duration increased as sea temperature decreased, showing strong negative correlation by day and by night. Study turtles made resting dives that were 3 to 4 times longer in median duration, and six times longer in maximum duration, at cool temperatures than they were at warm temperatures.

My visual observations of study turtles and other green turtles in the same area showed turtles made only fleeting appearances at the sea surface and none of them remained visible for longer than 2 s. However, the dive data revealed that collectively the study turtles spent more than 80% of their time at charted (low tide) depths of 3 m or less, suggesting that they consistently used the shallow margins of the bay where human activities tend to be concentrated, thereby potentially increasing their exposure to near-shore anthropogenic threats including vessel strike.

8.1.4 Objective 4

To test established and novel methods for recording fine-scale geographic movement by green turtles and gain preliminary insight into the spatial behaviour of turtles in shallow foraging habitat

Detail of spatial movements by foraging green turtles has remained obscure because turtles spend most of the time submerged (Chapter 6). This behaviour precludes continuous visual observation and severely limits the potential for automated electronic tracking with sufficient temporal and geographic resolution to reveal intra-day movements. To overcome this limitation I used boat-based ultrasonic tracking in conjunction with a novel Fastloc GPS

(FGPS) system with the capacity to obtain location data during surface intervals too brief for effective use of standard GPS equipment.

Accuracy evaluation under field conditions was a vital part of my study, in order to support inference about turtles' fine-scale space use. My test data, reported in detail in Chapter 7, showed FGPS spatial accuracy to be much higher than that provided by the Argos PTT system, which is currently the de facto standard for tracking marine turtles. Most importantly FGPS also greatly exceeded Argos PTT in location frequency. Overall my findings confirmed FGPS to be an effective new tool for this area of research. In contrast, although I achieved even higher accuracy in acoustic tracking than with FGPS, the logistical demands of boat-based tracking constrained the utility of that method.

My data revealed that the three adult-size green turtles tracked in this component of my study used modest short-term activity ranges with Minimum Convex Polygon area(mean ±SD) being 662 ha ±293.9 over 4.5 days. Within their modest ranges each turtle demonstrated day to day variation in the tortuosity of their fine-scale movements and diversity of areas traversed. They all remained within <4.7 km of their capture-release locations and favoured shallow water (86% of locations were at charted depths ≤3 m). The spatial data supported my inference derived from time-depth data (Chapter 6) that the larger sample of turtles in my study of diving behaviour predominantly used shallow margins of the bay.

Average rate of movement was significantly greater by day than by night and diurnal locations had greater seagrass density whereas nocturnal locations featured deeper bathymetry, albeit within the small overall depth range used by these turtles (deepest recorded location <6 m charted depth). During their respective tracking periods (4.5 to 16.8 days) turtles revisited some of their individual centres of activity on multiple occasions but none of them shuttled back and forth between the same day-night pair of sites as has been reported elsewhere.

8.2 Synthesis of behavioural findings

Green turtles evidently recognised a vessel as a threat but demonstrated very limited ability to evade moving vessels (Chapter 4). Turtles spent the majority of time submerged (Chapter 6) and hence not visible to vessel operators (precluding the latter taking evasion action) while remaining in danger of physical contact with vessels due to their occupation of shallow near-shore waters and proximity to the sea surface (Chapter 6 & 7).

8.2.1 Ability to evade vessels

Turtles' evasive responses (Chapter 4) depended significantly on vessel speed and turtles could be relied upon to flee only when the research vessel operated at extremely slow speed ($\leq$4 km h^{-1}). Furthermore, the characteristics of evasive responses recorded under the favourable conditions of my experimental trials (good daylight illumination, clear water, gentle wind and slight seas) implied no safety margin exists for less favourable conditions. If turtles responded at all, their responses were initiated at very close range with a median flight initiation distance of 4 m for encounters at 4 km h^{-1} and 2 m for encounters at $\geq$11 km h^{-1}. Response trajectories in 26% of cases were "unsafe" in that the turtle swam in or across the vessel's track. The direction of cross-track responses suggested that turtles fled preferentially towards deeper water.

The diminishing response rate by turtles as vessel speed increased and the differential rates of response according to vessel transit direction led me to infer that turtles in Moreton Bay may rely primarily on visual cues to detect the potential threat posed by an approaching vessel. Reliance on visual cues could explain the vulnerability of Moreton Bay turtles to vessel strike because physical limitations (due to light attenuation) on the distance at which a vessel could be seen by a turtle may afford insufficient time for reliable escape responses unless the vessel is moving very slowly (section 4.4.1).

My inference regarding the apparent importance of visual cues and apparent disregard of vessel noise during experimental transits does not imply that turtles cannot detect sounds. Turtles encountered during transits might have habituated to ubiquitous vessel noise, given that my study was designed to simulate the passage of normal vessel traffic through a turtle foraging area that regularly receives such traffic. As noted in Chapter 4, turtles have the auditory capacity to detect vessel noise (O'Hara and Wilcox, 1990; Moein et al., 1993; Moein Bartol and Musick, 2003; Ketten and Bartol, 2006) and undoubtedly vessel noise without visual cues may provoke a 'Flee' response by a turtle under some circumstances.

Beyond the scope of my PhD project I have watched turtles and vessels in many diverse situations but I have seen only sparse evidence of in-water turtles apparently responding to sound rather than visual cues. The instances I observed occurred only where 'rodeo' capture (Limpus and Reed, 1985) was used. This method involves one or more vessels travelling in pursuit of turtles to enable personnel to leap out and hand-capture individual animals for monitoring or study purposes. It seems plausible that turtles might become more attentive to vessel noise during 'rodeo' sessions than during experiments simulating normal vessel traffic.

Yet competent personnel can capture many turtles in a limited area (J Hazel personal observation). Capture success using noisy research vessels seems to contradict any hope that sound cues might prompt turtles to evade vessels reliably in a broader context.

A rigorous comparison of turtle responses to visual and aural cues would be valuable to expand current understanding of turtle behaviour in proximity to vessels. However to my knowledge such work has not been reported. A lack of data is unsurprising and difficult to rectify because substantial challenges obstruct behavioural studies of marine turtles on their foraging grounds (Chapter 3).

8.2.2 Diving behaviour and spatial movements

Study turtles occupied shallow near-shore areas of modest spatial extent within which they travelled between multiple sites in irregular sequences. Turtles were more active during the day than at night. Daytime rates of spatial movement were significantly higher than at night, and by day the study turtles made more frequent dives of shorter duration and shallower depth than at night.

There was an evident dichotomy between preferred daytime locations, characterised by very shallow depths with sparse to moderate seagrass, and preferred nocturnal locations with slightly deeper water and predominantly bare substrates. In the absence of hard structures, which provide rest sites for turtles elsewhere (e.g. Ogden et al., 1983, personal observation) the study turtles selected nocturnal resting sites that were typically local depressions in the substrate or intermediate positions on sloping gradients, yet these did not represent the deepest areas available within an individual’s activity range.

In combination my dive data and tracking data strongly suggested that turtles foraged intermittently during the day and rested for substantial parts of the night. Adherence to this pattern was variable and there were some instances where an individual remained at an inferred foraging site during part or all of the night or spent part of the day at an inferred nocturnal rest site. Although turtles favoured disparate locations for inferred foraging and resting, during their respective tracking periods (4.5 to 16.8 days) they did not repeatedly use the same pair of day and night locations, giving rise to considerably day to day variation in fine-scale movements.

8.2.3 Sea temperature dependent behaviour

In their diving behaviour the study turtles showed a notable response to seasonal changes in sea temperature over the 14ºC to 30ºC range covered by my field sessions. Resting dives at cool temperatures were much longer than resting dives at warm temperatures (median 3 to 4 times longer, maximum 6 times longer). In relation to their shallow depths the longest dives depicted in my data appear to have no precedents in the literature. Dives of similar and even more prolonged duration by green turtles have been recorded only in considerably deeper water (Broderick et al., 2007; Rice and Balazs, 2008).

During the coldest temperatures my study subjects remained within the study site and occasionally undertook bouts of activity that probably included foraging. Their behaviour presented a distinct contrast to the behaviour of green turtles in the Mediterranean, which was indicative of mid-winter diapause following a location shift to deeper water in response to falling water temperature (Godley et al., 2002; Broderick et al., 2007).

Year-round persistence of shallow water occupation and diel patterns that were maintained at colder and warmer temperatures suggested turtles' exposure to vessels does not vary greatly at different seasons despite the temperature related variation in longest dive durations. Nevertheless there may be a slight increase in exposure during the warmer months, inferred from a small positive association between mean water temperature and proportional time at depths 0 to 1 m below the surface.

8.3 Implications for conservation management

8.3.1 Mitigation of anthropogenic mortality

The specific focus of this thesis on one threat does not diminish the importance of other threats to marine turtles. The objective of maintaining Queensland turtle populations requires that cumulative anthropogenic mortality must be managed at a low level (Dobbs, 2001) and consequently managers must strive to minimise diverse sources of mortality while allocating scarce conservation resources as efficiently as possible among multiple threats to multiple species.

While vessel strike is one among multiple sources of turtle mortality, this mortality occurs at non-trivial levels with a high degree of spatial concentration (Chapter 2), offering the potential to achieve a substantial conservation benefit from narrowly targeted mitigation efforts. The high proportion of sub-adult and adult-sized turtles represented in recorded mortality from vessel strike provides added impetus for mitigation because the loss of turtles in these life stages implies a more deleterious effect on populations than would be the case if the mortality was concentrated on earlier life-stages (Heppel et al., 1999). In addition, if vessel management strategies are implemented to protect turtles, other species of conservation concern can be expected to benefit. The anticipated benefit would most notably accrue to dugongs, which often share habitat with turtles in Queensland and also suffer mortality from vessel strike (Hodgson, 2004).

In the absence of effective mitigation measures, future turtle mortality from vessel strike must be expected to increase because turtles demonstrate a very limited capacity to evade vessels (Chapter 4) and the intensity of vessel traffic is likely to rise, concomitant with very substantial growth projected for the human population in Queensland over coming decades (Wilson et al., 2004; Australian Bureau of Statistics, 2009). The risk of vessel strike may be further exacerbated by future advances in vessel design and construction that serve to increase vessel speeds generally and to produce yet larger and faster vessels able to travel in shallow water. This trend has already been identified as a factor in elevated levels of vessel strike for Florida manatees (Wright et al., 1995) and it would be expected to affect dugongs and turtles similarly, since all three taxa forage in shallow coastal waters subject to burgeoning vessel traffic.

8.3.2 Chelonian stocks threatened by vessel strike

As reported in Chapter 2, green turtles suffered the major share (76%) of recorded mortality from vessel strike while loggerhead turtles (14%) were also notably involved. Among the former, the majority probably comprised animals from southern Great Barrier Reef (sGBR) stocks, for which a stated management objective is to ensure annual anthropogenic mortality from all sources combined does not exceed a few hundred (Dobbs, 2001). Derivation of this target was not provided but its publication by the Great Barrier Reef Marine Park Authority implies support from expert sources. If true mortality from vessel strike substantially exceeds recorded cases (as seems likely because records depended on chance discoveries of turtle carcasses) then current levels of vessel strike probably constitute a serious challenge to this objective. For example, if green turtle mortality from vessel strike involved 75% sGBR turtles and 25% turtles from other stocks, then speculative estimates of true mortality, as set out in Table 2.2, would imply losses from sGBR stocks in the range from 122 to 576 green turtles annually due to vessel strike alone.

Loggerhead turtles warrant special consideration because stocks are severely depleted (Environment Australia Marine Species Section, 2003; Limpus, 2008). In comparison to large green turtle stocks in Queensland waters, the small loggerhead turtle population may be suffering proportionally greater mortality from vessel strike. A recently published biological review suggests that loggerhead turtle recovery could be compromised by mortality from an array of anthropogenic impacts including vessel strike, even if mortality from fox predation and fisheries bycatch could be eliminated immediately (Limpus, 2008).

It was not feasible to test loggerhead turtle responses to vessels during my study but if this species relies predominantly on visual cues to detect vessels, as I have tentatively inferred for green turtles, then loggerhead turtles will similarly have extremely brief opportunities to escape from approaching vessels. Inferior swimming speed and inferior turning ability of loggerhead turtles as compared to green turtles (Heithaus et al., 2002) implies that loggerhead turtles have inferior manoeuvring capacity when attempting to evade fast vessels. Thus in similar circumstances loggerhead turtles would be expected to have even greater risk of vessel strike than green turtles. Areas where loggerheads are present therefore warrant the most stringent risk reduction measures.

8.3.3 Vessel management for wildlife protection

Two vessel management options can be used to mitigate the risk of vessel strike: (1) routing vessels away from shallow waters regularly used by turtles, dugongs and other vulnerable species, and (2) restricting vessel speed within those areas.

Mandatory vessel routing for the purpose of wildlife protection has not to my knowledge been implemented in Queensland waters. This would be a potentially efficient strategy if localised areas of very high risk could be identified accurately. However, strong public opposition could be expected if popular and convenient existing routes thereby became unavailable.

Voluntary transit lanes recommended to vessel operators in the vicinity of Hinchinbrook Island have been reported to achieve very low compliance (Groom, 2003). Ad hoc route changes may arise when individual vessel operators choose to divert around a Go-Slow zone in order to maintain high speeds. However, that practice would be of uncertain benefit to wildlife and might increase collision risk along the margins of shallow Go Slow zones where turtles would tend to flee across the vessel's track towards adjacent deeper water. Therefore, as recommended in Chapter 4, Go Slow zones should include broad safety margins extending into deeper water.

Mandatory speed restrictions apply in defined Go Slow zones in some Queensland bays (Queensland Government, 2006; Queensland Government, 2008) although the spatial coverage of current Go Slow zones is modest. Compliance appears variable (e.g. Groom, 2003;

Hodgson, 2004, J Hazel personal observation; Queensland Environment Protection Agency, 2008) and potential risk reduction is unlikely to be fully achieved without effective enforcement.

Findings of my study suggest that mandated speeds in restricted zones may warrant reconsideration. In one area vessels >8 m in length are restricted to speeds ≤10 knots (19 km h^{-1}) while in most Go Slow zones all vessels must operate in non-planing displacement mode (Queensland Government, 2006; Queensland Government, 2008). The latter condition imposes an inexact limit because planing speed depends on the size and design of each vessel. As a result compliant vessels would have individual limits typically in the range10 to 20 km h^{-1} (J. Hazel unpublished data, Maitland et al., 2006). These speed limits might be relatively more effective in protecting dugong, which have in some instances been observed to initiate evasive responses at greater distances (Hodgson, 2004) than turtles. My data in Chapter 4 indicate lower speeds would be needed for optimal turtle safety.

8.3.4 Alternative mitigation measures

Over the course of my study I had opportunities for many informal discussions about vessel strike. People almost invariably expressed support for marine turtle conservation but many were opposed to restricting vessel travel and voiced expectations that alternative mitigation options must exist. The literature lacks support for that expectation and by inference from field observations and long-term boating experience I do not foresee technological solutions that could replace vessel management strategies.

Propeller guards were sometimes suggested in conversation. These devices comprise a mesh cage or ring that can be installed around an outboard propeller (for some examples see www.progeng.com.au, www.propguard.co.nz, www.allinflatables.com) and manufacturers assert utility in avoiding propeller damage (e.g. from striking rocks or entanglement in debris or aquatic vegetation) and in reducing the severity of injury in case of accidental contact with swimmers.

Logically one could expect little benefit from a propeller guard in the event of a collision at high speed because impact from any part of the vessel, including impact from the propeller guard itself, would cause severe injury. In contrast, a propeller guard could offer valuable protection in situations where a boat must closely approach a person (or animal) in the water and does so at very slow speed, thereby precluding injury from contact with any part of the boat except the spinning propeller. My observations tend to support this dichotomy. I have often noted propeller guards installed on small boats used to pick up divers in open water and on boats used by rescue services to retrieve swimmers in difficulty, but I have rarely seen propeller guards on vessels in general use.

Based on my understanding of protective potential, I would recommend propeller guards in addition to slow speed for vessels that routinely operate in close proximity to turtles and other species e.g. for eco-tourism or research purposes. However I infer that propeller guards would not under any circumstances remove or reduce the need for all vessels to travel at slow speed in turtle habitat. Given that high speed impact from any part of a vessel is likely to cause severe trauma, the requirement for slow speed in turtle habitat must also include vessels with no propeller, e.g. vessels propelled by a water jet drive and non-motorised sailing vessels.

For people reluctant to accept restrictions on their marine travel, the prospect of warning animals to “get out of the way” may seem an attractive alternative. Already substantial research effort has been directed to developing an acoustic device to warn Florida manatees of oncoming vessels (Gerstein, 2002) but utility of that device in the wild remains uncertain. The potential for warning turtles with acoustic devices seems even lower since turtles in a vessel traffic area apparently disregard noise as an indication of vessel approaches (Chapter 4).

If a device capable of provoking target species to flee from vessels does indeed become available in the future, its deployment could harm rather than help vulnerable species. Use of such a device might be appropriate only where a single vessel travels infrequently across a large area. In contrast, widespread deployment would have adverse implications for Queensland inshore waters that are typically used by multiple vessels travelling concurrently on diverse courses. In the latter situation the transmission of warning signals by many vessels would be liable to cause excessive disturbance of all target species within range. In addition, such transmissions would be likely to provoke animals to flee from one vessel into the path of another. Long term usage would be expected to cause either alienation of vulnerable species from favourable habitat (e.g. Richardson et al., 1995) or habituation to the signal (e.g. Cox et al., 2001) and hence loss of effectiveness.

Better potential might in principle be expected from equipment to warn vessel operators of animals in their path without disturbing the animals. Sonar detection and imaging is well advanced in both research and commercial applications that include monitoring of fish stocks, recording sea-floor detail, guiding submarine construction and documenting underwater archaeology (Wille, 2005). Current low-cost sonar equipment, e.g. a depth sounder designed for recreational craft, occasionally serves to identify a submerged turtle at close range (personal observation). One can speculatively anticipate future sonar technology with the capacity to detect individual turtles at considerable distance, a prerequisite for timely warning. However a practical and affordable warning system suitable for routine use on most vessels still seems a very remote prospect.

8.4 Future directions

8.4.1 Behavioural studies

The short term variation in turtle movements revealed by my study highlights the need for future fine-scale tracking to encompass more study animals and extend over longer periods than I was able to achieve. The advent of the FGPS system, which became commercially available only during the latter part of my PhD candidature, makes it feasible to propose fine-scale tracking studies of longer duration than mine. However, high costs and logistical difficulties are likely to remain challenging and technological refinements are needed as discussed below.

Fine-scale tracking data for extended periods should allow quantitative evaluation of factors potentially influencing movement patterns and habitat selection including turtle life stage, seasonal variation in water temperature and day length, and tidal currents. In this endeavour it would be especially valuable to obtain integrated spatial and dive data, and the latter ideally should be sampled at higher temporal resolution than was feasible in my study, in order to alleviate sampling bias (Chapter 5). Such data will have great value for advancing scientific understanding of turtles' energy and time allocation in the wild, to amplify the physiological insights gained from direct and indirect evaluation of turtles' metabolic rates (Wallace and Todd Jones, 2008). Behavioural insights may be further refined in the future by novel equipment such as an inter-mandibular angle sensor to record mouth-opening behaviour (Myers and Hays, 2006) or the use of a "daily diary" device capable of recording information about animal location, behaviour, energy expenditure and environmental conditions (Wilson et al., 2008).

Future fine scale tracking studies of extended duration will also be important in revealing whether turtles' known fidelity to foraging sites is continuous, except for breeding migrations, or discontinuous. Foraging site fidelity of green turtles has been inferred from multiple recaptures of marked animals at long-term monitoring sites (e.g. Limpus et al., 1994; Limpus et al., 2009) but data are lacking for continuous fidelity between widely spaced re-capture sessions. Local movements up to 25 km have been reported at one site (Whiting and Miller, 1998). These might be isolated cases or location shifts might occur more frequently, potentially in response to variations in forage availability or intra-specific competition. If location shifts are not rare events then insight into causative factors and frequency of occurrence will be important for conservation management.

8.4.2 Technological refinement

The FGPS system proved an important new technology for investigating fine-scale turtle movements (Chapter 7) but further work is required to realise the full potential of FGPS in demanding applications. Experimental trials at multiple locations are needed to elucidate the factors that influence the temporal resolution of FGPS locations achievable, the number of satellites used for individual locations and consequent geographic accuracy, and the proportion of locations that are successfully relayed via the Argos system. Findings of such trials will provide valuable guidance for the important task of pre-programming FGPS operating schedules to suit diverse research objectives and achieve an optimal trade-off between greater temporal resolution and longer battery life. In addition, there is a need for quantitative methods for screening FGPS data, as discussed in Chapter 7.

While accepting the fundamental constraint of turtle diving behaviour, there might be scope to enhance FGPS performance by optimising the presentation of a device at the sea surface. FGPS data acquisition under diverse sea conditions might be enhanced by small improvements in antenna orientation and duration of exposure, which might potentially be achievable by finding the most efficient physical configuration for the device and its method of attachment. However, the expense of field-testing alternative configurations in rigorous comparison trials would present a formidable obstacle. Importantly there is a crucial need to minimise risk of accidental damage or premature detachment of the FGPS device without compromising safety of the animal. Rigorous determination of the relative safety of diverse equipment deployed on threatened species in the wild presents an ethical dilemma that appears even more difficult to resolve than logistical and cost constraints.

Additional technical challenges arise for studies that rely on at-sea recovery of telemetry equipment, as mine did. An alternative strategy of remote data relay has been used in some studies where animal tracking devices were intentionally left adrift in the open sea, e.g. “pop-off” tags, see Swimmer et al. (2006) for an example of such usage. However remote satellite relay via the Argos system was not appropriate for my study. Bandwidth limitations constrain the volume of data that can be transmitted during each Argos satellite link. Therefore devices that record data with high temporal resolution typically transmit either a subset of the raw data collected or they transmit summary data, the latter being dependent on prior determination of summary values required. Neither alternative would have provided the detailed information about turtle diving and spatial movement that my study sought. Furthermore, there was no assurance of successful Argos transmission for devices left adrift in my study area. Devices released after attachment to study animals in this area might have drifted at sea indefinitely but these devices could also drift ashore in locations where data transmission would have been impossible, e.g. among rocks or mangrove forests. In addition to my considerations regarding data retrieval, the intentional abandonment of research equipment was prohibited under the terms of my research permits. Future telemetry studies of turtles in coastal foraging grounds are likely to face similar constraints so it would be valuable to develop better techniques for device attachment, release and recovery.

The methods I adopted for attaching equipment to turtles in my study represented a pragmatic solution for a low-budget study of short duration. Even in this limited usage, my reliance on fast-corroding galvanic links for automatic release was a notable limitation. These links rapidly become more fragile as they corrode, with increasing probability of premature breakage when deployed on an active animal. It would be preferable to use a durable link incorporating an electronic control circuit for release. I refer here specifically to the release device, which should not break prematurely, and stress that a separate ‘weak link’ must be provided to ensure that the turtle can safely shed the equipment if it accidentally snags on an obstruction. For deployments of longer duration in diverse habitats it would also be preferable to eliminate the tether and instead develop a two-part FGPS device with a separate base-plate for adhesion to the turtle carapace and an automatically detachable archival component, the latter having sufficient buoyancy to rise to the sea surface when released.

Electronic controls have been used for the automatic release of telemetry devices in various configurations, e.g. base-plate attachment on seals (Andrews, 1998), tether attachment on dugongs (Sheppard, 2008), but I was unable to source a sufficiently small and affordable electronic release for my FGPS research. This remains an important requirement for similar studies in the future, both to allow longer tracking sessions and to facilitate at-sea equipment recovery by releasing the device at a pre-determined time. Release triggered by a remote signal would potentially offer optimal convenience because the researcher could initiate equipment recovery under favourable weather conditions but unreliable performance in the field has hampered such usage in some studies (pers. comm. I. Lawler, J. Sheppard).

8.4.3 Spatial data for identification of high-risk locations for turtle

Data on the abundance and spatial distribution of green turtles and loggerhead turtles in neritic waters would be valuable for accurately targeting management strategies to reduce mortality from diverse anthropogenic sources including vessel collisions. However, distribution data remain an elusive goal due to the extreme difficulty of sighting turtles in the water. Records of turtle by-catch in commercial fish trawls (before the introduction of Turtle Excluder Devices) have been used as a proxy for turtle abundance and distribution (Robins, 2002; Dryden et al., 2008). These data could only be considered a valid proxy in regularly trawled areas as it would be erroneous to infer absence of turtles from absence of by-catch in large areas where trawling is infrequent or absent. Furthermore, fisheries data were aggregated in cells of 0.5º latitude and longitude and consequently the potential utility of these proxy data is further constrained by coarse spatial resolution.

Aerial surveys offer the most practical option for investigating marine animal distribution across Queensland's extensive coastal waters (Marsh and Saalfeld, 1989) but turtles present particularly challenging subjects for this method because of their relatively small size, the similar appearance of multiple species and their diving behaviour. Diving behaviour causes a proportion of animals to be unavailable for sighting, due to water turbidity and depth, while they are actually present in the survey area. In the context of aerial surveys for dugongs, quantitative methods have been developed to correct for this availability bias (Marsh and Sinclair, 1989) and correction techniques have subsequently been refined in several respects (Pollock et al., 2006). Enhancements included estimating the probability of dugongs being available for sighting, based on dive data from time-depth recorders. My dive data (Chapter 6) has potential application in analogous refinements for aerial surveys for turtles.

Resources are unlikely to become available for surveys of turtle distribution over the entire extent of the Queensland coast. However, survey effort could be narrowly targeted with respect to the specific threat of vessel strike, based on proximity to urban centres and ports as the main sources of vessel traffic. Even within these limited areas there will be substantial challenge in collecting fine-scale quantitative data on turtle distribution and corresponding data on vessel routes and traffic intensity, as discussed in Chapter 3. Nevertheless these data will be invaluable in defining locations where high traffic intensity and dense turtle occupation coincide, giving rise to high risk of collisions. It is in these locations that vessel management strategies would offer greatest conservation benefit.

8.4.4 Public support for conservation strategies

Once high-risk locations have been accurately identified it would be conceptually straight forward to design mitigation measures (bypass routes or speed restriction) based on scientific understanding of turtle behaviour. Nevertheless it may be extremely difficult to engender public support for such measures because constraints on preferred routes or preferred speeds would inconvenience vessel operators and vessel passengers. Indeed, substantial public opposition to a proposed go-slow zone in Moreton Bay (Young, 2008) attests to the unpopularity of such measures.

Future research must therefore extend beyond biological understanding and technology advances to the human dimensions of wildlife management. This relatively new field of study investigates the values that people ascribe to wildlife, their attitudes towards and influence on management strategies and the ways that management decisions affect people (Decker et al., 2001; Miller, 2009). It would be useful to investigate the scope for greater community involvement in decisions about vessel management strategies, as has been identified in a broader context (Miller and Jones, 2005) and to devise effective ways to increase public understanding of the rationale underlying regulatory constraints on vessel routes and speeds. The latter endeavour should encompass not only vessel operators but also the much larger population of stakeholders who travel as passengers on ferries, tour boats and private vessels.

While public understanding of regulatory constraints may be valuable, such understanding cannot be expected to ensure substantial compliance. In the context of road speed limits there is abundant evidence that enforcement remains the major strategy for enhancing compliance (e.g. see McCarthy, 1999; Son et al., 2009 and references therein). Similarly, I suggest, marine management agencies will need to direct resources towards planning and implementation of enforcement measures for go-slow zones. Research will be required to develop cost-efficient methods for this purpose because strategies and technologies applicable to road traffic may not be effective or even feasible for vessel traffic in diverse marine environments.

Finally I would recommend research into the inherent contradiction between widespread favourable sentiment towards iconic species like turtles and dugongs and apparent reluctance to accept inconvenience or restraint on human activity that may arise from measures to conserve these and other animals. Scientific understanding of wildlife biology, behaviour and population trends can guide efforts to reduce anthropogenic impacts but ultimately the successful protection of vulnerable species will depend on political will and public support.

8.5 References

ANDREWS, R. D. (1998) Remotely releasable instruments for monitoring the foraging behaviour of pinnipeds. *Marine Ecology Progress Series,* 175**,** 289-294.

AUSTRALIAN BUREAU OF STATISTICS (2009) Regional Population Growth, Australia, 2007–08 Canberra, Australian Bureau of Statistics.

BRODERICK, A. C., COYNE, M. S., FULLER, W. J., GLEN, F. & GODLEY, B. J. (2007) Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society of London B, Biological sciences,* 274**,** 1533-1538.

COX, T., READ, A. J., SOLOW, A. & TREGENZA, N. (2001) Will harbour porpoises (*Phocoena phocoena*) habituate to pingers? *J Cetacean Res. Mgmt.,* 3**,** 81–86.

DECKER, D. J., BROWN, T. L. & SIEMER, W. F. (2001) *Human Dimensions of Wildlife Management in North America,* Bethesda, MD, The Wildlife Society.

DOBBS, K. (2001) *Marine turtles in the Great Barrier Reef World Heritage Area,* Townsville, Great Barrier Reef Marine Park Authority.

DRYDEN, J., GRECH, A., MOLONEY, J. & HAMANN, M. (2008) Rezoning of the Great Barrier Reef Wold Heritage Area: does it afford greater protection for marine turtles? *Wildlife Research,* 35**,** 477-485.

ENVIRONMENT AUSTRALIA MARINE SPECIES SECTION (2003) Recovery plan for marine turtles in Australia. Canberra, Environment Australia.

GERSTEIN, E. R. (2002) Manatees, bioacoustics and boats. *American Scientist,* 90**,** 154-163.

GODLEY, B. J., RICHARDSON, S., BRODERICK, A. C., COYNE, M. S., GLEN, F. & HAYS, G. C. (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography,* 25**,** 352-362.

GROOM, R. A. (2003) The efficacy of the voluntary vessel transit lanes in Missionary Bay, Hinchinbrook Island, for dugong conservation management. *School of Tropical Environment Studies and Geography.* Townsville, James Cook University.

HEITHAUS, M. R., FRID, A. & DILL, L. (2002) Shark inflicted injury frequencies, escape ability and habitat use of green and loggerhead turtles. *Marine Biology,* 140**,** 229-236.

HEPPEL, S. S., CROWTHER, L. B. & R., M. T. (1999) Life table analysis of long-lived marine species with implications for conservation and management. *American Fisheries Society Symposium***,** 137-148.

HODGSON, A. (2004) Dugong behaviour and responses to human influences. *School of Tropical Environment Studies and Geography.* Townsville, James Cook University.

KETTEN, D. R. & BARTOL, S. M. (2006) Functional measures of sea turtle hearing. Woods Hole, MA, Woods Hole Oceanographic Institution.

LIMPUS, C. J. (2008) A biological review of Australian marine turtle species. 1. Loggerhead turtle, *Caretta caretta* (Linneaus). Brisbane, Queensland Environmental Protection Agency.

LIMPUS, C. J., BELL, I. & MILLER, J. D. (2009) Mixed stocks of green turtles foraging on Clack Reef, Northern Great Barrier Reef identified from long term tagging studies *Marine Turtle Newsletter,* 123**,** 3-5.

LIMPUS, C. J., COUPER, P. J. & READ, M. A. (1994) The green turtle, *Chelonia mydas*, in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum,* 35**,** 139-154.

LIMPUS, C. J. & REED, P. C. (1985) The green turtle, *Chelonia mydas*, in Queensland: a preliminary description of the population structure in a coral reef feeding ground. In GRIGG, G. C., SHINE, R. & EHMANN, R. (Eds.) *Biology of Australasian Frogs and Reptiles.* Sydney, Australia, Royal Zoological Society of New South Wales & Surrey Beatty.

MAITLAND, R., LAWLER, I. R. & SHEPPARD, J. K. (2006) Assessing the risk of boat strike on dugongs (*Dugong dugo*n) at Burrum Heads, Queensland, Australia. *Pacific Conservation Biology,* 12**,** 321-327.

MARSH, H. & SAALFELD, W. (1989) Aerial Surveys of Sea Turtles in the Northern Great Barrier Reef Marine Park. *Australian Wildlife Research,* 16**,** 239-249.

MARSH, H. & SINCLAIR, D. F. (1989) An Experimental Evaluation of Dugong and Sea Turtle Aerial Survey Techniques. *Australian Wildlife Research,* 16.

MCCARTHY, P. S. (1999) Public policy and highway safety: a city-wide perspective. *Regional Science and Urban Economics,* 29**,** 231-244.

MILLER, K. K. (2009) Human dimensions of wildlife population management in Australasia - history, approaches and directions. *Wildlife Research,* 36**,** 48-56.

MILLER, K. K. & JONES, D. N. (2005) Wildlife management in Australasia: perceptions of objectives and priorities. *Wildlife Research 32,* 32**,** 265–272.

MOEIN BARTOL, S. & MUSICK, J. A. (2003) Sensory biology of sea turtles. In LUTZ, P. L. & MUSICK, J. A. (Eds.) *Biology of Sea Turtles, Volume II.* Boca Raton, CRC Press.

MOEIN, S., LENHARDT, M., BARNARD, D., KEINATH, J. A. & MUSICK, J. (1993) Marine turtle auditory behavior. *Journal of the Acoustical Society of America,* 93**,** 2378.

MYERS, A. E. & HAYS, G. C. (2006) Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Marine Ecology Progress Series,* 322**,** 259-267.

O'HARA, J. & WILCOX, J. R. (1990) Avoidance responses of loggerhead turtles, *Caretta caretta*, to low frequency sound. *Copeia,* 1990**,** 564-567.

OGDEN, J. C., ROBINSON, L., WHITLOCK, K., DAGANHARDT, H. & CEBULA, R. (1983) Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. *Journal of Experimental Marine Biology and Ecology,* 66**,** 199-205.

POLLOCK, K. H., MARSH, H. D., LAWLER, I. J. & ALLDREDGE, M. W. (2006) Estimating Animal Abundance in Heterogeneous Environments: An Application to Aerial Surveys for Dugongs. *Journal of Wildlife Management,* 70**,** 255–262.

QUEENSLAND ENVIRONMENT PROTECTION AGENCY (2008) 'Go Slow' fine for Cleveland boat operator. Media Statement 31/10/08.

QUEENSLAND GOVERNMENT (2006) Marine Parks (Great Sandy) Zoning Plan 2006.

QUEENSLAND GOVERNMENT (2008) Marine Parks (Moreton Bay) Zoning Plan 2008.

RICE, M. R. & BALAZS, G. H. (2008) Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *Journal of Experimental Marine Biology and Ecology,* 356**,** 121-127.

RICHARDSON, W. J., GREENE, C. R., JR, MALME, C. I. & THOMSON, D. H. (1995) *Marine mammals and noise,* London, Academic Press.

ROBINS, J. B. (2002) *A scientific basis for a comprehensive approach to managing sea turtle by-catch: the Queensland east coast as a case study (PhD)*, James Cook University.

SHEPPARD, J. K. (2008) The spatial ecology of dugongs: applications to conservation management. James Cook University.

SON, H. D., FONTAINE, M. D. & PARK, B. B. (2009) Long-Term Speed Compliance and Safety Impacts of Rational Speed Limits. *Journal of Transportation Engineering,* 135**,** 536-544.

SWIMMER, Y., ARAUZ, R., MCCRACKEN, M., MCNAUGHTON, L., BALLESTERO, J., MUSYL, M., BIGELOW, K. & BRILL, R. (2006) Diving behavior and delayed mortality of olive ridley sea turtles *Lepidochelys olivacea* after their release from longline fishing gear. *Marine Ecology Progress Series,* 323**,** 253-261.

WALLACE, B. P. & TODD JONES, T. (2008) What makes marine turtles go: A review of metabolic rates and their consequences. *Journal of Experimental Marine Biology and Ecology,* 356**,** 8-24.

WHITING, S. D. & MILLER, J. D. (1998) Short term foraging ranges of adult green turtles (*Chelonia mydas*). *Journal of Herpetology,* 32**,** 330-337.

WILLE, P. C. (2005) *Sound Images of the Ocean: in Research and Monitoring,* Berlin, Springer.

WILSON, R. P., SHEPARD, E. L. C. & LIEBSCH, N. (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research,* 4**,** 123-137.

WILSON, T., BELL, M., HEYEN, G. & TAYLOR, A. (2004) New Population Projections for Queensland and Statistical Divisions. *People and Place,* 12**,** 1-14.

WRIGHT, S. D., ACKERMAN, B. B., BONDE, R. K., BECK, C. A. & BANOWETZ, D. J. (1995) Analysis of watercraft-related mortality of manatees in Florida, 1979-1991. In O'SHEA, T. J., ACKERMAN, B. B. & PERCIVAL, H. F. (Eds.) *Population Biology of the Florida Manatee.* Fort Collins, USA, National Biological Service.

YOUNG, R. (2008) 1513 petition against EPA Go Slows in southern Moreton Bay. *Bay Journal*.