The Hawksbill Turtle, *Eretmochelys imbricata*, (Linnaeus 1766): Ecological Insights of a Resident Population in the Northern Great Barrier Reef, Queensland, Australia

Thesis submitted by

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The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the National Statement on Ethics Conduct in Research Involving Human (1999), 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 turtle research methodology used in this thesis was conducted under the auspices of the Queensland Turtle Research Project's *Standard Operating Procedures*. The project received ethics approval clearance (EPA/2006/12/19) from the Queensland Government's Animal Ethic Committee.

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STATEMENT OF CONTRIBUTION

This research was co-supervised by Dr Lin Schwarzkopf, Dr Ivan Lawler and Dr Colin Limpus. All advisors contributed to the experimental design, provided technical support and assisted with statistical analysis.

Additional assistance was provided by many individuals and their contributions can be found in the Acknowledgements and at the beginning of chapters that have already been or are in the process of being published.

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ABSTRACT

The life history of *Eretmochelys imbricata* is complex and until now, there has been a paucity of data describing even fundamental population parameters for the species in the western Pacific Ocean. A baseline understanding of a population's structure, its dynamics and general foraging ecology are essential for determining its conservation status, and for developing management strategies if required. Ongoing monitoring is also vital to detect trends in population size, or if a population is responding to conservation management strategies.

In this thesis I provide a detailed description of the biometry, demographics, population dynamics, genetic structure, diet and growth rates of a population of *E. imbricata*, resident within a collection of reefs in the northern Great Barrier Reef. *Eretmochelys imbricata* were captured from a group of 13 reefs, which are collectively known as the "Howick Group". The area is remote, relatively undisturbed and falls within the Far Northern Section of the Great Barrier Reef Marine Park. Reef flats were searched using small outboard motor powered dinghies, and when spotted, *E. imbricata* were hand-captured by jumping from the boat.

I conducted eight annual surveys, of ~ 18 days duration (n = 143, R = 1 - 33; SD = 9.9) during the Austral winter period (June - July) between 1997 and 2008 at the Howick Group. Over this time, 665 *E. imbricata* were "first-time" captures with 148 turtles being recaptured on at least one other successive survey. This resulted in a total of 813 turtle encounters recorded.

An almost even number of juvenile, pubescent and adult *E. imbricata* were captured, with a high female to male gender ratio bias displayed across all three age-classes; adult *E. imbricata* comprised 9.0:1 (n = 243 f; 27 m), pubescent turtles: 4.7:1 (n = 221 f; 49 m) and juveniles displayed the highest proportion of females with a 10.0:1 ratio (n = 99 f; 9 m).

The mean curved carapace length (CCL) for adult female *E. imbricata* was 84.9 cm (n = 243; R = 74.5 - 97.7 cm; SD = 3.72 cm) and 82.5 cm (n = 27; R = 74.6 - 87.5 cm; SD = 3.2 cm) for males. The somatic growth rate of sub-adult turtles was non-monotonic, however the rate was monotonic and declined to zero growth upon reaching maturity. A Generalised Additive Modelling approach revealed a significant difference (P = 0.02) in growth rates between pubescent males and females. Pubescent males grew an average of 1.17 cm/yr (n = 7) compared to pubescent females, which grew 0.98 cm/year (n = 28). The mean growth rate for juvenile female *E. imbricata* was 0.32 cm/year (SD = 0.48 cm; R = -0.13 - 1.57 cm; n = 12), whereas the mean annual growth increment for the single juvenile male turtle caught was 0.8 cm/yr.

I used Bayesian Mixed Stock Analysis methodology to identify the genetic structure of turtles feeding in the Howick Group. From these data I determined the natal rookeries. The majority of *E. imbricata* (87%, 95% CI = 78 - 95%) came from eastern Bismarck-Solomon Sea eco-region natal beaches. Only 11% (95% CI = 2 - 21%) of *E. imbricata* originated from rookeries within the nGBR (e.g., Milman Island) and possibly the Northern Territory, and two percent from an unknown source.

Annual survival probabilities and population densities were determined using a Cormack-Jolly-Seber capture-mark-recapture model. Marked differences in survival probability between adult male (0.71) and female (0.92) *E. imbricata* were found. The mean annual population density estimates were consistently greater for adult female *E. imbricata* (n = 333.7; SD = 135.6; R = 221 - 581) than for adult males (n = 32.4; SD = 33.4; R = 8 - 98), with both adult males and females displaying high survivorship rates (71.1%; 92.2%, respectively). This was also apparent in immature age-classes, with male and female turtles showing similarly high survivorship likelihoods (78.0%; 93.0%, respectively).

I conducted gastric lavage sampling and examined the buccal cavities for prey items selected by 120 individual *E. imbricata*. A total of 467 gastric lavage and 71 buccal cavity ingesta items were identified. I found that during periods of high-tide, when access to the reef top was possible, turtles were primarily feeding on marine algae from the genera *Laurencia* and *Gelidiella*; refuting the commonly held notion that the species are principally spongivorous. During periods of low-tide, their diet principally comprised the same two algae, however a range of vertebrate and invertebrate prey, found typically occurring in a deeper (~ 6 – 8 m) water habitat were also recorded in diet samples. *Eretmochelys imbricata* were found to show strong fidelity to the reef upon which they were caught, with no movement of animals between reefs being recorded.

These data present an in-depth description of many life history aspects of all age classes of *E. imbricata* found in the northern Great Barrier Reef, which, until now, were undescribed for the western Pacific. The data, derived from this mark-recapture, genetics, diet and growth rate study, may now be used to develop management strategies to protect northern Great Barrier Reef *E. imbricata* populations in a rapidly changing marine environment.

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CHAPTER ONE

GENERAL INTRODUCTION AND SPECIES OVERVIEW

This study presents data describing key ecological aspects of a population of *Eretmochelys imbricata* found foraging in the Far Northern Section of the Great Barrier Reef Marine Park. This is the first study to determine the full range of life history variables, for both sexes and all age-classed *E. imbricata*, found feeding within the Great Barrier Reef. Attempts at assessing the robustness of marine turtle stocks within the Great Barrier Reef World Heritage Area requires an understanding of how, or if, populations are changing over time, and whether those changes are related to human impacts. Information on the status and natural variability of key indicator species, such as marine turtles, contributes to an essential body of knowledge to allow informed management of various marine and coastal ecosystems within an area of global conservation significance (Kinsey and Hopely 1991).

The demographic structure of an *E. imbricata* population, within a foraging habitat, is determined by a complex interaction of biotic and abiotic factors. Its population composition and size may be relatively stable, but is more likely to be stochastic, with individuals continually migrating into, out of, or through the habitat. Influencing this dynamic population structure are factors such as: the genetic make-up, age-class and gender cohorts, reproductive migrations, diet, growth rates and population trends. An understanding of these processes as a whole system, together with genetic structure and reproductive migratory routes, are needed to effectively manage turtle stocks (Bjorndal, 1999a). My study focused on elucidating the most relevant data from a high density population of *E. imbricata* found foraging in northern Australia. These data form the basis of continuing long-term studies in the northern Great Barrier Reef that may be extrapolated to provide an estimation of how the species is functioning in the western Pacific in general.

Species description

Eretmochelys imbricata is one of seven extant species of marine reptile that is estimated to have evolved in the Miocene period approximately 120 million years before present (Bowen *et al.*, 1993). They are a morphologically distinct species with a dorsal surface (carapace) characterised by "star-burst" shaped pigment patterns that change from light straw-coloured through reddish green to deep brown as the animal matures (Pritchard and Mortimer 1999). The ventral surface (plastron) colour also changes as the turtle moves through development, from white at first recruitment to a neritic feeding area, through pale cream, to dark orange at maturity (Pritchard 1979). In comparison with most other marine turtle species, adult *E. imbricata* are relatively small to medium-sized (60 - 90 cm curved carapace length, CCL) (Ernst and Barbour1989). They are readily differentiated from other marine turtle species because they possess a narrow, elongated snout, resembling a hawk's beak, with two pairs of prefrontal scales, two pairs of claws on each front flipper and four pairs of costal scutes (Witzell 1983). The heavily keratinised rhamphotheca and carapacial scutes are clearly imbricate (Figure 1.0), and marginal scutes are strongly serrated until adulthood, at which point they are likely to be abraded smooth, after turtles have taken up residence in neritic rocky or reef habitat.

Figure 1.0. An adult *Eretmochelys imbricata* showing thickly keratinised pointed snout adapted for foraging within rocky reef habitat. Photographer: Ken Knezick

Eretmochelys imbricata *population distribution*

Globally, *E. imbricata* foraging area lies within the circum-tropical regions of the Atlantic, Indian and Pacific Oceans (Witzell 1983), however there are reports of animals feeding in areas from latitudes as far north and south as Massachusetts in the United States (42°N) and the Solitary Islands off central New South Wales in Australia (30°S) respectively (Ernst *et al.*, 2009; Limpus and Miller 2000). Recognised *E. imbricata* foraging areas within Australia extend north from Moreton Bay (27°S) in south east Queensland, through reefs in the Torres Strait (9°S), west through Arnhem Land in the Northern Territory, and to at least Onslow (21°S) in Western Australia (Guinea *et al.*, 1999; Limpus *et al.*, 1994a; Limpus and Parmenter 1986; Pendoley 2005; Preen *et al.*, 1997).

The Australian nesting meta-population is comprised of two genetically distinct haplotypes: one dispersed through the northern Great Barrier Reef, Torres Strait and Arnhem Land; and the other found along the coastline of northern Western Australia (Limpus 2008). This genetic distinctiveness, coupled with data from tag returns, indicates that individuals from the two

subpopulations rarely interbreed (Broderick *et al.*, 1994). However, aggregations of *E. imbricata* found at foraging grounds may be comprised of a mixture of haplotypes, indicating that turtles from distinct natal beaches or genetic stocks come together to coexist within the same feeding ground[s] (Broderick and Moritz 1996; Lahanas *et al.*, 1998).

There is no accurate quantification of the size of *E. imbricata* foraging populations in Australian territorial waters. While several studies (Limpus 1992b; Limpus and Miller 2000; Whiting and Guinea 1998) have revealed both size and distribution of regional foraging populations, definitive estimates of the total number of animals found feeding in northern Australian waters are not available (Chaloupka and Limpus 1998; Guinea 1994; Limpus and Preece 1992; Miller 1994b; Robins 1995; Witzell 1983).

There are, however, estimates of annual *E. imbricata* nesting density and distribution in northern Australia (Dobbs *et al.*, 1999; Chatto and Baker 2008). Several thousand *E. imbricata* nest on beaches of northern Queensland through the Torres Strait (Limpus *et al.*, 1983), 2500 in the Northern Territory (Chatto and Baker 2008) and around 3000 nest in Western Australia annually (Preen *et al.*, 1997). Australia may support the largest breeding population of *E. imbricata* in the world (Limpus 2008).

The limited information available, describing *E. imbricata* feeding aggregations in northern Australia, does not necessarily reflect a lack of turtles, but merely that much of the coast and offshore islands are extremely remote, limiting turtle surveys. Limited survey effort also effects estimates of feeding aggregation size in the northern section of the Great Barrier Reef (nGBR) in Queensland. While *E. imbricata* clearly inhabit the region, no specific area supporting a high density *E. imbricata* feeding aggregation of both genders and all age-classes of turtle was

known, until the commencement of my study (Chaloupka and Limpus 1997; Limpus 1992b; Miller *et al.*, 1995; Robins 1995; Witzell 1983).

Ontogenetic stages

Several life history phases of *E. imbricata* remain poorly understood (Figure 1.1) (Musick and Limpus 1997). Generally *E. imbricata* exhibit the same life history pattern followed by most marine turtle species (Van Buskirk and Crowder 1994). Hatchlings that survive the transit across beach and reef flat to deeper offshore areas, are believed to enter regions of convergent water systems, or drift lines (Carr 1986; 1987), where they opportunistically shelter and feed on flotsam brought together by surface currents. A pelagic phase of unknown duration may occur in which post-hatchlings get caught in oceanic gyres and are carried hundreds to thousands of kilometres from their natal region (Miller 1997). Immature *E. imbricata* reappear once again when they recruit to neritic habitats, at around 35 – 45 cm carapace length (Limpus 1992b). Once established, typically within coral or rocky reef habitat, juvenile turtles may maintain strong site fidelity through puberty to adulthood (van Dam and Diez 1998b). Although unquantified in north-eastern Australia, a final developmental migration may occur during puberty to another neritic foraging habitat, where sexual maturity is attained (Chaloupka and Limpus 1997).

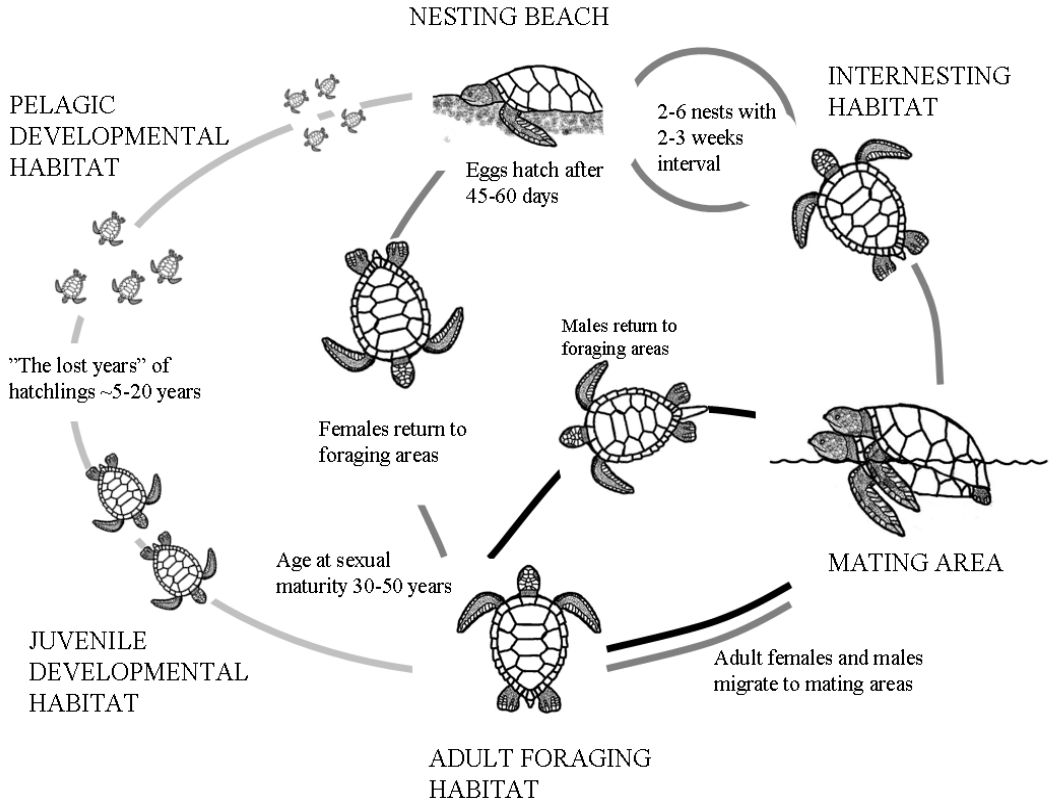

Figure 1.1. Generalised lifecycle for *Eretmochelys imbricata*. The duration of different life phases may vary among conspecific populations in the western Pacific. The figure is divided into hatchling / juvenile (light grey line), female (dark grey line) and male (black line) migration. Figure adapted from Lanyon *et al.*, (1989).

At an unknown age, thought to be 20 - 30 years, (Balazs 1985b; Limpus 1980), male and female turtles migrate to a nesting location which is often their natal region (Allard *et al.*, 1994; Meylan 1993). Several months prior to the commencement of nesting, competing males will try to couple with as many females as possible (Lee and Hays 2004). Courtship behaviour may include an aggressive rivalry between males, prior to and during copulation, typically in offshore waters adjacent to where nesting will occur (Owens 1980). At the end of a courtship period the majority of males return to their foraging areas (Fitzsimmons *et al.*, 1997a) and females commence oviposition, at approximately fortnightly intervals, at local beaches.

Eretmochelys imbricata are a highly fecund species laying between two and eight clutches of approximately 120 eggs, at approximately five year intervals throughout their adult life (Dobbs

et al., 1999). After spending several months at a nesting region, females then return to the foraging area from which they departed (Carr and Stancyk 1975; Miller *et al.*, 1998).

After an approximately 55 day incubation period, hatchlings emerge from the nest, their gender having been determined by ambient sand temperature during the middle trimester of development (Mrosovsky and Yntema 1982; Raj 1976). *Eretmochelys imbricata* hatchling gender ratios are poorly understood in the northern Great Barrier Reef, but are likely to be biased toward females (Dobbs *et al.*, 1999). This reproductive trait of high fecundity and female offspring bias is shared with other, late maturing and long-lived reptilian species, which, as a rule, are especially vulnerable to high immature age-class mortality (Heppell and Crowder 1996).

High fecundity is counteracted by high mortality of immature age-class turtles. In normally functioning populations, survivorship should increase as animals mature through ontogenetic life history phases until adulthood is reached, at which time annual survivorship is potentially high (Chaloupka and Limpus 1997). Several marine turtle population models, including those of *E. imbricata*, have shown that survivorship of large immature and adult turtles are particularly important for maintaining stable and viable populations (Olsen 1985).

Succession through ontogenetic stages may take decades to complete (Arthur *et al.*, 2008). Prolific offspring production, combined with delayed sexual maturity, may be a life history strategy that can serve as a "buffer", to compensate for high mortality or even total loss of several generations of immature turtles, and still maintain a stock of animals that will later mature and reproduce (Lutcavage *et al.*, 1997). However, species with low intrinsic rates of increase require considerable time to recuperate; hence, once reduced, it may take decades for population sizes to recover (Bjorndal 1999a).

Foraging habitat

Eretmochelys imbricata may occupy a diverse range of habitats at different ontogenetic stages, but upon reaching maturity most turtles are associated with healthy coral reefs (Leon and Diez 1999; Meylan 1985b). Studies in the Atlantic Ocean have described post-hatchling turtles (oceanic stage juveniles) as recruiting to a pelagic environment, taking shelter in floating algal mats and drift lines of flotsam and jetsam (Carr 1987). In the western Pacific, however, the post-hatchling habitat of *E. imbricata* juveniles remains undescribed but, like their northern hemisphere conspecifics, may include a pelagic phase (Chung *et al.*, 2009). It is believed that after a few years in the pelagic zone, small (approximately 38 cm carapace length) juvenile *E. imbricata* recruit to coastal foraging grounds within the nGBR (Limpus 1992b). It is likely that a shift in habitat type includes a change in feeding strategy, from surface opportunism to active selection of prey in a benthic rocky or coral reef environment (Meylan and Meylan 1998).

Diet

Historically, and primarily based on studies undertaken on feeding assemblages in the Caribbean, *E. imbricata* have been described as primarily spongivores (Meylan 1988), only consuming limited amounts of other benthic invertebrates (Leon and Bjorndal 2002). However my study shows that *E. imbricata* in the nGBR, unlike their northern hemisphere counterparts, display a strong preference for a small range of specific algal species and only a minor preference for a variety of other prey including: ascidians; bryozoans, molluscs, cnidarian, echinoderms, crustaceans and zooanthids and soft corals.

Threats

Nesting threats

Several long-term monitoring studies of *E. imbricata* nesting aggregations have shown major declines in population abundance (Groombridge and Luxmoore 1989; Baillie and Groombridge 1996), and while some populations continue this trend (Meylan and Donnelly 1999) others are starting to show signs of recovery (Beggs *et al.,* 2007).

Egg collection

Indigenous communities throughout the Western Pacific have opportunistically, and apparently sustainably, collected *E. imbricata* eggs as a seasonal source of dietary protein for many millenia. However, recent access to high-speed outboard-powered motor-vessels, combined with a centralised market system and a cash economy, has led to a level of take that is now likely to be unsustainable at many rookeries (Spring 1982; Kinch 2006).

Predators

Europeans introduced feral pigs (*Sus scrofa*) to Pacific islands in the 18th and 19th centuries (Gongora *et al.,* 2004). Since that time, their numbers have increased many fold, and because they possess particularly sensitive olfaction these animals are extremely well adapted to locating and consuming buried turtle eggs. In many parts of north Queensland and Papua New Guinea, a 100% predation of marine turtle eggs by feral pigs have been reported (Doherty 2005).

Collection of turtle shell

Historically, a demand for *E. imbricata*'s thickly keratinized scutes, to supply the Japanese "Bekko" ornamental trade, as well as other products, including leather, oil, perfume, and cosmetics has resulted in an unsustainable commercial exploitation and been the primary cause of species decline (Luxmore and Canin 1985). The British Virgin Islands, Cayman Islands, Cuba, Haiti, and the Turks and Caicos Islands (U.K.) all permit some form of legal take of *E. imbricata* (Beggs *et al.,* 2007). In fact, until recently, many of these countries were actively supporting a Japanese initiative to down-grade the conservation status of these turtles, under the

Convention of International Trade in Endangered Species (CITES), to allow export of *E. imbricata* products (Anon 1997). *Eretmochelys imbricata* products are openly available in the Caribbean and western Pacific, despite a prohibition on harvesting *E. imbricata* and their eggs (Brown *et al.*, 1982; Fleming 2001).

Marine environment threats

A wide variety of marine debris, including discarded fishing gear, plastics and packaging can entangle or maybe ingested by marine turtles including *E. imbricata* (Bjorndal *et al.*, 1994). Entanglement and ingestion probably occurs accidentally while swimming, feeding or scavenging (Laist 1987). Detrimental effects of entanglement with marine debris include strangulation, increased drag, lacerations, infection and loss of limbs **(**Mascarenhas *et al.*, 2004). Ingestion of marine debris may lead to the blockage and/or perforation of an individual's digestive system or potentially, poisoning by polychlorinated biphenyls (PCBs) (Muusse *et al.*, 2006).

Research objectives

The long-term (18y) *E. imbricata* nesting monitoring program undertaken at Milman Island in the nGBR has shown that the number of animals presenting to nest has been declining by between three and four percent per annum, over the course of the study (Dobbs *et al.*, 1999; Limpus and Miller 2000). In light of the current and predicted threatening processes occurring within nesting and foraging habitats, the long-term conservation outlook for *E. imbricata* populations in the western Pacific is generally poor (Meylan and Donnelley (1999). The unsustainable take of both reproductive and feeding turtles, combined with the collection of their eggs from multiple Coral Sea rookeries, is likely to drive down the population size to a point that it is unable to effectively function (Kinch 2006; Tuato-Bartley *et al.*, 1993). While nesting studies are important to determine trends in reproductive females, long term impacts at a meta-population scale cannot be accurately determined without robust baseline data describing both

the nesting and foraging life history phases (Miller 1994a). I chose reefs within the Howick Group to undertake a comprehensive examination of *E. imbricata* feeding ecology because they supported a high density feeding assemblage and, the area's remoteness ensured, as much as practicable, a lack of localised anthropogenic impacts. Additionally, 6 of the 13 reefs within the Howick Group are classified Marine Park "B" zones, which prohibits all extractive activities and is designated as the second highest level of conservation protection within the Great Barrier Marine Park.

Thesis outline

The research reported in the following chapters provides information on both genders and all age-classes of *E. imbricata* within their nGBR foraging grounds that will: 1) describe the sex and age-class ratios, morphometrics and distribution of turtles on and between reefs; 2) investigate the annual survivorship by gender and age-class, with estimations of total population size; 3) report on the genetic diversity and likely source populations; 4) re-evaluate the generally held belief that *E. imbricata* are primarily spongivores; and 5) describe the growth rates and age to maturity of a feeding cohort.

This thesis is divided into eight chapters; beginning with a general introduction, and general methods followed by four chapters on specific aspects of the study and a concluding chapter. Chapters two and three describe the study-site and methodology, chapter four describes the population morphology, while chapters five to seven examine population size and survivorship, genetic structure, diet and somatic growth rates and chapter eight provides some management recommendations and conclusions. The remainder of this, the first chapter, provides a brief general overview of the biology and conservation of sea turtles with an emphasis on green and hawksbill turtles in northern Australia.

CHAPTER TWO

STUDY SITE DESCRIPTION AND GENERAL METHODS

Study area

Collectively, the Howick Group comprises 16 coralline reefs, with their associated sand cays and several islands of granitic origin (Rees *et al.*, 2006). Ingram Island (140 25.29" S., 1440 52.54" E.) is close to the study area centre and was selected as a base for undertaking surveys. Geo-physically, this region of the Great Barrier Reef is characterised by an almost continuous line of outer-shelf-edge ribbon reefs enclosing a narrow (<50 km), shallow, continental shelf; with the neritic zone rarely exceeding the 40m isobath (Flood and Orme 1977).

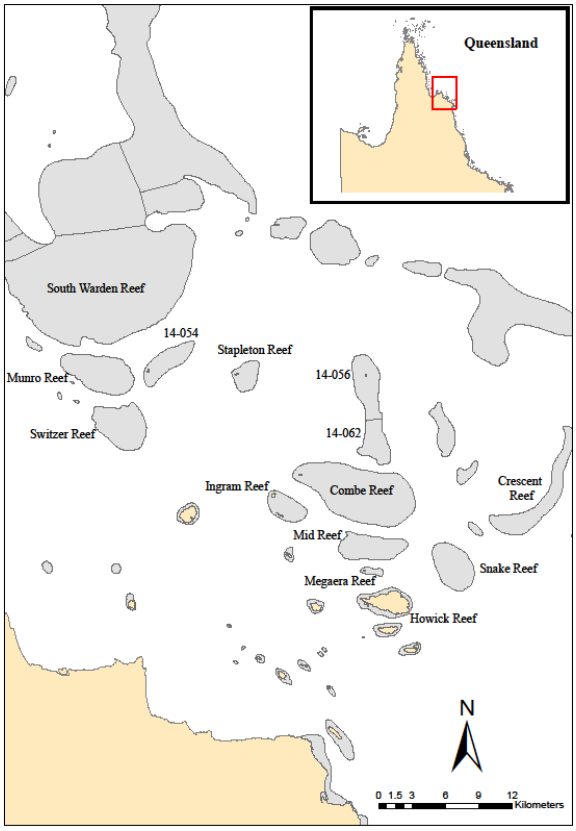

Figure 2.0. Location of the Howick Group of islands and reefs in the Far Northern Section of the Great Barrier Reef Marine Park, Queensland, Australia.

The majority of reefs within the Howick Group are classified as "inner shelf planer (or platform) reefs", however several (un-named reefs: 14-063; 14-056; 14-062; and Crescent) are

"crescentic" form reefs (Done 1982). The area is sheltered from large oceanic swells emanating from the South Pacific Ocean, by a line of ribbon reefs which form an almost continuous barrier. At a more regional scale, Lizard Island, a large granitic island, and Martin and Eyrie Reefs also shelter this region from the predominantly strong (~ 20 - 30 knots) south-east winds. Most reefs within the Howick Group have large sand-covered reef platforms, with active coral growth restricted to their margins. Two large rivers, the Starcke and Jeannie, drain a narrow coastal plain adjacent to the Howick Group.

Most reefs are oriented in a southeast to northwest direction and have a well developed rubble crest of up to 200m wide on the high-energy southeast end. Several reefs have shallow lagoons (<1m deep), and three of the 12 reefs support oval vegetated sand cays. They range in height from 1.0 - 3.5 m above highest astronomical tide (HAT). Cays are of variable dimensions ranging from 20 m long and 3 – 4 m wide to 500 m long and 200 m wide (Hopley and Harvey 1981).

The windward reef margins slope steeply to about 8m depth, are dominated by massive and tabulate coral forms and exhibit spur and groove morphology with gullies, caves and overhangs. Leeward reef margins slope gently to about 3m depth and are dominated by branching *Acropora* species (*pers. obs.*). The annual air temperature in the region ranges from 20 - 34°C; mean sea temperature is 27°C. Southeast trade winds predominate (March – September) and usually range from 15 - 30 knots and can generate up to 3 m swells for much of the year (Australian Bureau of Meteorology 2009).

Table 2.0. Reef names, geophysical structure, location, GBRMPA reef code and approximate number of visits to each reef within the Howick Group study area.

Reef name	Morphology	Area (km^2)	Latitude Deg. Min	Longitude Deg. Min	GBRMPA code	Approximate number of surveys
Combe	Planer	30.37	-14^0 25'S.	144^0 58'E.	14-063	81
Ingram	Planer	6.09	-14^0 25'S.	144^0 53'E.	14-064	34
Switzer	Planer	14.26	-14^0 21'S.	144^0 45'E.	14-061	8
Munro	Planer	13.29	-14^0 19'S.	144^0 45'E.	14-055	8
Stapleton	Planer	2.28	-14^0 20'S.	144^0 51'E.	14-054	6
Snake	Planer	11.18	-14^0 28'S.	145^0 01'E.	14-087	10
Mid	Planer	10.99	-14^0 27'S.	144^0 57'E.	14-066	34
Megaera	Planer	0.64	-14^0 28'S.	144^0 57'E.	14-072	7
Crescent	Crescentric	7.18	-14^0 26'S.	145^0 03'E.	14-082	2
Unnamed	Crescentric	4.69	-14^0 20'S.	144^0 57'E.	14-056	10
Unnamed	Crescentric	4.04	-14^0 23'S.	144^0 58'E.	14-062	10
Unnamed	Crescentric	7.76	-14^0 18'S.	144^0 47'E.	14-053	6
South Warden	Crescentric	69.88	-14^0 46'S.	144^0 46'E.	14-051	1

Implementing foraging studies in a northern Great Barrier Reef Eretmochelys imbricata *feeding area*

A number of factors influenced field research techniques. Surveys were undertaken during the austral winter (June - August) to maximise the possibility of encountering turtles that had returned from the previous seasons nesting, and encountering turtles that had yet to leave for the following season's nesting event. During this mid-year period, strong (15 - 25kts) and almost continuous "trade" winds prevail from the southeast. Undertaking open-ocean crossings between reefs, looking for and endeavouring to safely catch turtles using small vessels in rough seas with high winds meant some reefs were inaccessible on occasion. Turtle capture success was also influenced by a range of other variables, which included, but were not limited to: weather conditions (i.e., cloud cover); observer ability to spot and follow turtles, catcher ability to capture all age-class of turtle; vessel driver skill, and tidal conditions.

Flipper tagging techniques

The turtles were tagged with standard, self-locking, titanium turtle tags (Stockbrands Company, Pty. Ltd., Perth, Western Australia.). The tags' front had a unique alpha-numeric inscription, that typically consisted of a letter followed by 4 - 5 numbers. The reverse side of the tag was inscribed: "RETURN WILDLIFE BOX 155 BRISBANE 4002 QLD AUSTRALIA." Tags were

applied in the axillary tagging position of the front flippers (Eckert *et al.*, 1999; Limpus and Reed 1985; Mrosovsky and Shettleworth 1982). The axillary tagging position is through or immediately adjacent to the enlarged scale closest to the body on the posterior (trailing) edge of both the left and right front flippers. If the animal already carried tags, the condition of the tags was assessed and a decision made whether to add another tag(s) to the turtle. If greater than 50% of a tag extended from the trailing edge of the front flipper, a new tag was applied. Each turtle was released with a minimum of two, securely attached, titanium tags.

Mark-recapture classification of turtles

Eretmochelys imbricata captured over the course of the study were classified as follows:

1) Primary: a turtle with no evidence of tag scar and tagged for the first time;

2) Inter-season recapture (ISR): turtle tagged in a previous study season at the Howick Group or at a nesting site;

3) Inter-season recapture, re-tagged animal (ISR - RTA): a turtle with an obvious dermal tear or hypertrophic scarring, in the normal tagging position on the trailing edge of a front flipper, indicating that turtle was tagged during a previous survey or at another locality. The turtle was retagged and included in the total count tagged each season; or,

4) Within-season recapture (WSR): a turtle tagged and recaptured within the same survey period.

Eretmochelys imbricata *morphometrics*

Curved carapace measurements were taken using a flexible fibreglass tape measure (± 0.1 cm) laid over the anterior / posterior midline curve of the carapace. Due to stretching, fibreglass tapes were regularly calibrated using steel rules. Tape measure use was discontinued when its length exceeded 100 + 0.2 cm over a distance of 100.0 cm. Any large barnacles, typically *Chelonibia testudinaria*, present on the carapace, and likely to interfere with a measurement, were removed.

Curved carapace length (CCL)

A measurement taken along the midline from the junction of the loose skin of the neck and the nucal scute to the posterior edge of the post-vertebral scute.

Curved carapace width (CCW)

Measured perpendicular to the carapace midline axis, between the outer extremities of the marginal scales. This measurement was repeated at several positions to obtain the greatest value. For turtles whose carapace was reflexed upwards near the marginal scales, this measurement was made with the tape measure stretched tightly between the outer extremities of the marginal scales, i.e., it was not always in contact with the surface of the carapace for the full width. Reliably repeatable carapace measurements were difficult to obtain from some turtles due to either extensive damage to the post-vertebral scutes, or where the presence of burrowing barnacles, *Tubicinella cheloniae*, had caused extensive carapace deformity.

Head measurements

Head measurements were taken using stainless steel vernier slide callipers (± 0.01 cm). With large turtles it was necessary to support the turtle vertically (balanced on the posterior of its carapace) and deflect the head ventrally to enable measurements to be taken.

- *Head length (HL):* From the anterior tip of the maxillary sheath (upper beak) to the posterior margin of the supraoccipital process, keeping the arm of the callipers parallel to the dorsal surface of the skull.
- *Head width (HW):* Maximum width across the skull measured at the quadrate bones.

Plastron length (PL)

This was measured using a flexible tape measure (± 0.5 cm) along the midline from the anterior junction of the skin and plastron scutes to the posterior margin of the cartilaginous or bony plate.

Tail measurements

Tail measurements were taken to the tip of the straightened tail, using a steel tape measure (± 0.5 cm).

- Tail length from plastron (TLP): Measured from midline posterior of the cartilaginous/bony projection of the plastron.
- Tail length from carapace (TLC): Measured from the most posterior edge of the post vertebral scute. A negative value for this measurement indicated that the tail did not reach the carapace margin.
- Tail length from vent (TLV): Measured from the anterior margin of the vent.

Weight

Turtle mass was recorded after placing them on their backs and lifting via a spring balance attached by four ropes, each secured to the base of a flipper or by encasing the turtle in a continuous 4m long, figure of '8' strap. The turtles were weighed on either 10 (± 0.2) kg or 100 (± 0.5) kg spring scales depending on the size of the animal.

Surgical laparoscopy procedures

Given that marine turtles do not display external morphological characteristics of past or present breeding status, a surgical laparoscopic examination of their gonads is an ideal method to provide an unequivocal determination (Wood *et al.*, 1983; Limpus and Reed, 1985). Monitoring changes in the ratio of experienced to novel breeders in a foraging area can reveal if an over-harvest of reproductive females is taking place at nesting areas. The value of information that surgical laparoscopy provides, justifies use of this safe, but relatively invasive technique.

Study site remoteness necessitated that all laparoscopic examinations occurred *in situ*, either on the beach of a sand cay adjacent to the reef on which the turtle had been captured, or after transportation of the turtle, by vessel, back to Ingram Island. Turtles being prepared for an

examination were placed plastron-side up, in a recumbent position, on an aluminium examination frame and restrained by criss-crossed webbing straps. A 1.5 ml subcutaneous infusion of 10% lignocaine hydrochloride was administered by syringe to the dermis of the inguinal area as a local anaesthetic, five minutes prior to surgery. The right hind flipper was then extended and secured to the side of the frame to present the inguinal pocket. The frame was lifted at one end and the turtle presented for surgery with its head down and inguinal pocket exposed. Passage through the dermis occurred in the area immediately anterior to the hind limb in the inguinal pocket but posterior to the plastron, usually on the left side of the turtle. This site for cannula insertion was chosen specifically to avoid severing major blood vessels or puncturing vital organs. In addition, it is a site with few or no pain receptors, underlain mostly by fat and connective tissue with minimal muscle. Laparoscopy in the inguinal area caused a small wound, which healed rapidly.

Surgical instruments were immersed in 70% alcohol for cold sterilisation for several hours prior to laparoscopy. A four to five millimetre incision was made in the inguinal fossa, using a scalpel. A seven millimetre cannula, fitted with a matching trochar, was then inserted into the incision to separate mesentery, muscle, and connective tissue and penetrate the peritoneum. The trochar was then removed from the cannula and a 5mm diameter, 350mm long, 20^0 bevel Karl Stortz laparoscope was inserted through the cannula. Verification that passage through the peritoneum had been successful was confirmed by visual identification of a cross-section of intestine, ovary or lung. After confirming that the abdominal cavity had been entered, air was introduced via a manual pump to insufflate the area, facilitating clear vision of other organs including the gonads. After identifying the posterior end of the lung, the scope was swept laterally and slightly dorsally to locate and examine the gonads and their associated ducts.

Upon completion of the examination, the laparoscope was removed, and any excess air present in the abdominal captivity was expelled by opening the non-return valve on the cannula and depressing the turtle's plastron. The cannula was then removed and the incision manually closed with several soluble sutures.

Gonad interpretation

"Adult" age-class classification in *Eretmochelys imbricata* was based on several criteria and characteristics. A female was classified as an "adult" if the ovary displayed an expanded stroma and the oviduct was pink, very convoluted, strap-like, and at least 1.5 cm in cross section adjacent to the ovary (e.g., Limpus 1998). A female could be classified as an adult preparing to breed at the next nesting season, if yellow, vascularised, vitellogenic follicles (1.0 - 2.0 cm diameter) were present (Figure 2.2). A female could be identified as having bred in the past if *corpora lutea* (ovarian scars typically <5.0 mm in cross-section) were present (Figure 2.2). Additionally, female *E. imbricata* could be classified as a "first-time ever nester" if an ovary only displayed *corpora albicantia* (follicular scars) greater than 10mm diameter in cross-section, as clear evidence of an ovulation having occurred within the current, or most recent, nesting season (Figure 2.3). Mature male turtles had testis that were cylindrical (3 – 7 cm in cross section) and seminiferous tubules, with an enlarged (3 – 5 cm in cross section) pendulous, epididymis that was distinctly ridged and turgid (Figure 2.4).

A "pubescent" age classification in *Eretmochelys imbricata* was scored for females if the oviduct was only partly convoluted, oval in cross-section and 5 – 15 mm in diameter adjacent to the ovary, and no *corpora albicantia*, *corpora lutea*, or developing follicles were present. A pubescent male turtle had a non-pendulous, slightly ridged epididymis that protruded from the body wall into the peritoneum, and the testis were elliptical and approximately 3 – 5 cm in cross section. Periodically pubescent turtles could also be characterised by a tip of the tail to carapace length of 5 – 10 cm. Front and hind flipper claws of pubescent turtles displayed signs of becoming elongated and re-curved.

An allocation of a "juvenile" age-class classification was based on whether the turtle displayed: an ovary with a tightly bunched, non-expanded stroma; the oviduct was white, straight or only very slightly convoluted and cylindrical to oval in cross-section and the oviduct was less than 1.5 cm wide at a position that was opposite the ovary. Vitellogenic follicles, *corpora lutea*, *corpora albicantia* or atretic follicles were never present.

Juvenile male turtles displayed a flat or only slightly cylindrical testis and an epididymis that did not bulge from the body wall.

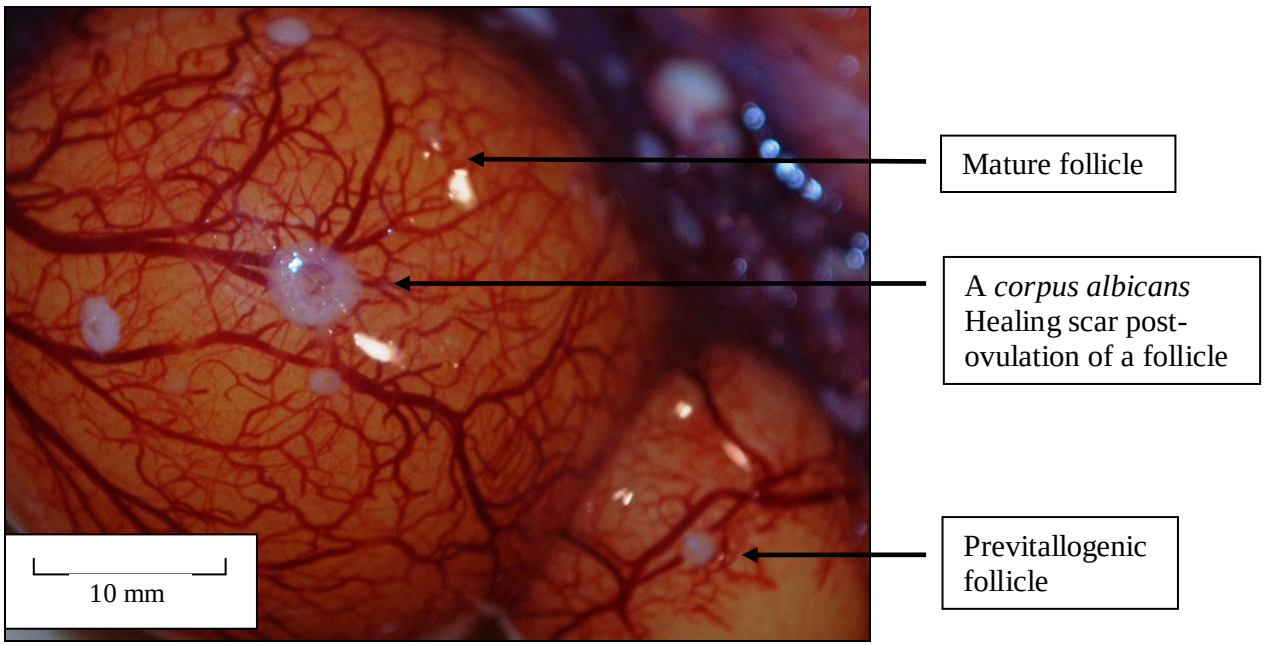

Figure 2.2. Photograph of a *corpus albicans*. The regressed scar of the *corpus luteum* remaining on the stroma of the ovary 1 - 2 years after the ovulation of a developed follicle.

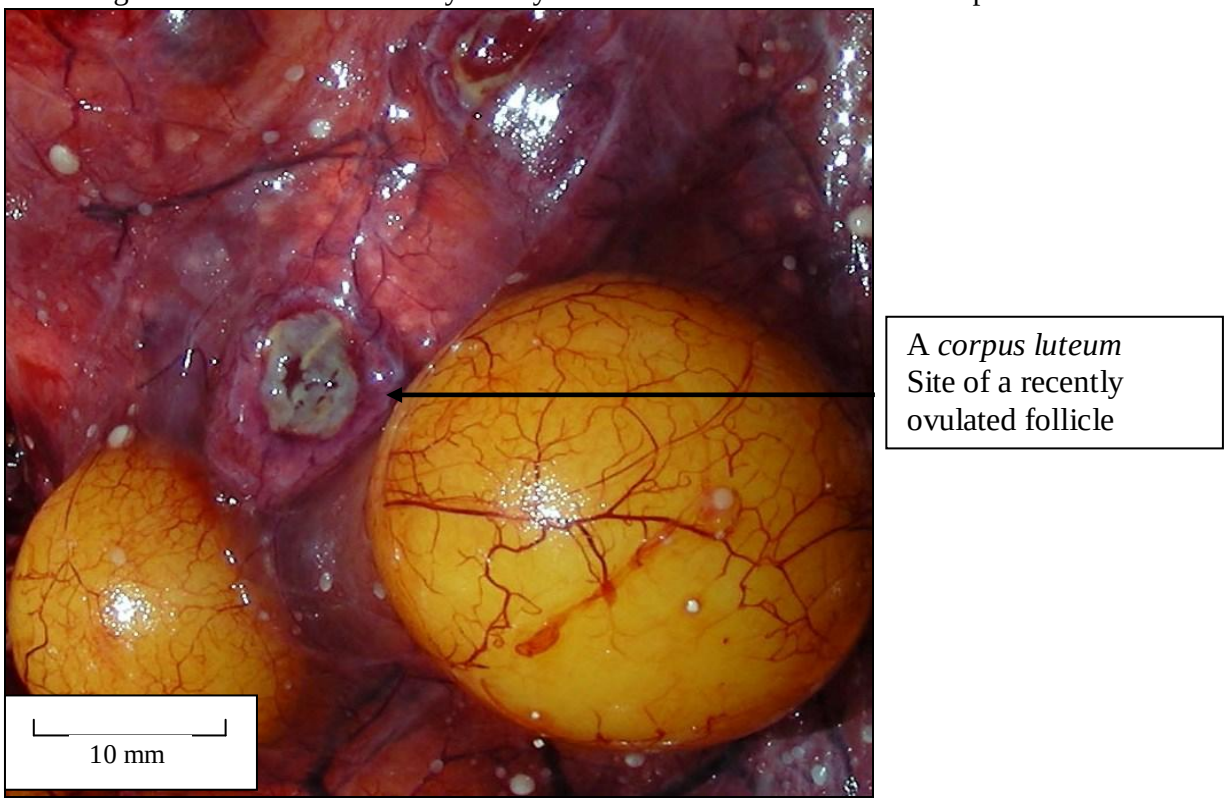

Figure 2.3. Photograph of a *corpus luteum* the scar remaining on the stroma of the ovary following the recent (~ 60 days) ovulation of a developed follicle.

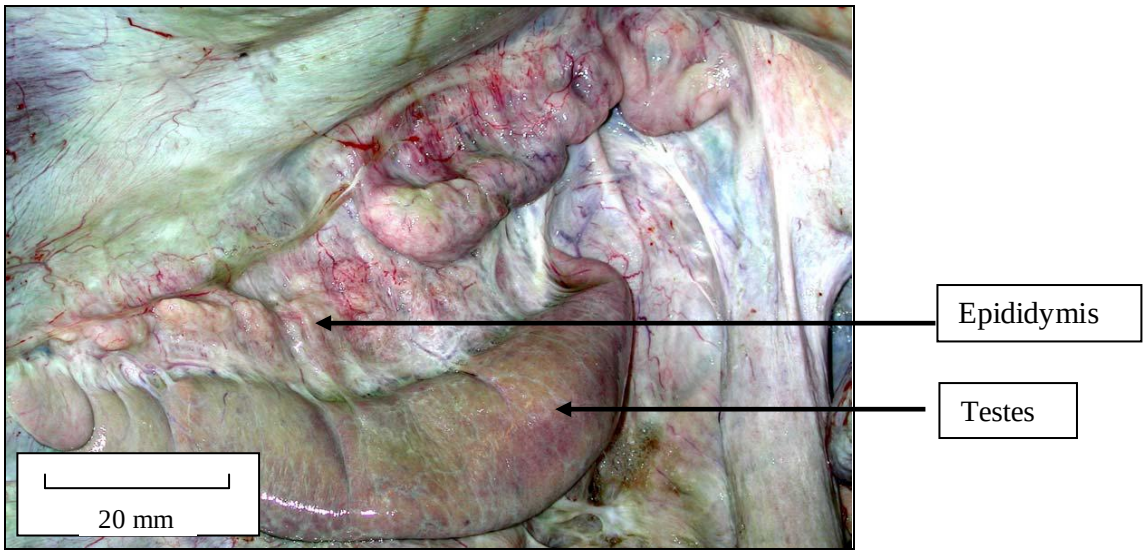

Figure 2.4. The epididymis and testes of an adult male *Eretmochelys imbricata* in spermatogenesis.

Evolution of survey techniques specific to the Howick Group of reefs

At the commencement of the study, turtle search pattern methodologies mirrored those used historically at other sites for different marine turtle species (Schofield *et al* 2006). More specifically, the entire reef flat or embayment were searched, by driving the vessels in a broad

zig-zag pattern. However, after several weeks of using this approach I discovered that while the centre of the reef flat contained broad sea grass meadows, with a high density population of green turtles, *Chelonia mydas*, *E. imbricata* were rarely encountered. *Eretmochelys imbricata* were however, most commonly seen, and subsequently caught, on the rocky rubble reef fringes, typically at the southern, high-energy end of reef flats. My sampling design subsequently changed to only rapidly scanning sea grass areas for *E. imbricata* and focussing the majority of search effort on the reef fringes instead. In order to avoid prematurely disturbing turtles, causing them to leave reef crests, vessels would move between reefs in either deep water, off the edge of the reef, or over the middle of the reef flat, to a point where the survey would commence. At this point, smaller, zig-zag patterns would be used to search the most likely habitat containing *E. imbricata.*

In order to safely and effectively catch a turtle, a distance of at least 75m was needed between the turtle and reef edge, to manoeuvre the catch vessel into position for a person to dive from the edge of the boat onto the back of the turtle. If a turtle was disturbed, generally by the sound of an approaching outboard motor, it rapidly swam towards the reef edge and dived into deep water, obviating chances of capture.

Research methodology considerations

Capturing marine turtles by jumping onto them from a small (4.5m), rapidly moving vessel, presents the researcher with some challenges. *Eretmochelys imbricata* are well camouflaged, with a dark brown, speckle-patterned carapace, making them highly inconspicuous within a reef habitat. Within the Howick Group, *E. imbricata* appear to be diurnal feeders; moving onto the reef flat when the tide is in and the water is deep enough, and departing for deeper water during at low tide (*pers. obs.*) They are extremely sensitive to any unfamiliar noise, such as that produced by an outboard motor, and they react by rapidly retreating from the shallow reef top to deep water when disturbed.

Figure 2.5. A research assistant preparing to jump from the bow of a catch vessel during rough weather conditions.

I secured project funding to undertake this research through a collaboration with a non-government organisation (Earthwatch Institute). Thus, many unskilled volunteers were engaged in turtle catching. Therefore, the first several days of every research trip were spent training people to safely undertake the work. The use of unskilled volunteers is likely to have caused an initial low catch rate during the first few days of each trip, with catch rate progressively improving. Typically, volunteers spent two weeks on the project.

My sampling methodology was designed to maximise the number of *E. imbricata* encountered. It took into account various environmental factors such as: tide height, tide time, prevailing wind strength and direction, and water clarity. To ensure that turtles were as far as possible onto the reef crest, thus maximising the distance catch vessels had to capture turtles, survey start times varied with diurnal tidal cycles and were timed to commence at approximately the peak of high tide. This allowed a period of approximately three hours for turtles to move onto the reef in search of prey. Searches continued until the entire reef crest had been searched, or the water was too shallow for a vessel to operate (~ 40 cm.).

The vessels used to catch turtles were specifically modified 4.5 m aluminium hulled, outboard-motor-powered dinghies. Vessels were crewed by one experienced driver and three trained turtle spotters/catchers. The vessel layout was such that all four people could maintain a watch for turtles from the bow of the boat. Typically a several hundred-metre-wide strip of reef crest was searched while working down wind and with the sun (as much as practicable) behind the boat to minimise glare and maximise chances of sighting turtles. Given that reefs in the Howick Group also host a large population of green turtles, visual differentiation between the species was at times difficult. *Eretmochelys imbricata* could be differentiated by their size, colour, body morphology and swimming style. Upon sighting an *E. imbricata*, the boat driver chased the turtle and manoeuvred the vessel into a position whereby a catcher could dive from the bow of the boat onto the turtle. Once the turtle was caught and restrained, the vessel was brought alongside the catcher and turtle, and both were loaded into the boat.

Following their capture, most *E. imbricata* were returned to a nearby island for processing. At this time, turtles were tagged or had their tags read, morphometric measurements were recorded and they were prepared for a laparoscopic examination of the gonads and lavage sampling. Once these processes were completed, turtles were released immediately into the sea, typically within three hours of being brought ashore. Turtles that were not returned to a beach for laparoscopy were processed and released within 10 minutes at the capture site.

Legislation

A Scientific Research Permit from the Great Barrier Reef Marine Park Authority was required to conduct research in the Great Barrier Reef Marine Park. Animal Ethics approval, from an authorised Animal Ethics Committee, was obtained to undertake the studies. It was also necessary to have approval under Section 18(1) from *Queensland Health under the Health (Drugs and Poisons) Regulation* 1996 in order to administer drugs (anaesthetics) to animals.

The three research vessels (4.5m aluminium dinghies) used during the study, were in 2C commercial survey to comply with the *Queensland Maritime Safety Act* 2002. A Safe Operation Manual and Risk Management Plans were developed to mitigate the likelihood of injury to staff and research assistants, as required under *Queensland Workplace Health and Safety Act* 1995.

Data management and analyses

Field data were entered and stored in Microsoft Excel©. These data were annually up-loaded to the Queensland Department of Environment and Resource Management's Turtle Research database. Data management and statistical analyses were performed using a range of software packages including: Microsoft Excel©, Statistica © 7.0, and Statistical package: Past v. 2.07 (Hammer *et al.*, 2001). xyExtract Graph Digitiser 2.4 was used to extract growth data from southern Great Barrier Reef *E. imbricata* presented by Limpus (1992b).

CHAPTER THREE

ERETMOCHELYS IMBRICATA: DEMOGRAPHICS, MORPHOMETRICS AND POPULATION DISTRIBUTION WITHIN A REEFAL HABITAT

Introduction

Eretmochelys imbricata are the most common species of marine cheloniid to be found feeding within coral reefs (Witzell 1983). Given that the Great Barrier Reef (GBR) is the most extensive reef ecosystem in the world (Hopely *et al.*, 2007) it would seem logical, therefore, that these reefs would provide substantial areas of suitable habitat for supporting *E. imbricata* foraging aggregations. However, while anecdotally *E. imbricata* were known to forage on reefs and within embayments, from Torres Strait (9^{o} S.) to at least Moreton Bay (27^{o} S.), no high density population foraging area, containing all age-classes, has been identified (Limpus *et al.*, 1994a; Limpus and Parmenter 1986).

Historically, most information describing *E. imbricata* populations had been collected by monitoring aspects of their nesting biology (Limpus 1992b; Dobbs *et al.*, 1999; Limpus and Miller 2000). However, while long-term monitoring of the reproductive period of a species is important, it describes only a relatively small aspect of their overall life history, and little about the total stock demography and trends. Conversely, mark-recapture programs, designed to detect trends in population dynamics within feeding aggregations, comprising all age-classes and both genders, are crucial in obtaining a population-wide perspective (Sandercock 2006).

Limpus (1992b) described several demographic and morphological aspects of an immature population of *E. imbricata* found on reefs in the southern GBR. Within Australia, Whiting and Guinea (1998) have also reported on various demographic and life history aspects of a population of juvenile *E. imbricata* from Fog Bay in the Northern Territory. Internationally, the

majority of in-water studies of have taken place in Central American countries: (Caribbean: Carrillo *et al.*, 1999; Leon and Bjorndal 2002; van Dam and Diez 1998a; Bjorndal *et al.*, 1993; Mexico: Clifton *et al.*, 1982; and Puerto Rico: Diez and van Dam 2002). However, descriptions of populations of mature *E. imbricata* within the southern hemisphere are lacking.

Prior to the present study, during June and July 1997, I conducted a vessel-based transect survey of inshore reefs between Torres Strait and Cairns to determine if a suitable site existed for conducting long term *E. imbricata* population monitoring. From this initial survey, I found that reefs that made up the Howick Group (14^0 25.29' S., 144^0 52.54' E.) supported a high-density assemblage of *E. imbricata* and were suitable for long term demographic studies.

Methods

The logistical challenges of catching marine turtles within their feeding habitat is likely to be one of the main reasons accounting for the limited number of in-water mark-recapture studies. Historically, various methods have been used, some of which are still employed, including: using SCUBA to hand-catch sub-adult turtles (Gilman *et al.*, 2010), snorkeling (van Dam and Diez, 1998a), netting, using turtles from fisheries by-catch, and conducting air surveys (Marsh and Sinclair, 1989; Robins 1995). Fortunately, *E. imbricata* in the nGBR come onto shallow, clear water (5.0 m) reef flats to forage at high tides, allowing the "turtle rodeo" capture technique (Limpus and Reed 1985).

Turtle capture method

To collect morphometric data, determine the age-class of immature turtles and allocate a reproductive status to mature turtles, *E. imbricata* were hand captured using the "rodeo" method (described in detail by Limpus and Reed 1985). Using this technique in clear shallow water can be very productive; however catchers need to be highly skilled to achieve a high (80 - 90%) success rate.

Eretmochelys imbricata found on Howick Group reefs generally preferred feeding in the high energy, wave-break, south-eastern end of reef flats. Operating small (4.5 m) vessels in 1 - 2 m breaking waves while trying to catch turtles that are swimming rapidly towards the edge of the reef and therefore into deep water, is clearly challenging. Being well camouflaged, *E. imbricata* are also hard to initially locate, and once discovered can be difficult to catch, as they are extremely powerful swimmers with swim speeds of up to 11.0 km/h (Eckert 2002).

Figure 3.0. An *Eretmochelys imbricata* foraging in a typical rocky rubble reefal area found in the Howick Group.

The Howick Group of reefs are classified as "remote", and are approximately a six hour one-way flight by helicopter from a hospital. While no serious injury occurred to researchers over the course of study, we periodically had to forgo catching multiple turtles for the sake of operational safely. Some reefs (e.g., South Warden and Crescent Reefs) were at the outer margins of what could be considered safe operating distances (~ 70 km round trip) from the research camp established on Ingram Island. It was a balance between carrying sufficient fuel to travel to these remote reefs, spend several hours searching for, and then returning to camp with a boat load of turtles within a safe margin of fuel.

Morphometrics

Standard curved carapace lengths (CCL) and turtle weights (WT) were recorded. All length measurements were recorded in centimetres (cm) and weights in kilograms (kg). Seven further measurements including: head length (HL), head width (HW), curved carapace width (CCW), tail length to plastron (TLP), tail length to carapace (TLC), tail length to vent (TLV) and plastron lengths (PL) were also recorded (as described by Limpus 1992b). The CCL is the most ubiquitous measurement reported in other marine turtle studies (Bjorndal and Bolten 1989) and therefore I used it preferentially as a comparison of morphometric parameters between this and other *E. imbricata* population studies.

Specific catch location for each turtle

During surveys conducted between 1997 and 2005, turtles were only identified to a specific reef. During the final three study seasons (2006 - 2008), individual turtles were identified to a specific geographic location (± 50m) on each reef using a hand held Global Positioning System (GPS), programmed to operate on the WGS 84 datum. Where practicable, position locations were recorded at first sighting of the turtle. However if this was not possible, the location was recorded immediately upon capture of the turtle.

Daily reef surveys

Although not logistically possible to quantify during the scope of this survey, I found that repeated (>3 consecutive) days of vessel operation over the same section of reef or on reefs of less than 10 km^2, would disturb the majority of *E. imbricata,* to the point that they moved off the reef flat and into deep (>6m) water. Once turtles had moved into deeper water, they were unavailable for capture. Weather and tidal heights permitting, searches were rotated among the 13 reefs, in an attempt to mitigate this disturbance.

Logistics of undertaking Eretmochelys imbricata *foraging surveys*

Cloud cover, wind speed, tide (amplitude and height), and declination of the sun, were the three main environmental factors that influenced the success rate of *E. imbricata* capture. The most favourable daytime conditions, for initially observing and subsequently catching turtles were: cloud free, mid-tide (falling), midday (sun at a 90° angle to the sea's surface) and no wind. With these conditions I achieved a ~ 90% catch rate of all *E. imbricata* seen. Alternatively, on cloudy days, at full or low tide, early in the morning or late in the afternoon, with greater than 10 - 15 knots of wind, meant virtually no turtles were seen or captured. Where necessary, search patterns and/or daily surveys were adjusted to maximise potential turtle encounters, given weather and tidal conditions.

To obtain the full range of data on a turtle, it was necessary to bring it to a beach to conduct laparoscopy, gastric lavage, tagging, measuring, weighing, etc. Some reefs in the Howick Group (South Warden, Crescent, Munro, Switzer and Stapleton Reefs) were located between 6.5 and 16 km to the north of where the research base was located on Ingram Island. Prevailing wind conditions during the middle of the year at the Howick Group, were strong (15 - 25 knots) and predominantly from the south and south-east. Surveys of reefs that were located to the north of Ingram Island were always logistically difficult due to large (2 – 3 m) ocean swells. A safe return to base camp with a vessel loaded with turtles, was only possible when wind speed fell below 15 knots. While an attempt was made to collect as much information as possible from every reef surveyed and *E. imbricata* caught, prevailing weather conditions frequently hampered attempts to do so.

Results

Approximately 57% of survey effort focussed on Combe Reef (n = 81 survey days) (Table 3.0). With an area of ~ 0.4 km^2, Combe Reef was the largest and most accessible reef, from a base

camp established on nearby Ingram Island. This level of survey effort was reflected in *E. imbricata* capture success, with ~ 50% of all turtles being caught on Comber Reef.

Table 3.0. Reefs surveyed, reef size, location and number of days allocated to searching for *Eretmochelys imbricata*.

Reef Code	Reef Name	Area km^2	Location Lat Lon	Number of visits per reef.
14.051	South Warden	69.88	14^0 46' S. 144^0 46' E.	1
14.053	Un-named	7.76	14^0 18' S. 144^0 47' E.	6
14.054	Stapleton	2.28	14^0 20' S. 144^0 51' E.	6
14.055	Munro	13.29	14^0 19' S. 144^0 45' E.	8
14.056	Un-named	4.69	14^0 20' S. 144^0 57' E.	10
14.061	Switzer	14.26	14^0 21' S. 144^0 45' E.	8
14.062	Un-named	4.04	14^0 23' S. 144^0 58' E.	10
14.063	Combe	30.37	14^0 25' S. 144^0 58' E.	81
14.064	Ingram	6.09	14^0 25' S. 144^0 53' E.	34
14.066	Mid	10.99	14^0 27' S. 144^0 57' E.	34
14.072	Mageara	0.64	14^0 28' S. 144^0 57' E.	7
14.082	Crescent	7.18	14^0 26' S. 145^0 03' E.	2
14.087	Snake	11.18	14^0 28' S. 145^0 01' E.	10

Survey dates and durations

Eight annual surveys were conducted between 1997 and 2008 on reefs within the Howick Group. The mean number of days per survey was 17.8 d (n = 143, R = 1 - 33; SD = 9.9) (Table 3.1).

Table 3.1. Survey dates, durations, number of turtles caught and mean number of turtles caught per survey.

Start date	Finish date	Sample days	Total number of *Eretmochelys imbricata* caught during the survey	Mean number of turtles caught / day
25/07/1997	25/07/1997	1	74	74.0
19/08/1998	26/08/1998	8	109	13.6
22/07/1999	24/08/1999	33	175	5.3
07/07/2004	31/07/2004	24	78	3.2
20/07/2005	11/08/2005	22	105	4.4
26/06/2006	15/07/2006	19	104	5.5
29/06/2007	20/07/2007	21	95	4.5
22/05/2008	06/06/2008	15	73	4.9
Total		**143**	**813**	**14.4**

Eretmochelys imbricata *population capture-recapture rates within the Howick Group*

Over the eight sampling periods, between July 1997 and June 2008, a total of 813 captures were made of 665 individual *E. imbricata* on reefs in the Howick Group. The sample included two turtles that had originally been tagged while nesting Milman Island, approximately 420 km north and one turtle that had changed feeding areas (Table 3.2). Ninety seven turtles were recaptured once again over the course of the study, 21 turtles were recaptured twice (= 42 captures) and three turtles were caught three times (= 9 captures) following the original capture. After an initially low, but expected recapture rate during the first three years of the study, the ratio of recaptured to primary caught turtles remained relatively stable at ~ 28% per year for the last five years of the study (Table 3.3.)

Table 3.2. Number of *Eretmochelys imbricata* recaptured by year following primary tagging. Does not include data from turtles tagged on nesting beaches or the one turtle that changed feeding areas.

		Number of recaptured *E. imbricata* by year following primary tagging.								
		1997	1998	1999	2004	2005	2006	2007	2008	Total
Primary tagging year	1997		4	2	1	4	2	2	1	**16**
	1998			16	8	5	5	7	1	**42**
	1999				10	19	3	9	6	**47**
	2004					6	6	4	4	**20**
	2005						4	4	3	**11**
	2006							3	3	**6**
	2007								3	**3**
Total			**4**	**18**	**19**	**34**	**20**	**29**	**21**	**145**

Table 3.3. Summary of primary, recaptured and nesting area *Eretmochelys imbricata* caught during the eight year study.

Survey Year	No. of primary turtles caught	Feeding area recaptures	Nesting recaptures (Milman Island)	Recapture of a turtle from a different feeding area	Total turtles caught	Percent recapture
1997	73	-	1*	-	74	1.4
1998	105	4	-	-	109	3.7
1999	155	18	1*	1	175	11.4
2004	59	19	-	-	78	24.4
2005	71	34	-	-	105	32.4
2006	84	20	-	-	104	19.2
2007	66	29	-	-	95	30.5
2008	52	21	-	-	73	28.8
Total	**665**	**145**	**2**	**1**	**813**	

*Note. Turtles were originally tagged while nesting on Milman Island and then subsequently caught in the Howick Group in 1999.

Eretmochelys imbricata *capture rate by reef and year*

The greatest survey effort (81 d) was undertaken on Combe Reef and resulted in the highest overall capture of 354 turtles (Table 3.4). This was almost twice the total number of turtles captured on all other reefs combined (n = 262).

Table 3.4. The distribution of primary captured *Eretmochelys imbricata* by specific reefs within the Howick Group, over all years of the study.

		Year								
Reef Code	**Reef Name**	**1997**	**1998**	**1999**	**2004**	**2005**	**2006**	**2007**	**2008**	**Total**
14-051	Sth. Warden	-	-	-	-	-	-	-	7	7
14-053	Un-named	-	-	-	-	-	15	-	5	20
14-054	Stapleton	-	-	-	-	-	6	-	-	6
14-055	Munro	1	2	-	-	-	4	-	1	8
14-056	Un-named	-	6	16	-	-		17	4	43
14-061	Switzer	-	9	15	-	6	4	8	1	43
14-062	Un-named	-	3		-	-	-	-	7	10
14-063	Combe	68	69	64	48	48	21	19	17	354
14-064	Ingram	-	9	8	7	9	-	-	-	33
14-066	Mid	1	7	17	-	5	8	11	4	53
14-072	Mageara	3	-	2	-	-	-	-	-	5
14-082	Crescent	-	-	-	-	-	19	-	-	19
14-087	Snake	-	-	33	4	3	7	11	5	63
Grand Total		**73**	**105**	**155**	**59**	**71**	**84**	**66**	**52**	**665**

The reproductive status of primary caught Eretmochelys imbricata *in the Howick Group, determined by surgical laparoscopic examination of the gonads over all years*

From a total of 665 primary captures, I confirmed the gender and reproductive status of 649 turtles by surgical laparoscopic examination of their gonads (Table 3.5). Of this total, 564 turtles were found to be female and 85 were found to be male. The gender and reproductive status of 16 turtles were not confirmed by surgical laparoscopy (using the methodology detailed in Chapter 2) due to either the logistical difficulty involved in landing them at a suitable site to undertake the procedure or equipment failure.

Female turtle demographics

From a total of 564 female turtles examined by laparoscopy, 244 were adult females of which 219 (90.1%) were identified as having ovaries containing ovarian scars (*corpora albicantia* or *corpora lutea*), and were therefore deemed to have bred in a previous nesting season. Twenty five percent (n = 61; R = 8 – 35%; SD = 13%) of the total pool of mature females were shown to be in vitellogenisis and were preparing to breed during the next November to February nesting season. This equates to 7.6 adult females per season preparing to breed at the nesting season following the survey. The remaining 25 adult female turtles showed no signs of ovarian scars and were subsequently scored as female turtles that had reached maturity, but were yet to breed. Of the remaining 320 female *E. imbricata* caught, 221 (39.3%) were classified as belonging to a pubescent age-class and 99 (17.6%) were classified as juveniles.

Male turtle demographics

From a total of 649 turtles examined laparoscopically, 85 turtles were male. Twenty seven turtles were classified as adults, 49 turtles were pubescent and nine were juveniles. One male turtle matured from a pubescent to an adult age-class between its first capture in 1999 and subsequent recapture in 2007. Twenty five adult male *E. imbricata* caught over the duration of the study were found to be in spermatogenesis which represented 92% of the mature male population. Two mature male turtles displayed gonads that were sexually mature but they were not in breeding condition. One of these turtles was equivocal as to whether it was a very mature

sub-adult or in fact an adult, however given the size of the epididymis it was scored as a non-breeding adult. The other mature male turtle presented with a missing front flipper which would have severely impeded his ability to successfully copulate with a female and it is likely that his reproductive capacity was reduced. One adult male turtle that was recaptured after an approximate 10 year interval (1997 - 2007) was found to be in breeding condition at both captures.

Eretmochelys imbricata *sex and age class ratios found in the Howick Group*

The total number of adult (n = 271) and pubescent (n = 279) turtles that were captured on Howick Group reefs were similar. However approximately only half as many juvenile turtles were captured (n = 115) than adults and pubescent turtles. The pooled sample of 270 adult *E. imbricata* of known gender, caught within Howick Group reefs, was strongly biased to females (9.0:1 female / male) (Table 3.6). The female to male sex ratio between pubescent turtles was also strongly biased towards females at 4.7:1and found to be even higher at 10:1 for juveniles.

Table 3.5. The reproductive and age-class structure of all primary caught *Eretmochelys imbricata* found feeding over reefs in the Howick Group determined by surgical laparoscopy.

		Age Class				
		Adult				
Sex	**Year**	**Experienced**	**Not bred**	**Pubescent**	**Juvenile**	**Total**
Female	1997	20	7	27	2	56
	1998	50	5	22	3	80
	1999	53	12	61	9	135
	2004	14	1	37	3	55
	2005	20	-	21	25	66
	2006	23	-	18	23	64
	2007	27	1	16	16	60
	2008	12	-	19	15	46
Total		**219**	**25**	**221**	**99**	**564**
Proportion of the female population		43.3%		39.2%	17.5%	
Male	1997	4	-	13	-	17
	1998	12	1	11	1	25
	1999	5	1	14	-	20
	2004	1	-	-	1	2
	2005	1	-	2	2	5
	2006	1	-	4	2	7
	2007	1	-	2	3	6
	2008	-	-	3	-	3
Total		**25**	**2**	**49**	**9**	**85**
Proportion of the male population		31.8%		57.6%	10.6%	
Sub-total		**244**	**27**	**270**	**108**	**649**
Sex undetermined	1997	-	-	-	-	-
	1998	-	-	-	1	1
	1999	-	-	-	-	-
	2004	-	-	-	2	2
	2005	-	-	-	-	-
	2006	-	-	9	2	11
	2007	-	-	-	-	-
	2008	-	-	-	2	2
Total				**9**	**7**	**16**
Grand total		**244**	**27**	**279**	**115**	**665**

Table 3.6. The gender and age-class structure of *Eretmochelys imbricata* that were captured over reefs in the Howick Group between 1997 and 2008.

Reef Code	Reef name	Sex	Age-class			Total
			Adult	Pubescent	Juvenile	
14-051	Sth. Warden	F	-	6	-	6
		M	-	1	-	1
14-053	Un-named	F	8	3	3	14
		I	-	5	1	6
14-054	Stapleton	F	1	-	-	1
		M	1	-	-	1
		I	-	3	1	4
14-055	Munro	F	2	2	1	5
		I	-	1	-	1
14-056	Un-named	F	16	15	1	32
		M	1	4	-	5
14-061	Switzer	F	16	11	4	31
		M	3	-	-	3
14-062	Un-named	F	2	1	1	4
		M	-	1	-	1
		I	-	-	2	2
14-063	Combe	F	151	135	53	339
		M	21	34	8	63
		I	-	-	1	1
14-064	Ingram	F	8	4	4	16
		I	-	-	1	1
14-066	Mid	F	21	11	8	40
		M	-	2	1	3
		I	-	1	2	3
14-072	Mageara	F	-	3	-	3
		M	-	1	-	1
14 -082	Crescent	F	4	7	7	18
		M	-	1	-	1
14-087	Snake	F	15	22	16	53
		M	1	5	-	6
Grand Total			**271**	**279**	**115**	**665**

Morphometric data

Adult turtles

The mean curved carapace length (CCL) for adult female *E. imbricata* was 84.9 cm (n = 242; R = 74.5 - 97.7 cm; SD = 3.72 cm) and 82.5 cm (n = 17; R = 74.6 - 87.5 cm; SD = 3.2 cm) for males (Table 3.7).

Table 3.7. The pooled morphometric data obtained from all adult *Eretmochelys imbricata* caught on reefs in the Howick Group over eight annual surveys between 1997 and 2008.

Measurement (cm)	Mean (cm)	N	Range (cm)	SD (cm)
Female				
Curved carapace length	84.9	242	74.5 - 97.0	3.72
Curved carapace width	73.6	179	66.4 - 88.7	3.52
Head length	18.7	109	10.9 - 21.8	1.50
Head width	11.9	109	8.1 - 19.8	1.07
Plastron length	63.7	49	58.0 - 68.5	2.57
Tail length to plastron	16.4	191	10.3 - 22.1	1.86
Tail length to carapace	3.2	245	-1.2 - 8.4	2.58
Tail length to vent	4.6	168	3.2 - 7.1	0.72
Weight	64.2	261	43.0 - 88.0	8.58
Male				
Curved carapace length	82.5	17	74.6 - 87.5	3.17
Curved carapace width	70.8	11	67.4 - 75.5	2.65
Head length	18.8	9	17.0 - 20.3	1.01
Head width	10.2	9	8.6 - 11.4	0.9
Plastron length	61.0	7	56.7 - 63.8	2.60
Tail length to plastron	30.9	15	25.6 - 35.6	3.17
Tail length to carapace	19.7	15	14.7 - 23.5	2.41
Tail length to vent	6.8	15	5.5 - 9.0	0.96
Weight	53.6	16	45.5 - 61.0	5.11

Pubescent turtles

The mean CCL for pubescent female turtles was 80.5 cm (n = 223; R = 63.3 - 98.3 cm; SD = 5.03 cm) (Table 3.8). The mean CCL for pubescent male turtles was 78.2 cm (n = 35; R = 66.8 - 85.5 cm; SD = 4.30 cm). There was a significant difference between the tail length to carapace of pubescent males and females (MWU test; U = 2018, n_1 = 216, n_2 = 35, P < 0.001).

Table 3.8. The pooled morphometric data obtained from all pubescent *Eretmochelys imbricata* caught on reefs of the Howick Group over eight annual surveys between 1997 and 2008.

Measurement (cm)	**Mean (cm)**	**N**	**Range (cm)**	**SD (cm)**
Female				
Curved carapace length	80.5	223	63.3 - 98.3	5.03
Curved carapace width	71.3	137	59.5 -79.8	3.27
Head length	18.0	94	14.7 - 21.0	1.35
Head width	10.1	93	8.5 - 12.7	0.69
Plastron length	60.9	38	52.5 - 68.8	3.42
Tail length to plastron	13.6	160	7.1 - 21.6	2.26
Tail length to carapace	2.2	219	-2.4 - 7.1	2.09
Tail length to vent	4.3	161	2.5 - 6.7	0.76
Weight	52.3	208	20.0 - 73.0	9.49
Male				
Curved carapace length	78.2	35	66.8 - 85.5	4.30
Curved carapace width	70.8	11	67.4 -7 5.5	2.65
Head length	17.2	15	9.6 - 19.8	2.33
Head width	10.0	15	8.9 - 11.0	0.69
Plastron length	60.4	9	55.5 - 64.4	2.97
Tail length to plastron	21.6	26	11.4 - 34.9	6.77
Tail length to carapace	8.7	35	0.0 - 22.2	7.41
Tail length to vent	5.5	29	2.9 - 8.0	1.39
Weight	46.1	30	24.5 - 59.5	8.21

Juvenile turtles

The mean CCL for juvenile female *E. imbricata* was 68.9 cm (n = 102; R = 34.0 - 83.8 cm; SD = 8.8 cm) and 64.8 cm (n = 11; R = 33.4 - 76.1 cm; SD = 14.4 cm) for juvenile male *E. imbricata* (Table 3.9). There was no significant difference between the tail length to carapace of male and female juvenile turtles (MWU test; U = 534.5, n_1 = 99, n_2 = 11, P = 0.921).

Table 3.9. The pooled morphometric data obtained from all juvenile *Eretmochelys imbricata* caught on reefs of the Howick Group over eight annual surveys between 1997 and 2008.

Linear measurements (cm) Weights (kg)	**Mean**	**N**	**Range**	**SD**
Female				
Curved carapace length	68.9	102	34.0 - 83.8	8.80
Curved carapace width	62.8	87	29.8 - 73.6	6.83
Head length	16.4	49	12.5 - 18.9	1.61
Head width	8.8	50	4.4 - 10.7	1.06
Plastron length	49.1	1	N/A	N/A
Tail length to plastron	10.4	59	6.4 - 15.8	1.72
Tail length to carapace	0.7	99	-2.9 - 5.0	1.32
Tail length to vent	3.3	61	2.0 - 4.6	0.61
Weight	33.9	96	3.0 - 54.5	10.5
Males				
Curved carapace length	64.8	11	33.4 - 76.1	14.40
Curved carapace width	57.7	11	32.0 - 67.7	12.30
Head length	14.7	6	9.9 - 16.7	2.58
Head width	7.7	7	5.0 - 9.1	1.79
Plastron length	42.7	3	27.8 - 50.7	12.91
Tail length to plastron	10.6	5	7.7 - 12.5	2.05
Tail length to carapace	1.5	9	0.0 - 5.0	1.84
Tail length to vent	3.0	7	1.4 - 3.9	1.02
Weight	30.3	11	3.5 - 45.5	14.14

Comparison of the curved carapace lengths of Eretmochelys imbricata *by gender and age-class that were captured in the Howick Group*

Significant differences in CCL were apparent between sexes of pubescent and adult age-class *E. imbricata* (Table 3.10). However, no significant difference was found between sexes of juvenile *E. imbricata* (Table 3.10).

Table 3.10. MWU tests of curved carapace lengths by gender of adult, pubescent and juvenile *Eretmochelys imbricata*, obtained from all turtles captured and recaptured turtles in the Howick Group between 1997 and 2008.

	Adults		**Pubescent**		**Juvenile**	
	Female (cm)	Male (cm)	Female (cm)	Male (cm)	Female (cm)	Male (cm)
Mean	84.7	81.6	79.6	76.9	67.9	66.9
Variance	14.51	9.41	23.8	34.3	92.0	168.6
n	238	27	220	49	98	9
U	1643		3935		432	
P	<0.001		0.003		0.924	

Comparison between the curved carapace length of female Eretmochelys imbricata *on Combe Reef compared with a pooled sample of female turtles captured on other reefs*

Individual reefs within the Howick Group were found to support morphometrically similar *E. imbricata* of both sexes across all age-classes. No significant differences existed between the CCL measurements of female turtles of all age-classes captured on Combe Reef compared to turtles captured on other reefs in the Howick Group (Table 3.11).

Table 3.11. A MWU test comparison of CCL measurements between female turtles captured on Combe Reef with a pooled sample of all female turtles captured on other reefs in the Howick Group. Insufficient male turtles were captured on "other reefs" to include in the comparative analysis.

	Female curved carapace lengths (cm)					
	Adult		**Pubescent**		**Juvenile**	
	Combe reef	Other reefs	Combe reef	Other reefs	Combe reef	Other reefs
Mean	84.6	84.2	79.1	78.7	65.7	66.9
Variance	12.6	16.1	26.1	22.8	108.3	90.1
n	143	67	129	68	43	37
U	6635		9083		1506	
P	0.836		0.748		0.442	

Somatic features indicating gender and / or age-class of Eretmochelys imbricata

There were no significant differences in tail length to carapace (TLC) measurements between juvenile male and female *E. imbricata* (P=0.921). However a turtle could be classified as a "pubescent" male, if the tail extended from the posterior of the carapace by more than 8.4 cm, but was less than 14.7 cm. An *E. imbricata* could be classified as an "adult" male if the tail extended beyond the carapace by more than 14.7 cm.

Eretmochelys imbricata *fidelity to specific reefs*

All *E. imbricata* found foraging in the Howick Group showed remarkably strong fidelity to specific reefs, with no recorded movement of turtles between these reefs over the course of the study. A sub-adult female *E. imbricata* (tag number T49229), that was tagged during a 1990 survey of turtles found foraging on Clack Reef, some 60 km north-west of the Howick Group, was recaptured as an adult on Munro Reef in the Howick Group during 1999 and 2003 surveys. Given that this turtle had been recaptured twice over a four year period, indicates that it is likely to have permanently shifted feeding locations.

Eretmochelys imbricata were typically found foraging within a rocky reefal substrate, that supported growth of alga of the genus' *Gelidiella* and *Laurencia* sp., (see Chapter 6). These approximate 100 – 450 m wide strips of rubble substrate areas most frequently occurred at southern and eastern facing reef edges, rather than in the sandy northern, western or mid reef areas. Eighteen turtles, each with site specific locations recorded by GPS (± 50 m), were caught in successive years between 2006 and 2008. Turtles displayed strong fidelity to specific locations on reefs with the greatest distance between capture locations of an individual turtle of only 4.6 km (Table 3.12). It appears that adult turtles displayed a stronger site fixity than sub-adult turtles with the mean distance between recaptures of only 52 m (n = 9; R = 109 - 757 m) for all adults.

Table 3.12. Distance in metres between annual recaptures of *Eretmochelys imbricata* in the Howick Group.

	Adult (m)	**Pubescent (m)**	**Juvenile (m)**
Mean	527	3231	2969
Standard Deviation	233	2202	2016
Range	109 - 757	1261 - 6716	47 - 4626
N	9	5	4

Discussion

Detailed information describing aspects of a foraging *E. imbricata* population such as gender ratios, age-class structure, biometric data and reproductive status within the Great Barrier Reef or indeed, throughout the western Pacific has been generally lacking (Limpus and Miller 2000). I found as part of this study that reefs within the Howick Group of islands, in the Far Northern Section of the Great Barrier Reef, supported a relatively high density foraging population of *E. imbricata* in comparison with other east Australian feeding sites (Limpus and Miller 2000). I therefore selected the Howick Group to undertake an in-depth study to address the paucity of population biology data.

Eretmochelys imbricata *gender ratios within the Howick Group*

With an overall population made up of ~ 79% female turtles, the Howick Group cohort comprised the highest ratio of females to males than any other known foraging population of *E. imbricata* (Mrosovsky 1994, 1995; Marcovaldi *et al.,* 1997). This high female to male gender bias was displayed across all three age-classes, but seen most prominently within the juvenile turtles with a 10:1 ratio.

Limpus (1992b) found a 2.6:1 female bias within a southern GBR *E. imbricata* feeding aggregation, while Whiting (1997) reported an immature population of *E. imbricata* in the Northern Territory with a sex ratio of 3.8:1. A propensity towards female biased sex ratios have also been reported for other *E. imbricata* feeding assemblages such as: 2.7:1in the Dominican Republic (Leon and Diez, 1999), and 5.4:1 in the U.S. Virgin Islands (Geis *et al.*, 2003).

Assuming the "catchability" of male and female *E. imbricata* in a feeding area is similar, the most likely cause of gender bias, is due to a greater production of female hatchlings from natal beaches.

Cheloniid offspring gender is a phenotypic trait determined by incubation temperature (Bull *et al.*, 1982, Deeming and Ferguson 1989). While several factors may influence the thermal dynamics and therefore the gender output from a nesting rookery, including sand colour, vegetative shading and the amount of metabolic warming generated within the clutch, female hatchlings are typically produced at higher incubation temperatures (>28.5^{0}C), with middle temperatures (~ 28.5^{0}C) yielding both sexes and low temperatures (<28.5^{0}C) producing primarily males (Mrosovsky 1995, Yntema and Mrosovsky 1980).

While a high female bias is unreported within foraging *E. imbricata* populations elsewhere, or indeed for many other cheloniids, some studies have found high female sex ratios to exist. Mrosovsky and Provancha (1991) reported a 9:1 female:male *Caretta caretta* hatchling production, over multiple years, from rookeries in Florida, USA. These high female biases would not however appear to be the norm and may highlight concern for population stability as the world enters a period of probable climate change with associated increased incubation temperatures (Godley *et al*., 2002; Poloczanska *et al.*, 2009). Even a modest increase (~ 1°C) in incubation temperature may radically alter offspring sex ratios of species that rely on temperature dependant sex determination (TSD) (Janzen 1994). Climate change could exacerbate the already skewed sex ratios hatchling outputs for some cheloniids. Multiple generations comprising only females could eventually result in an inability for females to breed and successive annual cohorts of hatchlings would be lost, ultimately leading to localised extinctions.

This has clear consequences for the fate of *E. imbricata* found feeding within the Howick Group, as mixed stock analysis of the genetic composition, combined with flipper tag returns (see Chapter 5), has shown that the source population for this feeding aggregation is from natal beaches located through the Bismarck-Solomon Sea eco-region. While, for this population, males may simply be feeding elsewhere or a high female bias may be needed for population functionality, more work needs to occur in order to determine if anthropogenic impacts on natal beaches are resulting in higher incubation temperatures and artificially skewing gender ratios in feeding areas.

Eretmochelys imbricata *age-class structure*

A life history strategy that requires the production of a large number of hatchings with low survivorship probability in order to maintain a viable adult cohort, with commiserate high survivorship, is well known for marine turtle populations (Chaloupka and Limpus 2002). *Eretmochelys imbricata* are long lived, iteroparous and highly fecund with a female capable of laying many hundreds of eggs during a nesting season, which can occur at several yearly intervals upon reaching maturity (Dobbs *et al.,* 1999). Depending on hatching success rates, annual hatchling recruitment to the population from nesting rookeries in western Pacific should be high (Caldwell. 1969; Chung *et al.,* 2009; Limpus and Millar 2000). While hatchling loss can be high, survivorship is believed to increase as a turtle progresses though ontogenic phases to adulthood (Chaloupka and Limpus 1997).

A similar ratio of pubescent to adult *E. imbricata* within the Howick Group feeding population was not expected and differed from most other species of marine turtle (Mrosovsky *et al.*, 1984). Juvenile female turtles made up the smallest proportion of the female population (17.5%), and pubescent and adult turtles comprised an almost even ratio. Juvenile male turtles contributed the smallest proportion of the male cohort (10.6%), adults only made up approximately a third (31.8%), while pubescent males accounted for over one half of the male population (57.6%).

A possible explanation of this atypical age-class structure may lie in the possibility that sub-adult *E. imbricata* are undertaking a developmental migration (Meylan and Meylan 1998; Bolten *et al.*, 1998) from other feeding areas. Limpus (1992b); reported similar, albeit the opposite, skew in age-class structure within a sGBR feeding area. Sub-adult turtles, of both genders, formed the highest proportion of *E. imbricata* found in the Capricorn-Bunker Group of Islands, with adults making up only ~ 1.0% of the total population captured (Limpus 1992b). Whether these sub-adult turtles are making their way north to populate reefs in the nGBR as they mature is unknown.

Morphometrics

The considerable variation in the world wide morphometric parameters recorded for *E. imbricata* allows a distinction to be made between conspecifics (Witzell 1980). The biometric information obtained from adult female *E. imbricata*, found foraging in the Howick Group, indicated that they were morpholometrically more closely aligned with nesting populations using Solomon Island nesting beaches (Witzell 1980). This is a surprising result given the close proximity (~ 300 km.) to regionally high density *E. imbricata* nesting sites located in the nGBR and Torres Strait, rather than the ~ 700 to 1400 km they travel to reach rookeries located in Papua New Guinea and the Solomon Islands.

Studies by Dobbs *et al.*, (1999) have shown that the mean nesting CCL of *E. imbricata* on Milman Island (the index nesting beach for monitoring this regional cohort) is 81.6 cm (n = 1236; R = 63.5 - 91.9; SD = 3.67), some 2.3 cm smaller than the mean adult female size recorded in the Howick Group. However the mean CCL of 84.6 cm (n = 43; R = 60.0 - 91.5) reported for reproductively active females in the Solomon Islands by Witzell (1980) was very similar to the CCL (84.9 cm; n = 242; R = 74.5 - 97.0) reported for mature females in this study.

Additionally, the mean mass of *E. imbricata* nesting on Milman Island was reported to be 50.4 kg (n = 582; R = 32 – 72 kg) by Dobbs *et al.*, (1999). The mean mass of adult female *E. imbricata* residing in the Howick Group was 64.2 kg (n = 261; R = 43 – 88 kg), some 13.8 kg heavier than nesting females on the nGBR. Several reports (McKeown 1977; Vaughan 1981) of Solomon Island nesting females show mean masses between 66.3 - 57.8 kg, which are far more closely aligned with masses reported in the Howick Group feeding turtles.

Similarities between morphometric parameters of adult female *E. imbricata* residing in the Howick Group with females nesting at Bismarck-Solomon Sea rookeries corroborates evidence from tag recoveries and genetic analysis (Chapter 5). The molecular technique of sequencing a portion of the mitochondrial DNA (mtDNA) of nesting females has been a successful tool in identifying the genetically discrete composition of a feeding population (stocks) of most marine turtle species (Bowen 1996; Dethmers *et al.*, 2006).

Density of foraging Eretmochelys imbricata *found in the Howick Group*

Specific reef areas supported a greater density of *E. imbricata* feeding than other parts of the reef. The highest number of turtles observed, and subsequently caught, was over rocky-rubble crests that occurred on the south-east facing aspect of each reef. Reporting *E. imbricata* densities as a result of capture effort over an entire reef would therefore be misleading, as the great majority of reef flat does not provide suitable foraging habitat. The rubble crest area on Combe Reef (with an area of ~ 1400 ha) could conceivably be classified as a "high density" *E. imbricata* feeding area, with approximately 3.5 turtles per hectare caught over the duration of the study. The remaining area (~ 95%) of reef platform occurring on Combe reef (~ 28974 ha), was found to support a population density of turtles (3.34 turtles/km^2) that was similar to the number of immature conspecifics found foraging within the Capricorn-Bunker Group of reefs in the sGBR (Limpus 1992b).

Turtle foraging density data reported here is also likely to be a ~ 10 - 20% underestimate of the total number of *E. imbricata*, as it only reports turtles actually caught and not those that avoided capture. A minimum distance (~ 75 m) between the turtle and reef edge was required to be able to manoeuvre the vessel into a position that would allow a diver to catch the turtle. If the turtle was seen too close to the reef edge and therefore escape into deep water or if a diver[s] failed in their attempt to capture the animal, it was not included in the census.

Somatic features indicating the gender and / or age-class of Eretmochelys imbricata

Upon reaching maturity, *E. imbricata* display strong sexual dimorphism (van Dam and Diez 1998a). Mature Howick Group male *E. imbricata* frequently displayed a tail that extended posteriorly from the carapace (TLC) by up to three times that of a mature female. However, it was found that turtle size or CCL alone was not a sound metric for allocating an age-class or gender to a turtle. The maximum curved carapace lengths of both male (n = 2), and female (83.8 cm; n = 102) juvenile turtles were recorded exceeded the minimum CCL length of both mature males (74.6 cm) and female turtles (74.5 cm).

It was found that the most reliable algometric indicator of gender was the distance that the tail extended past the carapace. The largest TLC recorded by a mature female *E. imbricata* was 8.4 cm, therefore a turtle presenting with a tail of greater length was likely to be a male.

A significant difference ($p<0.05$) in male turtle tail length existed, when the pooled data of adult and pubescent age-classes were compared. However multiple pubescent males were caught during the study with TLC measurements of up to 22.2 cm, which was only 1.5 cm shorter than the maximum recorded for mature males, precluding differentiation between pubescent and adult status. Given that the minimum CCL of pubescent male and female turtles was recorded at 66.8 cm and 63.3 cm respectively, turtles captured with a CCL less than 63.0 cm were likely to be juvenile.

Foraging reef fidelity displayed by Eretmochelys imbricata *within the Howick Group*

Site fixity has long been described in foraging populations of other marine turtle species, such as *C. mydas* (Carr and Carr 1972; Fitzsimmons *et al.*, 1997b), *C. caretta*, (Limpus 1989), and *E. imbricata* in the Caribbean (Richardson *et al.*, 1989) and Philippines (Alcala 1980). However these are the first data to be presented on a foraging population in the nGBR. No interchange of foraging turtles between reefs at the Howick Group was recorded over the duration of the study. All recaptured turtles were found back on the reef where the were initially caught after intervals of between 1 - 9 years; indicating a strong adherence to a localised home range for extended periods.

In contrast to the suggestion of van Dam and Diez (1998b), this study found no evidence of researcher induced disruption of home range finding ability. The majority of *E. imbricata*, that underwent a laparoscopic surgical examination, were returned to the research base at Ingram Island for processing. Following the procedure, turtles were released into the ocean at Ingram Island. All recaptured turtles were subsequently found back at the reef upon which they were originally caught with return distances ranging from 2.5 - 16 km. This post-release homing ability of turtles to return to their original capture reef, and in some cases the actual capture site, provides further evidence of strong home range fidelity (Meylan *et al.*, 1990). While it is possible that turtles may have migrated to take up residence on reefs outside the Howick Group, evidence presented here, and from studies in the southern GBR, indicates otherwise.

Conclusion

This is the first study to describe the morphometric, age-class and gender structure of a feeding assemblage of *E. imbricata* in the northern Great Barrier Reef and has elucidated several key factors previously undescribed in this population. Biometric, genetic and tag return data all suggests that many *E. imbricata* found foraging on reefs in the Howick Group are likely to belong to an assemblage of turtles which have originated from natal beaches in the Solomon-

Bismarck Sea region, some 800 km distant. The study has also shown that the *E. imbricata* foraging population on reefs of the northern GBR has a female gender bias of a magnitude that is unseen in other feeding assemblages of cheloniid.

These two factors raise concern about the long-term conservation outlook for this cohort, given that these turtles are crossing geo-political boarders and leaving the relative protection of marine protected areas. However, with a high proportion of turtles tagged, this study site can now function as an index site from which to determine if trends in gender and age-class structures are continuing over temporal or spatial scales.

CHAPTER FOUR

HIGH SURVIVORSHIP OF AN ANNUALLY DECREASING AGGREGATION OF HAWKSBILL TURTLES, *ERETMOCHELYS IMBRICATA*, FOUND FORAGING IN THE NORTHERN GREAT BARRIER REEF

Chapter overview

This chapter presents findings on the survivorship, population size and trend of *Eretmochelys imbricata* found foraging over reefs of the Howick Group, in the Far Northern Section of the Great Barrier Reef Marine Park.

The chapter is a manuscript accepted for publication in the Journal: *Aquatic Conservation: Marine and Freshwater Ecosystems*. The work presented is my own, with intellectual and technical input from other collaborators.

Authors: Ian Bell, Lin Schwarzkopf and Carryn Manicom.

CHAPTER FIVE

MOLECULAR TECHNIQUES AND FLIPPER TAG RETURNS: POWERFUL METRICS FOR DETERMINING THE MIGRATION PATTERNS OF *ERETMOCHELYS IMBRICATA*

Chapter overview

This chapter presents findings on the genetic structure of *Eretmochelys imbricata* found foraging over reefs of the Howick Group, in the Far Northern Section of the Great Barrier Reef Marine Park. The chapter is presented as a manuscript for publication, listing the authors involved, although it has not yet been submitted. The work presented is my own, with intellectual and technical input from other collaborators.

Authors: Ian Bell, Dr Michael Jensen

Abstract

We used molecular techniques to assess the mitochondrial DNA(mtDNA) diversity within a cohort of foraging hawksbill turtles, *Eretmochelys imbricata* that were captured on thirteen reefs in the Far Northern Section of the Great Barrier Reef (nGBR), Queensland Australia. We then used a mixed stock analysis (MSA) approach to determine the proportion that each nesting population contributed to this feeding aggregation. The MSA estimated that the majority (87%; 95% CI = 78 - 95%) *E. imbricata* in the feeding area had originated from nesting beaches located in the Bismarck-Solomon Sea region, whereas only 11% (95% CI = 2 - 21%) had originated from rookeries within the nGBR (e.g., Milman Island) and possibly the Northern Territory. We then corroborated these findings through the use of flipper tags returns which identified 18 international reproductive migrations by *E. imbricata* between the Howick Group foraging area and rookeries within the Bismarck-Solomon Sea region. These 18 turtles make up 86% of all known migration recaptures from the Howick Group and ~ 7.4% of all mature female *E. imbricata* (n = 242) that were captured over the duration of the eight year study.

Introduction

Eretmochelys imbricata are listed internationally as a Critically Endangered species of cheloniid (IUCN 2003) and populations continue to decline in many areas of the south Pacific (Mortimer and Donnelly 2008). Major cause of this decline was, and in some countries still is, the take of animals to supply carapacial scutes or "tortoise shell / Bekko" for the Asian curio trade (Groombridge and Luxmoore 1989; Meylan and Donnelly 1999).

Eretmochelys imbricata, are known to nest in relatively large numbers (~ 700/yr) on specific islands and coral cays of the nGBR and throughout Torres Strait in north Queensland, Australia (Limpus *et al.*, 1983; Limpus and Miller 2000, Miller *et al.*, 1995, Dobbs *et al.*, 1999). Anecdotally it was thought that north Queensland nesting populations, such as those at Milman Island and through the Torres Strait, were likely to be the primary source of *E. imbricata* recruiting to feeding areas along the Great Barrier Reef. However, until 1997, no major *E. imbricata* feeding aggregation had been identified in the region. Following several vessel-based surveys to sample ~ 800 km of nGBR reefs, between latitudes 100 - 170 S., the 13 reefs comprising the Howick Group were found to support a regionally high-density *E. imbricata* foraging population (Limpus 2008).

Historically, the application of flipper tags was the only method available to determine and monitor demographic change, elucidate reproductive migration pathways or identify breeding areas (Balazs 1976; Limpus 1997). However, a combination of tag loss (van Dam and Diez 1999; Parmenter 1993a,b), inability to tag hatchlings (Bjorndal 1980) and low tag recovery rates (Balazs 1999; Witherington 1994) have hindered attempts to identify the natal regions that are supplying *Eretmochelys imbricata* to feeding aggregations. Now genetic markers combined with flipper tag returns, have provided a useful metric for identifying distinct natal regions, therefore breeding destinations of mature *E. imbricata* from feeding areas (Bowen *et al.*, 1992, Karl *et al.*, 1992).

The mtDNA is female inherited, passed only from mother to offspring, making it a useful tool for looking at differences between *E. imbricata* breeding populations. We now know that adult female *E. imbricata* are highly philopatric to their natal regions (Bass 1996). As a result of this natal homing behaviour, there is strong genetic similarity between female turtles nesting within the same region, resulting in genetic partitioning (of their mtDNA) between nesting regions that are generally separated by distances greater than 500 kilometres. The molecular technique of sequencing a portion of the mtDNA control region or "d-loop" of nesting females has been a successful tool in identifying genetically discrete nesting populations (stocks) of most marine turtle species (Bowen *et al.*, 1997, Laurent *et al.*, 1998, Roberts *et al.*, 2004). This genetic structuring provides a useful metric for defining the spatial extent of breeding populations.

By sequencing the mtDNA control region, we are able to identify specific haplotypes. This allows the identification of fixed or nearly fixed differences in haplotype frequencies between breeding stocks, thereby creating a characteristic genetic signature of each breeding population (Bowen 1995; Norman *et al.*, 1994). Knowing the nesting turtle haplotype diversity that exists within a feeding stock can be a useful tool for identifying a turtle's natal region (Broderick and Moritz 1998). The mtDNA structure of regional breeding populations has been defined for: the Solomon Islands, north Queensland, Northern Territory, Western Australia and Malaysia. All sequences were accessed through Genbank, an annotated collection of all publicly available DNA sequences. This effectively provided the necessary reference "library" in order to trace-back the nesting origin of the Howick Group *Eretmochelys imbricata* feeding aggregation.

Conservation management becomes complicated when feeding or breeding activities result in species crossing geo-political boundaries, leaving the relative protection of marine parks or passing through unregulated fishing areas (Laurent *et al.*, 1998). Having an understanding of population connectivity and the implications of migration between feeding and breeding locations is fundamental in developing effective conservation management strategies for such species (Bass

et al., 2007; Parmenter 1983). While the nGBR is known to host some of the last remaining, relatively high density nesting and feeding assemblages in the world, these too may be under threat from unsustainable take in neighbouring countries (Skewes 1990; Mortimer and Donnelly 2008).

The purpose of this paper is to: (i) describe the source and relative contributions of turtles from spatially distinct nesting regions of *Eretmochelys imbricata* within the Indo-Pacific to foraging assemblages in the Howick Group; and (ii) corroborate genetic work findings with multiple flipper tags returns from *E. imbricata*, that had migrated from the Howick Group to nesting sites in the western Pacific.

Methods

Study site description

The Howick Group are an uninhabited group of 13 coralline reefs that collectively cover an area of ~ 113 km^2 and lie within a 20 km radius of 14^0 25.29" S., 144^0 52.54" E., in the nGBR. The majority of reefs are classified as "inner shelf planar (or oval platform) reefs"; however several (un-named reefs: 14-063; 14-056; 14-062; and Crescent) are "crescentic" in shape (Hopley *et al.*, 2007). Sand/rubble reef-top platforms support growth of a diverse range of algal (Price and Scott 1992) and seagrass species (Coles *et al.*, 2000) with active coral growth restricted to the inter- and sub-tidal margins.

Survey timings and duration

Two sampling events were conducted during years 1997 - 2008, on reefs within the Howick Group. Surveys took place during the austral winter period (June - August) with the aim of maximising the potential of capturing the greatest number of *E. imbricata*. Given that the peak nesting period for western Pacific *E. imbricata* occurs during the austral summer (Dobbs *et al.*, 1999), it was believed that a mid-year sampling period would maximise the likelihood of

capturing pre- and post-migrating turtles, while minimising the chances of sampling turtles that may be migrating through the area.

Turtle capture, tagging and laparoscopy

Eretmochelys imbricata were captured using the "rodeo" capture technique (Limpus and Reed 1985). Following capture, turtles were double tagged on the trailing edge of the front left and right flippers if they were new to the study, or had their tag numbers recorded if they had been tagged in a previous survey. *Eretmochelys imbricata* were double-tagged with self-locking standard titanium tags (Stockbrands Company, Pty. Ltd., Perth, Western Australia). The tag's upper surface carried a unique alpha-numeric inscription and a postal address was stamped on the underside, to facilitate a return should it be found. Tags were applied immediately adjacent to the enlarged scale, closest to the body, on the trailing edge of both front flippers (Limpus 1992a). If a turtle already carried a tag[s], the condition was assessed and if more than 50% of the tag extended from the trailing edge of the front flipper, a new tag was applied. Each turtle was released with a minimum of two, securely attached, titanium tags. Tag and biometric data were stored in the Queensland Turtle Research Database (dBXL/dBASE III 3+, WordTech Systems, Inc. 1987). Standard surgical laparoscopic techniques, as described by Limpus and Reed (1985), were used to establish both gender and age-class of all *E. imbricata* captured. The current reproductive status of mature male (spermatogenesis) and female (vitellogenesis) turtles was determined; in addition to assessing the breeding history of females, which was evident by the presence (or absence) of ovarian scars.

Genetic sampling and DNA analyses

A tissue sample (0.5 g) was taken for genetic analysis from the trailing edge of one front flipper and placed in a vial containing 20% dimethyl sulfoxide (DMSO), 250 mM ethylenediaminetetraacetic acid (EDTA), and saturated with sodium chloride (NaCl). A salting-out procedure, as described by FitzSimmons *et al.*, (1995), was used to extract DNA. Samples were then checked for DNA quality and quantity by electrophoresis on a 1.2% agarose gel. DNA was replicated by polymerase chain reaction (PCR) techniques using the primers LTEi9 and H950, (Abreu-Grobois *et al.*, 2006) to amplify ~ 770 base pairs (bp) of the mtDNA control

region. The PCR protocol was: 94°C for 5 mins, followed by 35 cycles at 94°C for 1 min, 52°C for 30 sec and 72°C for 30 min with a final extension at 72°C for 5 min. PCR products were again analysed for quality and quantity by gel electrophoresis and successfully amplified samples were purified using polyethylene glycol (PEG) prior to sequencing. To reduce the likelihood of encountering orphan haplotypes through sequencing errors, PCR product was sequenced in both forward and reverse directions and only sequences that showed multiple base-pair differences from known haplotypes were accepted as being orphan haplotypes.

Sequencing was conducted by Macrogen Inc (Korea) and results compiled using Geneious Pro (V5.1.6) software. Sequences were aligned using Clustal W (Larkin *et al.*, 2007), implemented within Geneious. Haplotypes were identified by running a search against known *E. imbricata* haplotypes from the Indo-Pacific region in Genbank (www.ncbi.nlm.nih.gov), an annotated collection of all publicly available DNA sequences. Unknown haplotypes were identified by running a BLAST search in Genbank and if still unidentified, they were classified as new haplotypes. New haplotype naming followed a standardized nomenclature for Indo-Pacific *E. imbricata* using the prefix "EIIP"-followed by the next sequential number.

Statistical analysis

Program "BAYES" was used to estimate the relative contribution of the five source populations to the feeding aggregation (described by Pella and Masuda 2001). This program is based on a Bayesian model and outputs a Marcov Chain Monte Carlo (MCMC) sample of the stock proportions. Analysis was conducted for five different chains, one for each baseline stock, using different starting points for each chain. The Gelman-Rubin diagnostic was used to verify convergence of the chains. Convergence was assumed when the shrink factor was less than 1.2 (Pella and Masuda 2001). Chains were run for 20,000 steps discarding the first 10,000 steps as burn-in. Mixed stock composition was estimated from the mean of all five chains after 50,000 steps in total and the 95% credibility interval computed. The program "CHIRXC" (Zaykin and Pudovkin 1993) was used to apply a randomised chi-square test to detect significant shifts in haplotype frequencies between the two sampling years and age-classes.

Results

Dermal tissue samples were obtained from 91 *Eretmochelys imbricata* of both sexes and across all age-classes from 2007 - 2008. All turtles were captured in water depth of 0.5 - 5.0 m over 13 reef flats. The gender, age-class and reproductive history (if any) of all turtles was successfully confirmed by laparoscopic gonad examination for all but three turtles. From the 91 tissue samples collected, 38 were from adult *E. imbricata* (37 females and one male), 27 were from sub-adult turtles (22 females, four males and one unknown sex), and 26 juvenile turtles (23 females, one male and two turtles of undetermined gender).

Table 5.1. Identification of the *Eretmochelys imbricata* haplotypes, identified from samples sourced from turtles at 5 nesting rookeries in the western Pacific, southeast Asia and the frequency that they, and orphan haplotypes, were found at in turtles foraging within the Howick Group.

Location	EIP—1	EIP--2	EIP--3	EIP--4	EIP--5	EIP--6	EIP--7	EIP--8	EIP--9	EIP-23	EIP-24	EIP-26	EIP-28	EIP-29	EIP-31	EIP-33	EIP-34	EIP-35	EIP-36	EIP-37	EIP-38	EIP-43	EIP-45	EIP-46	EIP-47	EIP-48	EIP-49	EIP-5-	EIP-51	EIP-52	EIP-53	EIP-54	TOTAL
Solomon Islands	-	-	17	-	-	-	-	-	-	2	1	-	-	-	-	17	3	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	41
Milman Is./ N.E. Australia	-	1	-	2	-	-	5	37	37	-	-	2	-	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	89
W. Australia	-	-	-	-	-	-	-	37	-	-	-	-	3	-	-	-	-	-	-	3	3	-	-	-	-	-	-	-	-	-	-	-	46
Turtle Is., Malaysia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	7	10	1	1	1	-	-	25
Peninsula Malaysia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	1	23
Howick Group	**2**	**-**	**11**	**3**	**2**	**2**	**1**	**6**	**1**	**-**	**-**	**-**	**-**	**-**	**-**	**56**	**2**	**2**	**1**	**-**	**-**	**-**	**1**	**1**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**91**

Note: shaded numbers indicate unknown (orphan) haplotypes.

Haplotype diversity

All tissue samples were successfully PCR-amplified and sequenced. Fourteen separate mtDNA control region haplotypes were found: seven that had been previously identified from Indo-Pacific rookeries; and seven unknown (orphan) haplotypes: EIIP-01, EIIP-05, EIIP-06, EIIP-35, EIIP-36, EIIP-45, EIIP-46. These were only found in low frequency, comprising 12.1% of the total sample (Table 1).

Mixed stock analysis

Given that there was a lack of nesting density data from most of the Pacific rookeries analysed by Broderick (1994; 1996), we had little support for using weighted prior probabilities (e.g., by giving a higher probability to larger breeding populations) for the Bayesian MSA. Thus, the analysis was conducted using uniform priors only, making each of the five source rookeries an equally likely contributor. The MSA estimated that most (87%; 95% CI = 78 - 95%) feeding *E. imbricata* originated from nesting beaches in the Bismarck-Solomon Sea region, whereas only 11% (95% CI = 2 - 21%) of *E. imbricata* on the feeding ground originated from rookeries within the nGBR (e.g., Milman Island) and possibly the Northern Territory (Table 5.2).

Table 5.2. Estimates of the percent that each origin rookery contributed to *Eretmochelys imbricata* haplotype frequency found within the Howick Group, based on Bayesian estimations using 5 major source rookeries characterised for a 780 bp sequence as a baseline. The posterior probability estimates, median and the 95% confidence intervals are shown for estimates using uniform weighted priors.

Source rookery	Mean%	SD%	2.5%	Median%	97.5%	MCMC Sample
Solomon Islands	86.90	4.50	77.54	87.09	95.35	50000
Milman Is./ N.E. Australia	11.20	4.79	2.12	11.10	20.96	50000
W. Australia	1.40	2.31	0.00	0.26	8.28	50000
Turtle Is., Malaysia	0.25	0.55	0.00	0.03	1.93	50000
Peninsula Malaysia	0.25	0.56	0.00	0.03	1.87	50000

Effect of year and age-class on haplotype frequency

There was no evidence of significant temporal variation in the haplotype frequencies of *E. imbricata* sampled between years 2007 (n = 33) and 2008 (n = 58) (χ^2 = 17.49, P = 0.11), nor were there significant differences between age-classes: adults (n = 38) versus sub-adults (n = 27) (χ^2 = 7.59, P = 0.916), adults versus juveniles (n = 26) (χ^2 = 13.41, P = 0.472), and sub adults versus juveniles (χ^2 = 11.94, P = 0.418). Due to the highly female biased sex ratio no test was made to determine the effects of gender on haplotype frequency.

International tag recoveries

The return of flipper tags has identified 18 international reproductive migrations by *E. imbricata* between the Howick Group foraging area and nesting rookeries within the Bismarck-Solomon Sea region (Figure 1). These 18 turtles make up 86% of all known migration recaptures from the Howick Group and ~ 7.4% of all mature female *E. imbricata* (n = 242) that were captured over the duration of the eight year study. The mean, one way migration distance between Howick Group foraging area and nesting areas in the Bismarck-Solomon Sea was 1150 km, (n = 18; R = 628 - 1536 km, SD = 319.4 km). The time interval between original capture at the Howick Group and subsequent recapture at a breeding area ranged between 1 - 8 years ($\bar{x}$ = 4.5, SD = 2.1, n = 18).

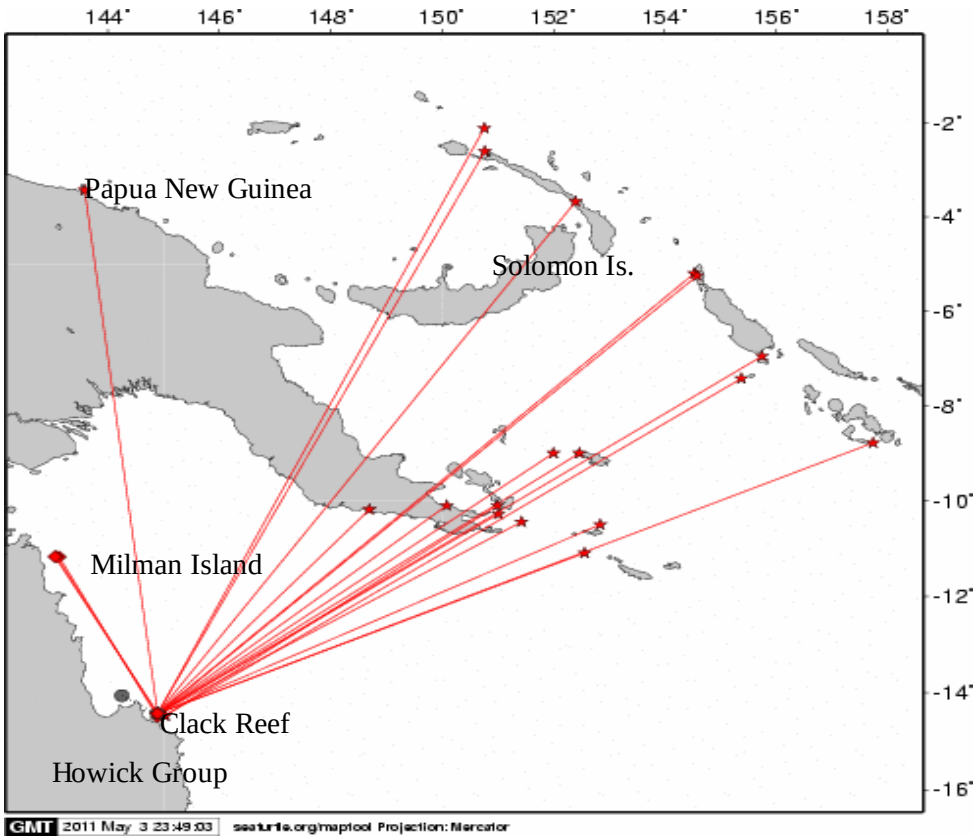

Figure 5.0. Within country and international tag recoveries from *Eremochelys imbricata* that were tagged in the Howick Group and were captured after undertaking breeding migtrations or having changed a foraging reef.

Regional (within country) tag recoveries

Two *E. imbricata* (T55332, T55372), that were originally tagged while nesting at Milman Island, located approximately 420 km to the north, were recaptured foraging on Combe Reef in the Howick Group (Figure 1). One turtle (K5637), tagged while nesting on Crocodile Cay, a sand island adjacent to Milman Island, was recaptured on Mid Reef, which also lies within the Howick Group. These three turtles make up ~ 14% of all reproductive migration recaptures.

Discussion

The use of a Bayesian MSA to determine the source of turtles found within foraging areas has indicated that the majority of *E. imbricata* recruiting to the Howick group were likely to have originated from rookeries located in neighbouring countries (87%). These findings were supported by the return of flipper tags from 18 turtles (86%) that had completed reproductive

migrations to nesting sites within the Bismarck-Solomon Sea region, which were between 800 - 1000 km distant from the Howick Group.

While *E. imbricata* are widely accepted as reproductive migrants of various distances between foraging and nesting sites (Bell *et al.*, 1998; Miller *et al.*, 1995; van Dam *et al.*, 2007) it was thought that a relatively large proportion of the feeding cohort was likely to have originated from regional nesting rookeries. A finding that the majority (>80%) of *E. imbricata* had recruited from the Bismarck-Solomon Sea region was unexpected. It is not immediately obvious why this apparently high proportion of long distance recruitment is occurring and warrants further investigation.

One possible explanation may lie in the preliminary work described by Fabrice and Lagerloef (2002), on sea surface currents off the east coast of Australia. An off-shoot of the South East Equatorial current, the Northern Vanuatu Jet, streams east to west and is conducive for ferrying hatchlings westward towards the northern Great Barrier Reef from nesting sites in the eastern Bismarck-Solomon Sea region. Alternatively, the relatively large number of *E. imbricata* hatchlings emanating from high-density nesting rookeries in the nGBR, such as Milman Island, and those in Torres Strait, may be carried by the North Queensland Current (NQC) to the New Guinea Coastal Current (NGCC) finally taking up residence in coastal waters of the Torres Strait or Bismarck-Solomon Sea region (Brassington *et al.*, 2007).

Temporal change in haplotype frequency

Previous studies have shown that the haplotype frequencies of *Eretmochelys imbricata* foraging aggregations varied among years, especially within the cohort of turtles recruiting to feeding areas (Bowen *et al.*, 2007; Bass 1999; Bjorndal and Bolton 2008; Velez-Zuazo *et al.*, 2008). However no significant between yearly difference in haplotype ratios, within the Howick Group feeding aggregation, was apparent. However this may be an artefact of the short two-year

sampling period used in this study. Nonetheless, an understanding of how the genetic structure within a feeding aggregation of marine turtles may shift temporally is an important metric for monitoring impact[s] or change, either negative or positive, that may be occurring within breeding cohorts (Bowen and Bass 1997, Davenport 1997). A recent study of foraging green turtles from the Howick Group shows large differences in stock origin between juvenile and adult turtles that could be attributed to temporal changes in the reproductive output of the main breeding stock (Jensen 2010). This highlights benefits of long term monitoring at the feeding ground to detect if changes in haplotype frequencies are occurring as a result of reduced (or increased) output from source populations (Bass *et al*., 2004). If for example, the unsustainable take of adult *E. imbricata* and their eggs continues at current levels, at nesting sites within the Bismarck–Solomon Sea region (Leary and Laumani 1989), then it is likely that we will see a shift to a higher proportion of haplotypes from nGBR nesting sources appearing within the Howick Group foraging cohort in the future (e.g., EIIP-08 and EIIP-09).

The ratio of flipper tag returns, from natal regions in the Bismarck-Solomon Sea (~ 86%) and the nGBR (~ 11%), has corroborated the results of origin of the genetic stock contributions obtained from MSA of the Howick Group feeding aggregation. Turtle fate data that accompanied the 18 Howick Group tag returns from the Bismarck-Solomon Sea, all reported that the turtles were attempting to nest. Two turtles, that were tagged while nesting on Milman or adjacent islands in the nGBR, were captured upon return to Howick Group foraging areas.

Implications for conservation

Based on information supplied with the flipper tag returns, it is known that all 18 Howick Group *Eretmochelys imbricata* were killed post-migration for consumption or scute collection, by indigenous fishers, within neighbouring countries of the Bismarck-Solomon Sea. While comprehensive conservation covenants exist within the Great Barrier Reef Marine Park, via a

multi-use conservation zoning approach (Dobbs *et al.*, 2007), few strategies are in place for protecting marine turtle species that cross geo-political boundaries (Hamann *et al.*, 2010; Vaughn 1981). Ineffectual or a complete lack of conservation strategies at turtle nesting rookeries, that are subject to an unsustainable take of both nesting turtles and/or their eggs, is likely to have major implications for migratory species survival within protected areas (Leary and Laumani 1989; Skewes 1990).

An understanding of how the genetic structure within a feeding aggregation of marine turtles may shift temporally is an important metric for monitoring impact[s] or change, either negative or positive, that may be occurring within breeding cohorts (Bowen and Bass 1997). This study highlights the importance of identifying the genetic composition of feeding and nesting assemblages to be able to determine the source populations that are supplying recruits for feeding regions (Bass *et. al.*, 2007; Bowen *et al.*, 1996). This knowledge will ultimately allow for the development of conservation management strategies to protect *E. imbricata* throughout all life-history stages.

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CHAPTER SIX

ALGIVORY IN HAWKSBILL TURTLES: *ERETMOCHELYS IMBRICATA* PREY SELECTION WITHIN A NORTHERN GREAT BARRIER REEF FORAGING AREA.

Chapter overview

This chapter presents my findings on the diet of *Eretmochelys imbricata* found foraging over reefs of the Howick Group, in the Far Northern Section of the Great Barrier Reef Marine Park. It is presented as the manuscript that has been published in the Journal: *Marine Ecology*.

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Running heading: Algivory in hawksbill turtles

Abstract

This paper describes the prey selection of hawksbill turtles, *Eretmochelys imbricata*, using reefs of the Far Northern Section of the Great Barrier Reef Marine Park (nGBR) during 2006 and 2007. A total of 467 gastric lavage and 71 buccal cavity ingesta items were collected from 120 individual *E. imbricata*, comprising adult female and immature turtles of both sexes. Nineteen *E. imbricata*, that were captured in 2006 were recaptured and sampled again in 2007. Within the totalled pooled buccal and lavage sample (n = 538), the occurrence of prey items was dominated (72.7%) by only three algal taxonomic divisions. Rhodophyta (red alga; 53.7%; n = 289); Chlorophyta (green alga; 11.0%; n = 59) and algae from the division of Phaeophyceae (brown alga; 8.0%; n = 43). The remaining total (buccal and lavage) ingesta sample comprised sponges (10.4% n = 56), soft corals and a wide variety of possibly nutritionally important invertebrate species, (12.6% n = 68) and a small percentage (5.4% n = 22) of inorganic material.

Generally *E. imbricata* are considered to be primarily a sponge feeding specialist and secondarily an omnivorous species within coral reef habitats and, in various parts of the world, this is the case. However, this study has shown that *E. imbricata*, found foraging on reefs of the nGBR, are primarily algivorous and secondarily omnivorous. A feeding strategy that relies on a predominantly algal diet may infer important benefits to the species if the impacts of climate change and ocean acidification inhibit coral growth while promoting algal density and distribution within the Great Barrier Reef ecosystem.

Key words

Eretmochelys imbricata, diet, feeding, marine turtle, Great Barrier Reef

Introduction

For most animals, the single most important factor to either promote or limit growth rate and reproductive periodicity is the availability of nitrogenous food (White 1978). This holds true for marine turtles, whose life history strategy is one of high fecundity but low survivorship of immature age-classes. It makes sense therefore that immature turtles grow rapidly, but this relies on access to high quality forage. *Eretmochelys imbricata* are the most likely species of marine turtle to be associated with coral reef habitat, with their dietary requirements being supplied by these ecosystems (Meylan 1988, Leon & Bjorndal 2002)

Post-hatchling *E. imbricata*, produced from rookeries throughout northern Australia and the Bismarck-Solomon Sea region, are likely to spend time drifting in the western Coral Sea before recruiting to foraging areas along the Great Barrier Reef (GBR). Post-hatchling feeding habits are not well known, although a few diet descriptions suggest an omnivorous existence while in the pelagic environment, with feeding occurring within marine debris drift lines that form at intersections of surface currents (Bjorndal *et al*., 1994; Mayor *et al*., 1998; Meylan 1988).

Sargassum sp. and floating debris such as Styrofoam, tar droplets, and plastic fragments, which also occur in these convergence zones, have been reported in the stomachs of post-hatchling *E. imbricata* that strand in Texas (Plotkin & Amos 1990; Almendor & Avila 1994).

Juvenile turtles recruit to neritic habitats, such as those of the Howick Group at approximately 40 cm curved carapace length (min = 33.5 cm CCL), after spending several years (the actual length of time is unknown, but thought to be between 1 – 10 y) at sea (Bolten 2003). Upon taking up residence in these inshore habitats, *E. imbricata* mature through puberty to adulthood, and at this point in their life cycle have historically been considered to be primarily spongivorous (Meylan 1985a). *Eretmochelys imbricata* may also shift habitat types to meet their changing dietary requirements during ontogeny in order to maximize growth rates, minimize mortality risk or to minimize the ratio of mortality risk to growth rate (Werner & Gilliam 1984; Dahlgren & Eggleston 2000). While little is known of the foraging ecology of mature turtles in the western Pacific, the dietary descriptions of *E. imbricata* from the Caribbean region, have reported that sponges were the turtles' predominant food item (Hill 1998), and that spongivory for the species was likely to be a worldwide feeding habit (Meylan & Whiting 2008).

A contemporary baseline understanding of species' dietary breadth and therefore niche utilisation within the Great Barrier Reef, is important for allowing predictions to be made on how populations may respond to, or cope with the ramifications of a changing climate (Holt 1990). For example, an increase in mean sea level combined with an increase in oceanic acidification due to carbon dioxide uptake, may have profound, albeit unknown implications for global coral reef diversity (Hoegh-Guldberg *et al*., 2007). These data contribute to knowledge on the current habitat requirements to sustain *E. imbricata* populations within the nGBR and allow for the development of more targeted conservation strategies that will allow the identification and protection of critical reefal areas, if the

predicted climate-change induced alteration to foraging habitat eventuates (Hoegh-Guldberg *et al*., 2007).

This study was conducted over 12 reefs that make up the "Howick Group" in the Far Northern section of the GBR Marine Park (nGBR). A prior survey of 56 inshore reefs between the Torres Strait (latitude 12° 15" E.) and Cairns (16° 51"S.), identified a large regionally restricted *E. imbricata* foraging population using the inter-tidal rubble flats of the Howick Group. This study provides the first description of the range of ingesta items found in the buccal cavity and from gastric lavage sampling of *E. imbricata* found foraging at Howick Group reefs.

Methods

Three purpose-built marine turtle capture vessels were used to search Howick Group reefs for foraging *E. imbricata*. Daily surveys were undertaken over an approximately 5 week period during the austral winters (June - Aug) of 2006 and 2007. Field work was undertaken during this time to maximise the likelihood of capturing mature turtles that had returned from, or had yet to depart on breeding migrations.

Survey area

This study was undertaken on 12 reefs that form part of the Howick Group. Ingram Island (14° 25.29" S.; 144° 52.54" E) is proximate to the study area centre and was selected as a base for undertaking surveys (Figure 1). Geo-physically this region of the Great Barrier Reef is characterised by an almost continuous line of outer ribbon reefs that enclose a relatively narrow (<50 km wide) shallow continental shelf; with the neritic zone rarely exceeding the 40 m isobath (Flood & Orme 1977). The line of ribbon reefs shelters the area from oceanic swells emanating from the South Pacific Ocean. The majority of reefs within the Howick Group are classified as "inner shelf planar (or platform) reefs", however several are "crescentic" in form. Most reefs have

large, sand-covered reef platforms with active coral growth restricted to their margins. Most reefs are oriented in a southeast - northwest direction and have a well developed rubble crest of up to 200 m wide on the high-energy, south-east facing end of the reef platform. Many reefs support a sand cay formation on the northern, sheltered end of the reef flat, which range in height from 1.0 - 3.5 m above highest astronomical tide. For a more detailed description of this section of the GBR see Orme and Flood (1980).

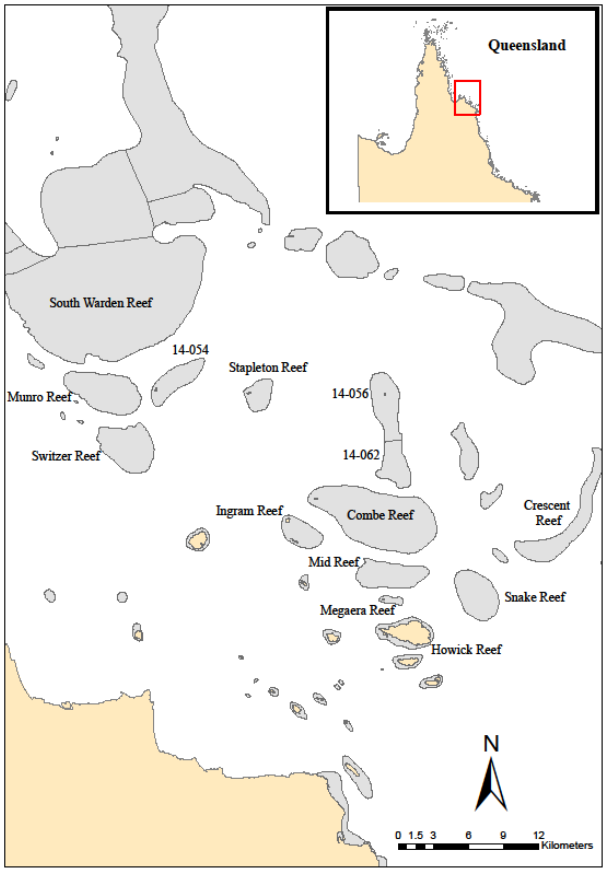

Figure 6.0. The location of the Howick Group of reefs in the Northern Section of the Great Barrier Reef Marine Park, in north Queensland, Australia.

Tidal amplitudes within the Howick Group can fluctuate greatly; with some high tides failing to reach a level that allow turtles access to the reef flat, whereas at other times turtles can remain on the reef flat during low tide periods (Anon 1997 - 2008). Typically, however, reef flat access was

only possible for approximately six of every 12 hours; i.e. three hours before and after the highest point in the tide.

Turtle capture, tagging and measurements

Eretmochelys imbricata were captured over shallow (<6 m) clear water reef flats using a "turtle rodeo" capture technique described by Limpus & Reed (1985). Briefly, this method involved using a small outboard motor powered aluminium dinghy to search for turtles over reef flats, when tidal depth allowed. If spotted, turtles were pursued until a "catcher" was able to dive from the vessel in an attempt to restrain the animal. Once the turtle was under catcher control, the vessel would return to haul both the catcher and turtle on-board. Captured turtles were lifted on board the vessel and two uniquely coded titanium tags were applied to the trailing edge of each front flipper as close to the body as possible and maximum curved carapace length measurements were taken (after Limpus & Reed 1985).

Ingesta sample collection

Turtles were only caught on reef flats when sufficient tide height allowed vessel access, and for the majority of tides, reef flats were only accessible for several hours one either side of the high tide period. Therefore samples collected from the buccal cavity were taken to be representative of the most recent items the turtle had consumed. Gastric lavage sampling of stomach contents provided ingesta items that are likely to have been consumed sometime during the ~ 12 hour period when the reef flat was too shallow for turtles to access.

Buccal cavity sample collection

Once in the vessel captured turtles were manoeuvred into a vertical position as soon as possible, so as to be resting on their post-vertebral scutes with the head held in an upright position. A veterinary mouth gag was then inserted between the upper and lower rhamphotheci, to prise apart and maintain the jaws in an open position. The buccal cavity was then visually examined for the presence of prey

items, which, if found, were removed by forceps (Figure 2). Following collection, samples were placed in 50 ml plastic specimen containers containing a solution of 4% sea-water-buffered formalin.

Figure 6.1. Research assistant fitting a veterinary gag between the jaws of a recently caught *Eretmochelys imbricata* prior to make a search of the buccal cavity for ingesta items.

Gastric lavage sample collection methodology

Gastric lavage sampling was undertaken using techniques described by Balazs (1980); Forbes & Limpus (1993); Legler (1977). The only modification I made to these techniques was the use of a finer (500 µm) mesh net to collect discharged ingesta (Figure 3).

On several occasions the successful introduction of the lavage tube into the stomach was not possible. This seemed to occur if the gastro-oesophagus sphincter was restricted or orientated at an acute angle. The procedure was abandoned when it seemed likely that entry to the stomach was unsuccessful, and further forceful tube insertion may cause undue stress or injury to the turtle. Following collection, samples were placed in 50 ml plastic specimen vials containing 4% sea-water buffered formalin.

Figure 6.2. A research assistant inserting a PVC tube into the oesophagus of an *Eretmochelys imbricata*, in order to commence a gastric lavage.

Ingesta item identification

A dissection microscope was used to sort and describe prey items to the lowest possible taxonomic level. Algal samples were identified to genus or species level using reference material, and dichotomous keys from the on-line Algaebase (Guiry 2008) and descriptions by Cribb (1996). Sponge identification was aided by the guide produced by Hooper (2003).

Laparoscopy

Standard surgical laparoscopic techniques, as described by Limpus & Reed (1985), were used to determine both sex and maturity status of all *E. imbricata* when possible.

Data analysis

Data analysis were undertaken to detect similarities or differences in the percentage of the total occurrence of prey species, within the gut or buccal cavities of turtles using different reefs, due to sex, maturity status or over successive years. Because it was not possible to obtain rigorous volumetric quantities of prey species samples from *E. imbricata* under field conditions a non-Metric multi-Dimensional Scaling (nMDS) approach (Clarke & Green, 1988; Clarke, 1990) within the

software package PAST (Hammer *et al*., 2001) was used to determine if variables such as: reef, year, maturity status or sex influenced ingesta item occurrence. A Bray-Curtis similarity coefficient was used as a meaningful and robust similarity measure within both the nMDS and ANOSIM tests (Clarke 1993). A nMDS distance matrix was generated and the results displayed as a 2D scatter plot to detect if clustering or overlap in the presence of prey species existed. Data were then fitted with a 95% confidence ellipses to detect if clustering and / or outliers occurred among animals.

A one-way-crossed Analysis of Similarity test (ANOSIM) (Clarke 1993), was used to test for significant differences in prey item presence between: sex, maturity status, gastric lavage and buccal cavity samples, Combe and "other" reefs, and between 2006 and 2007. An ANOSIM is a non-parametric, modified version of the Mantel Test based on a standardized rank correlation between two distance matrices (Anderson 2001). All ANOSIM tests involved 10,000 simulations and were performed using the software package PAST (Hammer *et al*., 2001). To mitigate the likelihood of pseudo-replication of ingesta items, only oesophageal lavage and buccal cavity data, that had been collected from different turtles within years, or the same turtle between years, were used in analyses. Statistical significance was accepted at $P<0.05$.

All ingesta items

A data set that included all prey items found in *E. imbricata* were analysed using a nMDS ordination approach and an ANOSIM test for similarities or significant difference prey items were selected by turtles according to sex, maturity status, gastric lavage and buccal cavity samples, or turtles resident on Combe and "other" reefs and the same turtle captured in 2006 and 2007.

Major ingesta items

A subset, comprising 14 of the most abundant prey items found, was created from the pooled buccal cavity and gastric lavage samples. This subset of prey species excluded inorganic material (sand, rubble), items that were likely to be epibionts of the target species or items that contributed less than

the mean pooled number of ingesta item types found within all turtles ($\bar{x}$ = 9; SD = 15.2; n = 61). Again a nMDS ordination approach, combined with ANOSIM tests, were used to detect if similarities or significant differences existed between turtle prey selection by sex, maturity status, gastric lavage and buccal cavity samples, Combe and "other" reefs and between sampling years (2006 - 2007).

Results

A total of 467 gastric lavage and 71 buccal cavity ingesta samples were collected from 120 individual *E. imbricata*, comprising adult and immature females and immature males, captured while foraging over Howick Group reefs (Table 6.1). Turtles were predominantly found foraging within the 70 - 200 m wide coral rubble substrate occurring at the south-eastern end of reef flats. Nineteen individual turtles were sampled in both 2006 and 2007. While an attempt was made to capture all turtles seen, no mature male *E. imbricata* were captured over the course of the diet study.

Table 6.1. The number of different prey types collected from *Eretmochelys imbricata*, according to sex, maturity status, capture reef in the Howick Group over both years of sampling. A = adult; SP = sub-adult pubescent; J = juvenile turtles; ? = unknown sex.

	Number of gastric lavage samples collected							**Number of buccal cavity samples collected**					
	Female			Male				Female			Male	?	
Reef	A	SP	J	A	SP	J	**Total**	A	SP	J	J	SP	**Total**
14.053	-	-	-	-	-	-	**-**	2	-	-	-	4	**6**
14.069	8	-	-	-	-	-	**8**	-	-	-	-	-	
14-056	29	64	5	-	8	-	**106**	3	-	-	-	-	**3**
Combe	52	56	65	-	9	5	**187**	10	23	8	2	-	**43**
Crescent	-	-		-	-	-	**-**	1	-	-	-	-	**1**
Mid	49	11	17	-	-	3	**80**	4	-	1	-	-	**5**
Munro	-	-		-	-	-	**-**	1	-	-	-	-	**1**
Snake	26	14	44	2	-	-	**86**	7	-	1	-	-	**8**
Stapleton	-	-		-	-	-	**-**	1	-	-	-	-	**1**
Switzer	-	-		-	-	-	**-**	3	-	-	-	-	**3**
Total	164	145	131	2	17	8	**467**	32	23	10	2	4	**71**

The percentage of occurrence of ingesta items within the total pooled collection of buccal cavity and gastric lavage samples for both years and all turtles (n = 538), was dominated by only three algal taxonomic divisions. Rhodophyta (red alga; 53.7%; n = 289); Chlorophyta (green alga; 11.0%; n = 59) and algae from the division of Phaeophyceae (brown alga; 8.0%; n = 43) made up 72.7% of the entire sample collected. The remaining ingesta sample component comprised sponges (10.4% n = 56), soft corals, a wide variety of possibly nutritionally important invertebrate species, (12.6% n = 68) and a small percentage (5.4% n = 22) of inorganic material (Table 6.2).

Table 6.2. The sample size and relative percentage that each prey item contributed to the total amount of buccal cavity and gastric lavage sampling of *Eretmochelys imbricata* at the Howick Group. Both buccal cavity and gastric lavage ingesta items were collected from 19 turtles, either between or within a sampling period.

	Sample source			
	Buccal cavity		**Gastric lavage**	
	2006 (N = 17 turtles) Ingesta items n (%)	**2007 (N = 17 turtles) Ingesta items n (%)**	**2006 (N = 26 turtles) Ingesta items n (%)**	**2007 (N = 79 turtles) Ingesta items n (%)**
Rhodophyta	24 (61.9)	19 (59.4)	49 (48.5)	197 (54.4)
Chlorophyta	3 (7.7)	5 (15.6)	18 (18.0)	33 (9.0)
Phaeophyceae	3 (7.7)	1 (3.1)	10 (10.0)	29 (8.0)
Algal components	**77.0%**	**78.1%**	**76.5%**	**71.4%**
Sponge	5 (12.5)	2 (6.3)	8 (8.0)	41 (11.2)
Cyanobacteria	-	-	-	16 (4.4)
Copepod	-	-	-	9 (2.5)
Actinaria	1 (2.5)	1 (3.1)	-	5 (1.4)
Foraminifera	-	1 (3.1)	1 (1.0)	5 (1.4)
Anthozoa	-	-	2 (2.0)	4 (1.1)
Thalassia hemprechii	-	-	1 (1.0)	4 (1.1)
Ascidiacea	1 (2.5)	-	4 (4.0)	3 (1.0)
Hydozoa	-	-	1 (1.0)	1 (0.3)
Unknown leaf	0	1 (3.1)	-	-
Mollusc	1 (2.5)	-	-	-
Nudibranch	-	-	1 (1.0)	-
Marine worm	-	-	2 (2.0)	3 (1.0)
Non-algal components	**20.0%**	**15.6%**	**20.0%**	**21.0%**
Inorganic ingesta				
Sand	1 (2.5)	2 (6.3)	3 (3.0)	13 (3.6)
Small rubble	-	-	1 (1.0)	2 (0.5)
Total percentage of inorganic components	**2.5%**	**6.3%**	**4.0%**	**4.1%**

From a total of 22 different species of red algae identified within pooled ingesta samples, *Gelidiella acerosa* (27.6%; n = 79) and *Laurencia* sp. (26.2%; n = 75) were recorded the most frequently. The remaining 48.4% of samples identified from the genus Rhodophyta comprised 20 other algal types (Tables 6.3, 6.4).

All ingesta items

Ingesta items found only in buccal cavity samples

Twenty five different prey types, comprising both organic and inorganic material, were identified within turtle buccal cavities. Rhodophyta (red algae) were the most frequently recorded (60.5%) ingesta items. From a total of 21 different species of red algae identified, *Gelidiella acerosa* was the most prolific, accounting for approximately 36% of the ingesta. Sponges were the most frequently occurring non-algal ingesta item (9.9%). Chlorophyta (green algae) and Phaeophyta (brown algae) were also common, but were recorded less frequently than Rhodophyta, while the remaining fraction contained trace amounts of invertebrate species including ascidians, soft corals and inorganic material (Table 6.3).

Ingesta items found only in gastric lavage samples

The gastric lavage sample contained almost twice (n = 53) the diversity of ingesta types compared to the buccal cavity fraction. However microalgae again dominated in the percentage of occurrence with *Laurencia* sp., accounting for 15.2% of the total pooled gastric lavage sample. *Gelidiella acerosa* was the second most frequently recorded item followed by sponge material. A range of algal species from the phyla Chlorophyta (green algae) and Phaeophyta (brown algae) were also common, but were recorded less frequently, while the remaining fraction contained trace amounts of a range of diverse invertebrate species including ascidian spp., anemone, copepods and soft corals. Inorganic material, such as sand and rubble comprised a surprisingly high percentage (4.2%) of the total lavage sample (Table 6.4).

A comparison of prey type presence between age classes and sex

There was a high degree of similarity in the presence / absence of prey items from immature male and female, and adult female *E. imbricata (*Figure 6.3). However no significant difference was apparent in prey items between adult and immature female *E. imbricata* (one-way crossed ANOSIM, P = 0.27).

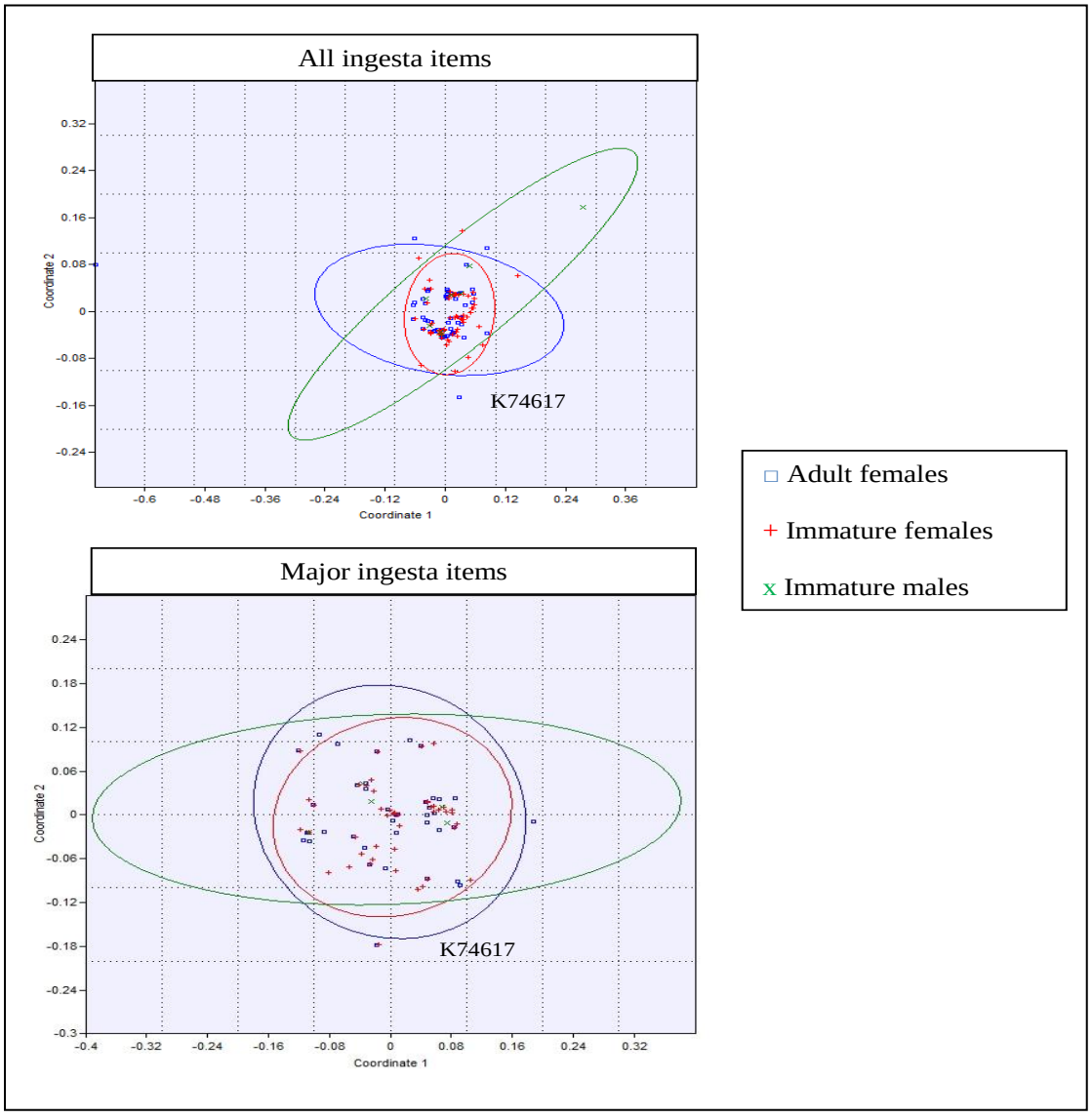

Figure 6.3. A two dimensional, nMDS ordination, using a Bray-Curtis similarity measure, showing the ellipses plots of 95% probability regions of adult female and immature male and female *Eretmochelys imbricata* with all ingesta items included and only frequently observed or organic material identified. Points that appear closer together are more similar in their diet composition than points farther apart.

Similarly, no significant difference existed between immature males and females (P = 0.13) and mature females and immature males (P = 0.26). Turtle K74617, an adult female turtle captured in 2007 with a single piece of rock present within the gastric lavage sample, did not unexpectedly present as an outlier.

Table 6.3. The percentage of occurrence and type of ingesta items found and the percentage that each item contributed to the pooled *Eretmochelys imbricata* buccal cavity samples for turtles of known maturity status.

Ingesta Items	Mature turtles n = 15		Immature turtles n = 18				Total	
	Adult	%	Pubescent	%	Juvenile	%	N	%
Rhodophyta								
Gelidiella acerosa	13	39.4	7	26.9	5	41.7	25	35.2
Gelidium sp.	2	6.1	2	7.7	1	8.3	5	7.0
Laurencia sp.	2	6.1	2	7.7	1	8.3	5	7.0
Chondrophycus sp.	1	3.0		-	1	8.3	2	2.8
Leveilla jungermaniodes	1	3.0	1	3.8	-	-	2	2.8
Acanthophora spicifera	1	3.0	-	-	-	-	1	1.4
Chondria sp.	-	-	1	3.8	-	-	1	1.4
Hypnea spinella	1	3.0	-	-	-	-	1	1.4
Lomentaria sp.	-	-	1	3.8	-	-	1	1.4
Chlorophyta								
Valonia utricularis	2	6.1	-	-	-	-	2	2.8
Valoniopsis pachynema	1	3.0	1	3.8	-	-	2	2.8
Anadyomene sp.	-	-	-	-	1	8.3	1	1.4
Cladophora sp.	-	-	1	3.8	-	-	1	1.4
Codium sp.	-	-	1	3.8	-	-	1	1.4
Halimeda sp.	1	3.0	-	-	-	-	1	1.4
Phaeophyceae								
Sargassum sp.	1	3.0	1	3.8		0.0	2	2.8
Dictyota sp.	-	-	1	3.8	-	-	1	1.4
Lobophora variegata	1	3.0	-	-	-	-	1	1.4
Sponge	3	9.1	4	15.4	-	-	7	9.9
Soft coral	-	-	1	3.8	1	8.3	2	2.8
Anadara sp.	-	-	1	3.8	-	-	1	1.4
Ascidiacea sp.	1	3.0	-	-	-	-	1	1.4
Foramnifera sp.	-	-	-	-	1	8.3	1	1.4
Terrestrial plant leaf	1	3.0	-	-	-	-	1	1.4
Sand	1	3.0	1	3.8	1	8.3	3	4.2
Total	**33**		**26**		**12**		**71**	**100**

Table 6.4. The percentage of occurrence, ingesta items type found and the percentage that each item contributed to the pooled *Eretmochelys imbricata* gastric lavage samples by age-class.

Ingesta Items	Mature turtles n = 43		Immature turtles n = 61				Total	
	Adult	%	Pubescent	%	Juvenile	%	N	%
Rhodophyta								
Laurencia sp.	27	16.8	23	14.2	20	14.4	70	15.2
Gelidiella acerosa	19	11.8	18	11.1	17	12.2	54	11.7
Chondrophycus sp.	5	3.1	10	6.2	12	8.6	27	5.9
Gelidium sp.	9	5.6	5	3.1	6	4.3	20	4.3
Hypnea spinella	3	1.9	3	1.9	4	2.9	10	2.2
Acanthophora spicifera	3	1.9	3	1.9	3	2.2	9	1.9
Leveilla jungermaniodes	2	1.2	2	1.2	3	2.2	7	1.5
Amansia glomerata	3	1.9	1	0.6	2	1.4	6	1.3
Gracilaria sp.	2	1.2	4	2.5	-	-	6	1.3
Cladophoropsis sp.	2	1.2	2	1.2	1	0.7	5	1.1
Chondria sp.	2	1.2	3	1.9	-	-	5	1.1
Jania adhaerens	2	1.2	2	1.2	1	0.7	5	1.1
Champia parvula	1	0.6	3	1.9	-	-	4	0.9
Eucheuma denticulatum	1	0.6	1	0.6	-	-	2	0.4
Gelidiopsis sp.	7	4.3	1	0.6	-	-	8	0.4
Sphacelaria sp.	3	1.9	3	1.9	2	1.4	8	0.4
Amphiroa sp.	-	-	-	-	1	0.7	1	0.2
Hypnea cf. pannosa	-	-	-	-	1	0.7	1	0.2
Spyridia filamentosa	1	0.6	-	-	-	-	1	0.2
Taenioma nanum	1	0.6	-	-	-	-	1	0.2
Meristotheca procumbens	1	0.6	-	-	-	-	1	0.2
Chlorophyta								
Valonia utricularis	5	3.1	4	2.5	-	-	9	1.9
Dictyophaeria cavernosa	1	0.6	3	1.9	3	2.2	7	1.5
Valoniopsis pachynema	4	2.5	3	1.9	-	-	7	1.5
Valonia sp.	2	1.2	3	1.9	1	0.7	6	0.9
Pseudocodium floridanum	-	-	2	1.2	2	-	4	0.9
Caulerpa racemosa	-	-	1	0.6	2	1	3	0.7
Halimeda sp.	1	0.6	2	1.2	-	-	3	0.7
Anadyomene sp.	3	1.9	2	1.2	3	2.2	8	0.4
Cladophora sp.	-	-	2	1.2	-	-	2	0.4
Ventricaria ventricosa	-	-	-	-	2	1.4	2	0.4
Boergesenia forbesii	1	0.6	-	-	-	-	1	0.2

Veloniacea sp.	-	-	1	0.6	-	-	1	0.2
Phaeophyceae								
Sargassum sp.	4	2.5	7	4.3	7	5.0	18	3.9
Dictyota sp.	3	1.9	-	-	2	2.8	7	1.5
Lobophora variegata	-	-	2	1.2	3	1.0	5	1.1
Padina sp.	-	-	1	0.6	1	0.7	2	0.4
Cyanobacteria	7	4.3	3	1.9	6	4.3	16	3.5
Other diet components								
Sponge	18	11.2	15	9.3	16	11.5	49	10.6
Copepod.	2	1.2	5	3.1	2	1.4	9	1.9
Ascidian.	1	0.6	4	2.5	2	1.4	7	1.5
Foramnifera sp.	1	0.6	3	1.9	2	1.4	6	1.3
Hydroid	2	1.2	2	1.2	2	1.4	6	1.3
Soft coral	1	0.6	1	0.6	3	2.2	5	1.1
Worm	1	0.6	3	1.9	1	0.7	5	1.1
Anemone	-	-	-	-	1	0.7	1	0.2
Cnidarian.	-	-	-	-	1	0.7	1	0.2
Nudibrach	-	-	-	-	1	0.7	1	0.2
Thalassia hemprichii	1	0.6	1	0.6	4	2.9	6	0.9
Sand	8	5.0	6	3.7	2	1.4	16	3.5
Small rubble	1	0.6	1	0.6	1	0.7	3	0.7
Grand Total	**161**		**162**		**139**		**462**	**100**

A comparison of prey types present by age class and sex.

A high degree of similarity in the presence / absence of major prey items found in immature turtles of both sexes, and adult female *E. imbricata* was apparent (Figure 6.3). Again, turtle K74617 presented as an outlier, likely due to the presence of only *Gelidiella* sp., within the buccal cavity. However, no significant difference was apparent in the subset of major prey items found in the stomach and buccal cavities of both sexes of immature turtles ($P = 0.590$) and between immature and adult female *E. imbricata* (females: $P = 0.123$; males: $P = 0.782$).

Table 6.5. Pooled buccal cavity and lavage ingesta items collected from sampling of the same turtles captured in 2006 and recaptured in 2007. F= female; A = adult; SP = pubescent.

Turtle CCL (cm)	Reef	Sex	Age-class	Source	Ingesta item	Ingesta item
					2006	2007
K8361 (84.7)	Combe	F	A	Lavage	*Gelidiella acerosa*	Sponge
				Lavage	*Laurencia* sp.	Sand
				Lavage	*Anadyomene* sp.	
				Lavage	*Valonia utricularis*	
K75051 (81.2)	14-056	F	SP	Lavage	*Gelidiella acerosa*	*Gelidiella acerosa*
				Lavage	*Acanthophora spicifera*	*Amansia glomerata*
				Lavage	*Chondria simpliciuscula*	
				Lavage	*Laurencia* sp.	
				Lavage	*Valonia utricularis*	
				Lavage	*Valoniopsis pachynema*	
				Lavage	*Padina* sp.	
				Lavage	Hydroid	
				Lavage	Sponge	
K58141 (76.5)	Combe	F	SP	Buccal	*Gelidiella acerosa*	
				Buccal	Sponge	
				Buccal	*Gelidium* sp.	
				Lavage		*Caulerpa racemosa*
				Lavage		*Dictyophaeria cavernosa*
				Lavage		*Laurencia* sp.
				Lavage		*Gelidiella acerosa*
				Lavage		Sponge
K74617 (83.8)	Combe	F	A	Buccal	*Gelidiella acerosa*	
				Lavage		Rock
K75032 (71.2)	Snake	F	J	Lavage	*Cladophoropsis* sp.	*Amphiroa fragilissima*
				Lavage	*Gelidiella acerosa*	*Gelidiella acerosa*
				Lavage	*Laurencia* sp.	*Laurencia* sp.
				Lavage	*Anadyomene* sp.	Ascidian
				Lavage	*Ventricaria ventricosa*	Sponge
				Lavage	*Dictyosphaeria cavernosa*	*Thalassia hemprichii*
				Lavage	*Sargassum* sp.	

				Lavage	Foramnifera	
				Lavage	Sand	
				Lavage	Worm	
				Buccal		Soft coral
K74619 (67.6)	Combe	F	J	Buccal	*Gelidiella acerosa*	
				Buccal	*Gelidium* sp.	
				Lavage		*Gelidiella acerosa*
				Lavage		*Gelidium* sp.
				Lavage		Sponge
K74848 (65.4)	Combe	F	J	Lavage	Sponge	
				Lavage	Nudibranch	
				Lavage	*Amphiroa* sp.	
				Lavage	Ascidian	
				Buccal		*Gelidiella acerosa*
				Buccal		*Chondrophycus papillosus*
				Buccal		*Laurencia* sp.
				Buccal		*Anadyomene* sp.

Effect of reef and year on prey item selection

A high degree of MDS overlap of prey species was evident between *E. imbricata* using Combe Reef (n = 61) compared to turtles sampled on all other reefs (n = 78) (Figure 6.4). However, a one-way crossed ANOSIM indicated that a significant difference ($P<0.05$) existed between the subset of major ingesta items collected from turtles foraging at Combe Reef when compared with turtles found on all other Howick Group reefs.

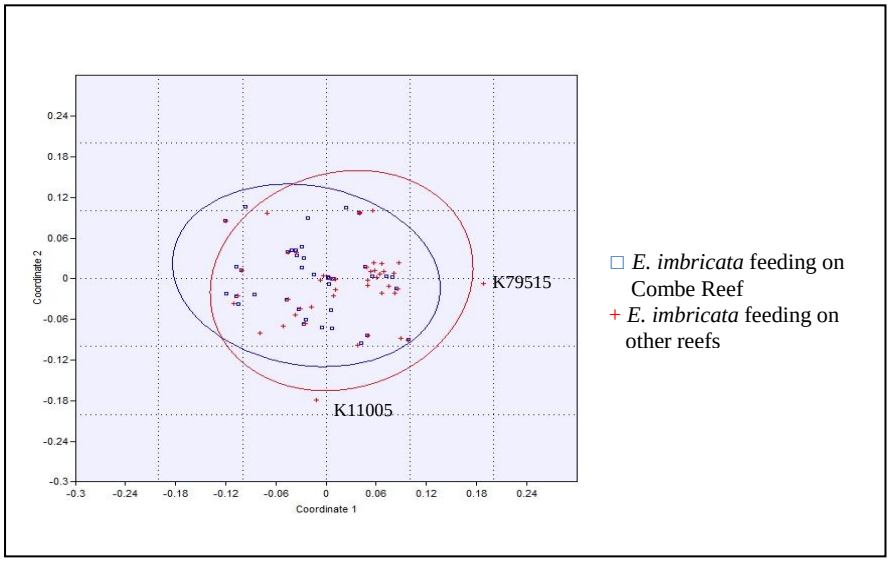

Figure 6.4. A two dimensional, nMDS ordination, using a Bray-Curtis similarity measure, showing the ellipses plots of the 95% probability regions of the subset of frequently observed ingesta items found in *Eretmochelys imbricata* on Combe Reef compared with turtles found on other reefs of the Howick group. Points that appear closer together are more similar in their diet composition than points farther apart.

Conversely there was a high degree of nMDS overlap and no significant difference (one-way crossed ANOSIM P = 0.2) apparent between the ingesta items found in turtles foraging in the Howick Group, between 2006 (n = 37) and 2007 (n = 80) was apparent (Figure 6.5). The two adult female turtles (K11005 and K79515) that presented as outliers in Figure 6, were found to have only a single prey species present (Cyanobacteria sp., and Sargassum sp., respectively) in their gastric lavage samples.

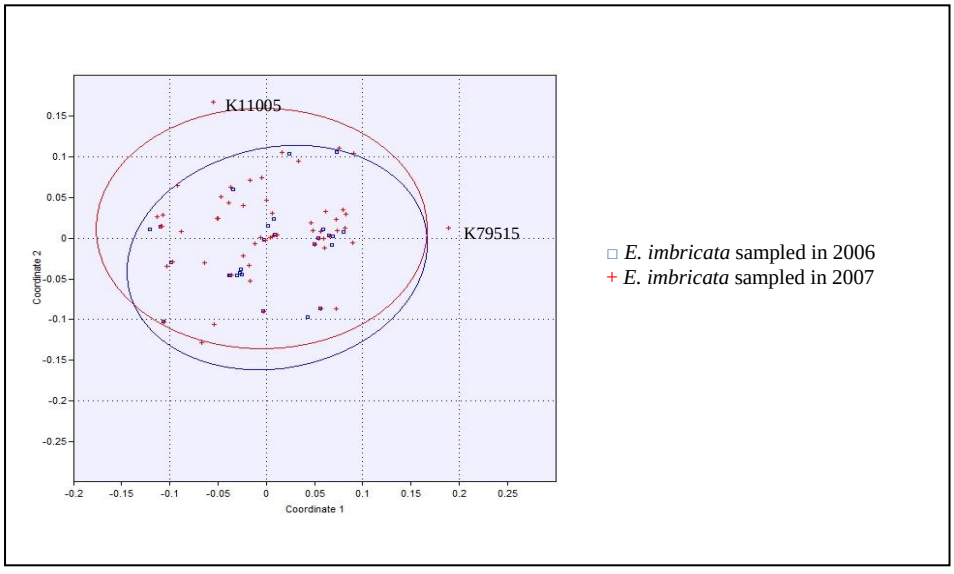

Figure 6.5. A two dimensional, nMDS ordination, using a Bray-Curtis similarity measure, showing the ellipses plots of the 95% probability regions of the subset of frequently observed ingesta items found in *Eretmochelys imbricata* in 2006 and 2007 on other reefs of the Howick group. Points that appear closer together are more similar in their diet composition than points farther apart.

Major ingesta items found

A comparison of gastric lavage and buccal cavity ingesta item diversity

In spite of a notable overlap of the 95% probability ellipse plots, a one way ANOSIM showed a significant difference in prey species diversity between the buccal cavity and gastric lavage subset of major ingesta items consumed by turtles foraging on Howick Group reefs (one-way crossed ANOSIM $P<0.05$) (Figure 6.6). This finding was unexpected given that buccal cavity samples are likely to be a subset of the lavage component, for as the turtle feeds, ingesta would logically travel from the buccal cavity through the oesophagus and into the stomach.

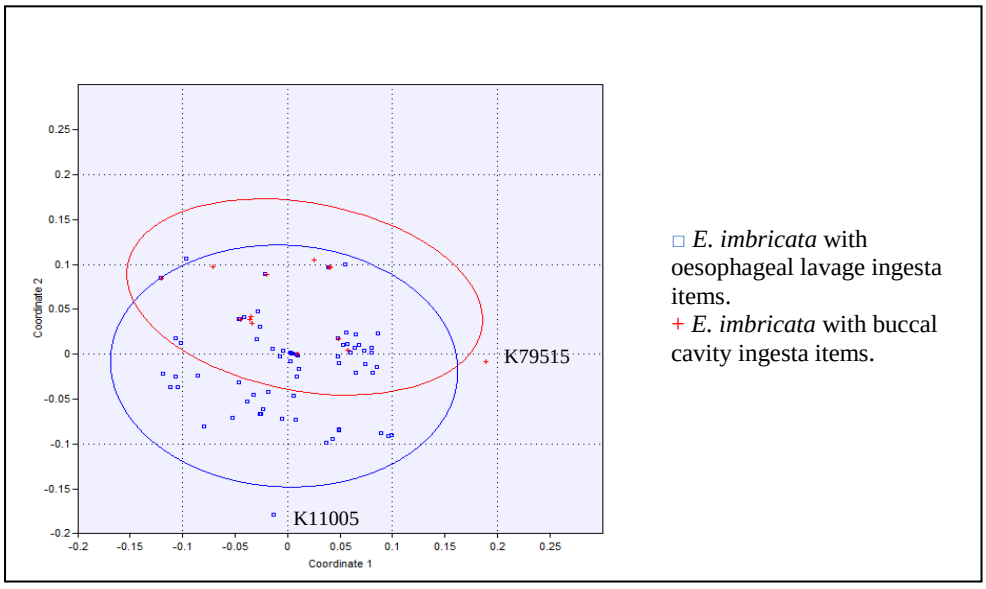

Figure 6.6. A two dimensional, nMDS ordination, using a Bray-Curtis similarity measure, showing the grouping of ingesta items (buccal cavity and gastric lavage) by all foraging *Eretmochelys imbricata* found within the Howick Group. Points that appear closer together are more similar in their diet composition than points farther apart.

Discussion

This study presents the first detailed description of prey selection by the largest known feeding aggregation of *E. imbricata* within the Far Northern Section of the Great Barrier Reef. Surprisingly, *E. imbricata* were found to most frequently consume marine algae. While there is certainly some overlap in prey species reported here and those found in diet studies elsewhere (Meylan & Whiting 2008), a predominantly algal diet is atypical for this species. *Eretmochelys imbricata* have been reported to select a diverse variety of prey species in other parts of the world (Acevedo *et al*., 1984) including: sea anemones and other coelenterates; sponges; oceanic squid; gastropods and crustaceans (Den Hartog 1980; Steinbeck & Ricketts 1941; Vicente 1994). Some of the earliest accounts of *E. imbricata* diet composition (Carr & Stancyk 1975) concluded that they were a relatively indiscriminate feeder of benthic invertebrates, however other studies rejected this idea in favour of strict spongivory (Meylan 1988, Anderes & Uchida 1994, van Dam and Diez 1997).

In comparison, the dietary range of the cohort of *E. imbricata* captured on northern GBR reefs would appear to be comparatively narrow, given the strong preference for only several species of red alga. While an understanding of the frequency that food items consumed by turtles occur is important, it does not convey the nutritional value or biomass a particular food item infers (Abbas *et al*., 1992).

Surprisingly, a frequently occurring ingesta item, in fact the fourth most prevalent, was inorganic material (rock/sand). While rocks and sand may be purposely consumed by some species, as an aid to digestion, it is not commonly reported in chelonians (Taylor 1993). Thus, I suggest that the presence of this material was probably due to incidental consumption. This incidental ingestion may also account for other items present in the gut, such as copepods and worms, which may have inadvertently been consumed as a consequence of being an epibiont of target dietary species. However, the nutritional value of these secondary dietary items should not be underestimated, as they may be an important source of micronutrients (Westoby 1974; Wood & Wood 1981).

Noteworthy challenges were associated with conducting oesophageal lavage on *E. imbricata* in field conditions during this study including intubation of flush water and insertion of a collection tube into the turtle's stomach. Adherence to strict animal ethics protocols and time limits resulted in the collection of presence / absence of prey selection, rather than volumetric / quantitative data. However buccal cavity and gastric lavage samples collected from this study were comprised of approximately 73% algal species, demonstrating that *E. imbricata*, found foraging within the northern Great Barrier Reef, are most frequently selecting an algivorous prey.

Buccal cavity and gastric lavage samples: a balance between energy expenditure and energy gain in foraging strategies

Eretmochelys imbricata were rarely encountered during surveys of either the sandy seagrass and algae dominated reef flat centres, or on the sheltered coralline substrate occurring at the northern, less energetic reef ends. Instead, turtles were predominantly found foraging within the 70 – 200 m wide coral rubble substrate, which was exposed to strong (~ 20 knot) south easterly trade winds, occurring at the south-eastern end of the reef flat. This rocky substrate is likely to provide the micro-habitat type necessary to support growth of the two algal species (*Gelidiella* sp. and *Laurencia* sp.) that were found to be most often selected by *E. imbricata* (Cattaneo & KalffSource 1979).

Unlike some other species of cheloniid, *E. imbricata* have evolved various morphological traits, such as thickly keratinised carapacial and plastron scutes and powerful angular jaws, that provide a high level of protection against an abrasive substrate, allowing them to forage on target species that may be occurring within these turbulent areas of the reef (Wyneken 2001). A far higher level of energy expenditure is likely to be required for *E. imbricata* to target prey species within these areas of high energy wave conditions, than if they foraged in calmer areas of the reef. This suggests that a high degree of nutritional benefit is conferred to turtles by undertaking this feeding behaviour. Both *Gelidiella* and *Laurencia* sp., are known to contain high levels of protein (6.3 - 9.2% respectively) (Abbas 1992) and carbohydrate (14.3 - 67.7% respectively) (Hong *et al*., 2007), in comparison with the range of other forage available on the reef flat (Manivannan *et al*., 2009). The elevated carbohydrate and protein content these two algae provide, may therefore offset the higher activity levels required to forage, during turbulent conditions, and infer a higher net energetic gain than feeding on other forage types.

Comparison of diet on Combe Reef with all other reefs

There was a significant difference in the prey type selected by turtles foraging on Combe Reef when compared with animals foraging on other Howick Group reefs. While turtles on Combe Reef had fewer prey species in their guts, they had a greater proportion of the two most prevalent algal types. Combe Reef, with a reef flat area of 30.4 km^2 is approximately three times larger than that of any other reef in the Howick Group. Because of its size this reef also provides the greatest area of rocky rubble substrate, and as a consequence, was likely to support a greater spatial coverage of the two principal algal species found in turtle diets: *Gelidiella* and *Laurencia* sp. Possibly, turtles foraging on Combe Reef are able to consume the preferred diet, and therefore had no need to consume other prey types. Turtles feeding on smaller reefs may have had less opportunity to access their preferred diet and therefore must forage over a greater dietary breath.

This study has revealed that the high propensity for algal prey selection by *E. imbricata* found foraging within the Howick Group contrasts with the dietary niche described for conspecifics in the Caribbean and indeed in many other parts of its distribution (Meylan 1988). While this study only sampled from turtles found on the small number of reefs that comprise the Howick Group, this foraging aggregation is also likely to be a good proxy indicator of the animal's dietary preference throughout the northern Great Barrier Reef in general. However some caution should be exercised in the interpretation of these results given sampling methodology utilized resulted in collection of presence / absence data, of varying sample sizes, to describe prey selection rather than a quantitative description of the entire gut content. Additionally, this study was only undertaken during the austral winter months and it warrants further investigation to determine if feeding strategies changed in response to prey availability at other times of the year.

An understanding of the nutritional requirements driving immature *E. imbricata* growth rates and the reproductive capacity of mature animals, within western Pacific foraging areas is fundamental

for determining how populations are functioning. Dietary composition, and potentially net nutrition, within and between foraging grounds are likely to differ, causing variation in growth rates, age to maturity and reproductive output among feeding cohorts (Carr & Carr, 1969; Bjorndal, 1982).

Clearly *E. imbricata* are selecting a variety of prey items in different parts of the world (Bjorndal 1985), however habitats containing the preferred prey items may be changing due to a variety of anthropogenic impacts, in particular through the implications of climate change (Gardener *et al*., 2003). Some high biodiversity marine areas, such as the Great Barrier Reef, are expected to experience elevated temperature regimes and significant ENSO-related bleaching events that will likely result in present day reef habitats in the Pacific Ocean becoming "marginal" within the next several decades (Guinotte *et al*., 2003). Under conditions expected in the 21st century, global warming and ocean acidification may compromise carbonate accretion, with corals becoming increasingly rare on reef systems. The result will be less diverse reef communities and carbonate reef structures that fail to be maintained. Climate change also exacerbates local stresses from declining water quality and overexploitation of key species, driving reefs increasingly toward the tipping point for functional collapse (Hoegh-Guldberg *et al*., 2007). This study has shown that the diet of *E. imbricata* foraging within the northern GBR already contains a high algal component, therefore an increase in algae density and distribution, as a consequence of climate change, may actually infer a benefit to the species. However the importance of continuing this work, over time and space to detect if change is occurring should not be understated given the species has been listed on the International Union for the Conservation of Nature (IUCN) Red List as "Critically Endangered" since 1975 and maybe facing an uncertain, climate changed induce future.

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CHAPTER SEVEN

SOMATIC GROWTH RATES OF ERETMOCHELYS IMBRICATA FOUND IN A NORTHERN GREAT BARRIER REEF FORAGING AREA

Chapter overview

This chapter presents findings on the growth rates of *Eretmochelys imbricata* found foraging over reefs of the Howick Group, in the Far Northern Section of the Great Barrier Reef Marine Park. The chapter is presented as a manuscript published on 2nd February 2012 in the journal: *Marine Ecology Progress Series*.

The work presented is my own, with intellectual and technical input from Dr David Pike.

Authors: Ian Bell and Dr David Pike.

CHAPTER EIGHT

SYNOPSIS, ISSUES OF CONSERVATION CONCERN AND FUTURE MANAGEMENT CONSIDERATIONS FOR MAINTAINING *ERETMOCHELYS IMBRICATA* POPULATIONS IN THE WESTERN PACIFIC

A general global decline in marine turtle populations has been recognised by the World Conservation Union (IUCN), by assigning the status of "Endangered" to all species except *E. imbricata* and *Dermochelys coriacea*, which are listed as "Critically Endangered" (IUCN Red list). The Australian federal and Queensland state governments have also recognised that the long-term conservation prospects for *E. imbricata*, residing on reefs of the northern Great Barrier Reef, look similarly poor, assigning a classification status of "Vulnerable to Extinction" via the relevant conservation legislation (Environmental Protection and Biodiversity Conservation Act 1999; Queensland Nature Conservation Act 1992).

Prior to European contact, only indigenous Australians took marine turtles and their eggs. However, following the Second World War, Australia embraced industrialisation and the economy and population grew rapidly. Marine turtles, particularly *E. imbricata* and *Chelonia mydas*, were subject to unsustainable take for their meat or shells until 1971 (Groombridge and Luxmoore 1989). In addition, the increased exploitation of commercial fish also caused increased bycatch, including marine turtles (Oravetz 1999). Expanding industrialisation, with concommitant population growth, continues to have multiple negative impacts on *E. imbricata* populations. Some of these impacts include: mortality from ingestion and entanglement in marine debris, boat-strike, and unsustainable levels of indigenous hunting, reduced reproductive success caused by loss or degradation of nesting habitat, and human and feral animal predation on eggs, reduced condition caused by loss of foraging habitat, and marine pollution (Laist 1987; Mortimer and Donnelly 2008).

In an effort to address a historical (King 1982) and ongoing decline of Australian marine turtles, the Federal Government developed a National Recovery Plan for Marine Turtles in Australia (Environment Australia 2003). The recovery plan highlighted a shortfall in detailed demographic and life history information on feeding populations of *E. imbricata*, hindering the development of sound conservation management. The recovery plan identified a "*significant need to sample and analyse resident feeding ground populations to determine the relative composition of the representative populations. This information will be added to monitoring and mortality data to determine the impact of mortality on each population. Ultimately it will assist in judging the security of Australian populations in relation to the levels of mortality at any time"* (Australia 2003, p. 21). In this study I have begun identifying and addressing information gaps about feeding populations of *E. imbricata* in the south-western Pacific.

Understanding demography

An understanding of the demographic structure within a foraging marine turtle population is critical to predicting the impact of anthropogenic, or environmentally induced change (Fuentes *et al.*, 2010). Many characteristics of *E. imbricata's* reproductive biology, such as internesting periodicity and hatchling gender output from natal beaches, are directly coupled to thermal conditions at both foraging and nesting areas (Miller 1985). Change in a feeding population's demographic structure may identify a range of impacts including, but not limited to: an unsustainable take of nesting turtles or eggs, sex ratio or offspring survival consequences of future global temperature changes, and influences of degradation of nesting or feeding habitat (Fuentes *et al.*, 2009; Hawkes *et al.*, 2007). The strong female bias (6.7:1 female to male) I observed in the Howick Group feeding population raises questions about the capacity of rookeries to cope with increased incubation temperatures in the future, if it causes further biasing of offspring sex ratios (Limpus *et al.*, 1985).

Biometrics

Prior to the advent of molecular techniques to determine a species' genetic phylogeny, the use of an animal's body dimensions was one of several principal methods biologists used to describe or categorise animals within a population. Even today, biometric data can be an effective, non-intrusive method of determining life history stages or reproductive state of particular animals within a population (Myers *et al.*, 2007). Morphometric data collected in this study indicated that adult females were mostly from the nesting cohort that used islands in the Bismarck-Solomon Sea, rather than from regional nesting stocks identified by Miller and Limpus (1991) in the nGBR and Torres Strait. These findings were corroborated with genetic analysis and flipper tag-return data.

Genetic structure

A mixed-stock analysis of the genetic composition of turtles found within the Howick Group foraging population revealed that the majority originated from nesting areas widely distributed around the Bismark-Solomon Sea (Broderick 1994; 1996). Monitoring trends in the genetic structure of *E. imbricata* within the Howick Group foraging area may provide an indication of level or severity of impacts occurring in these natal regions. Similarly, a large percentage of the *E. imbricata* population that nest on islands of the the nGBR and though Torres Strait have recruited from foraging areas distributed over a vast area of the Indo-Pacific region. Introducing strategies that would mitigate impacts in foraging and nesting regions would be clearly challenging, but not impossible, for the relevant Australian management agencies. There are many examples of the Australian Federal Government providing financial incentives to neighbouring countries to assist in the implementation of strategies that promote sustainable ecosystem and wildlife management (Anon 2007).

Diet

The composition of dietary items in the stomach and buccal cavities of *E. imbricata* foraging on reefs of the nGBR, revealed a strong preference for several species of marine algae. These algae occurred on rubble reef flats, which turtles could only access at high tides. When water over the reef flats was too shallow, *E. imbricata* selected a more varied diet that included sponges and more closely resembled conspecifics in other regions (Anderes and Uchida 1994). Daily bimodal feeding patterns, dictated by tidal amplitudes, have not been described for other species of marine cheloniid.

Implications of climate change on forage composition

The large scale degradation of coral reefs around the world, due to global climate change (Gardner *et al*., 2003), overfishing of apex predators, and eutrophication (Diaz-Pulido *et al.*, 2009), may (ironically) benefit *E. imbricata* residing on the Great Barrier Reef, due to their dietary preferences. For several decades, climate change models have been warning that an increased frequency and severity of warming-induced coral bleaching events will lead to increases in coral mortality and an increase in algal overgrowth (Davenport 1989). A study conducted by Diaz-Pulido *et al.*, (2009) showed that after coral died, the remnant calcareous skeleton became covered by macroalgae (*Lobophora variegate)*. This species of alga was found in both buccal cavity and lavage samples of *E. imbricata* in the Howick Group, indicating that it is consumed along with *Gelidiella* and *Laurencia* sp., the two most selected forage species. Paradoxically, reef recovery may depend on the grazing effort of *E. imbricata* reducing algal assemblages, and allowing regeneration of corals, if their larvae can successfully recolonise damaged reefs after grazing (Rasher and Hay 2010).

Growth rates

Growth rates calculated from *E. imbricata* from an nGBR foraging ground provided a robust, quantitative baseline from which a long term perspective may be gained on the population if

monitoring is continued. The rate at which turtles are growing at the Howick Group may be used as a direct measure of fitness and habitat quality, and provide an early warning measure if conditions change.

Threats

The current and projected level of [un]sustainable harvest of reproductive females, combined with a degradation of nesting and feeding habitats, due to various anthropogenic impacts including climate change (Pandolfi *et al.*, 2003), has resulted in a poor long-term prognosis for a viable population of *E. imbricata* on the northern Great Barrier Reef. Many foraging and nesting regions in the nGBR, Torres Strait and island nations of the south Pacific, that historically have provided suitable habitat for hundreds to thousands of turtles annually, now support only low density foraging aggregations (Kinch and Burgess 2009; Chaloupka *et al*., 2004).

Globally the conservation outlook for this species is also dire, primarily due to the already significantly reduced population densities and loss or alteration of feeding and nesting habitats, in every ocean basin (Gibson and Smith 1999). The poor conservation outlook may be compounded by an inability to adapt to impacts of climate change (Poloczanska *et al.*, 2009). Breeding populations may be two orders of magnitude below pre-exploitation levels (Meylan 1989; Bjorndal and Jackson 2003) and a review of data from 25 globally distributed nesting sites show an 84 - 87% decline in annual nesting over the last three *E. imbricata* generations (~ 50 yrs) (IUCN 1995). The outlook for foraging populations is no better, with over 80% of post-oceanic feeding habitat severely damaged (Jackson 1997; McClenachan *et al.,* 2004).

A bleak survival outlook for *E. imbricata* in almost all western Pacific regions, including the nGBR, raises the question of why state and federal protected-area-management agencies have been unable to perceive, and therefore act on, these threatening processes. Successful implementation of regional, national or international conservation strategies that can infer some

level of resilience in *E. imbricata* populations, to cope with anthropogenic impacts, will require cooperation among a range of shareholders. Strategies will rely on detailed information, such as that presented in this study, to generate and implement actions that protect *E. imbricata* feeding and nesting habitats and migration pathways (Donnelly 1991; Eckert 1999).

Future research and monitoring requirements

My study, describing previously unknown demographic and biophysical aspects of a foraging population of *E. imbricata*, goes some way to providing a contemporary understanding of trends and life history traits displayed by these animals in a nGBR protected area. However, while this study has provided a "baseline" of various life history traits, there is a need for ongoing work to determine the consequences of past and present human actions.

Long-term demographic studies of foraging *E. imbricata* should be continued at study sites such as the Howick group, to determine if apparent trends in population size continue (Bjorndal 1999b). My study of *E. imbricata* at the Howick Group highlights the power of long-term demographic, mark-recapture data. The complete stock structure, including the boundaries of distinct populations, need to be determined, for all age-classes of turtles. Without this knowledge the effects of impacts on nesting beaches, foraging grounds and migratory corridors cannot be evaluated for individual cohorts.

Genetic diversity

Natural variation in specific rookery output from fluctuations in annual nesting densities, natural catastrophes and predation is expected, and the genetic composition of *E. imbricata* foraging populations are unlikely to be temporally static. However a rapid change (5 - 10 yrs) in the haplotype ratio of juveniles recruiting to the Howick Group of reefs may be an early warning indication that output from a nesting region is being reduced (Davenport 1997). Further genetic sampling of turtles nesting throughout the Bismarck-Solomon Sea eco-region, New Caledonia

and Vanuatu needs to occur as a priority, to determine haplotype diversity of nGBR source stocks. Ongoing monitoring of the genetic diversity within the Howick Group *E. imbricata* turtle stock will detect changes in output from these rookeries, should any occur.

Feeding habitat

Long-term monitoring of *E. imbricata* foraging habitat will be required to detect if degradation is occurring as a consequence of increased mean sea temperature and heights, or changes in ocean chemistry due to acidification (Doney *et al.*, 2009). The range, frequency, and scale of human impacts on coral reefs are increasing to the extent that reefs are threatened globally (Diaz-Pulido *et al.*, 2009). Projected increases in carbon dioxide and temperature over the next 50 years exceed the conditions under which coral reefs have flourished over the past half a million years (Hughes *et al.*, 2007). International integration of management strategies that support reef resilience need to be vigorously implemented, and complemented by strong policy decisions to reduce the rate of global warming (Hughes *et al.*, 2003). These processes usually take years to decades to bring a reef back to coral dominance (Gardener *et al.*, 2003).

Migration destinations

A more detailed understanding of natal beach locations, and what proportion of *E. imbricata* make intra- and international reproductive migrations to these nesting rookeries will allow the development of more focussed, and hopefully effective, conservation strategies (Aidely 1981). While flipper tagging can determine nesting beach use, more sophisticated technology such as satellite telemetry can identify important migratory corridors, courtship areas and internesting habitat associated with breeding cycles (Balazs 1994). This study has clearly identified islands scattered widely throughout the Bismarck-Solomon Sea region as destinations for a large percentage of nGBR breeding *E. imbricata*. Identification of these rookeries and the specific impacts associated with them will be important for developing threat mitigation strategies.

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