Gyuris, Emma (1993) ***Insights into the ecology of hatchlings of the green turtle, Chelonia mydas: implications for the life histories of the marine turtles.*** **PhD thesis, James Cook University.**

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Insights into the Ecology of Hatchlings of the Green Turtle, *Chelonia mydas* : Implications for the Life Histories of the Marine Turtles.

Thesis submitted by
Emma Gyuris B.Sc., M. Sc. (Monash)
March 1993

for the degree of Doctor of Philosophy
in the Department of Zoology at
James Cook University of North Queensland

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E Gyuris
28 March 1993

Note: Part of the work presented in Chapter 3 is to be published by the journal "Coral Reefs" under the title "The rate of predation by fishes on the hatchlings of the green turle (*Chelonia mydas*)." Part of the work presented in Chapter 4 has been published under the title "Factors controlling the timing of green turtle hatchling emergence from the nest" Wildlife Research 20(3): 345-353

PERMITS

Appropriate permits and approvals to carry out the experimental work described in this thesis were granted by the following state and federal agencies and authorities: Queensland National Parks and Wildlife Service; Fisheries Branch, Queensland Department of Primary Industries; the Great Barrier Reef Marine Park Authority and The James Cook University of North Queensland Animal Research Ethics Committee.

ACKNOWLEDGEMENTS

I wish to thank the following individuals for their help during my candidature.

Helene Marsh (JCU), took on the task of supervising this project. I am grateful for her advice, for making herself available whenever needed and most of all for her belief in me. Several times the reason to keep going was a sense of duty engendered by her trust and belief.

Barry Goldman (Research Associate, Australian Museum) and **Glen De'Ath** (JCU) gave guidance and invaluable advice on statistical analysis of my data. **Barry Goldman** functioned as surrogate supervisor during my lengthy absences from the University.

Col Limpus (Queensland Dept. of Environment and Heritage), introduced me to turtles, and was an integral part of this work in the initial stages of developing methodologies.

David Hannan (Coral Sea Imagery) gave his time, equipment and expertise to help make the short audiovisual presentation documenting some aspects of my work.

Ian Somers (CSIRO Div.of Fisheries) provided generous help by making his computerized population model available to me.

The comments of an **anonymous reviewer** facilitated significant improvements on the earlier drafts of Chapter 4.

Many student **volunteers** and some personal friends assisted in patrolling the beach, spearfishing and following the hatchling turtles in the water - often a tiring and sometimes scary exercise. Without these people the project would never have got off the ground. I hope they will remember the sights, sounds and scents of coral cays for many years to come.

In addition to the above I received help and assistance of a more personal nature from several people. I am particularly thankful to my husband, for his support, encouragement, and the many discussions that generated some good ideas. Most of all for remaining cheerful while enduring several months on Yap alone, without his family.

I am indebted to my parents, , for taking loving care of our daughter, , during the last few months of the writing of this thesis. And to for being a such a good little girl. Zoli Florian and Carden Wallace took me into their homes, looked after me and provided company during these last few months of completing this thesis.

To all these people I give my heartfelt thanks.

ABSTRACT

By reviewing the literature, I examined the validity of earlier explanations of the differences in body size, fecundity and other life history parameters amongst testudines. I concluded that while many life history parameters, such as survivorship, growth and age to maturity are similar for marine, terrestrial and freshwater turtles, the large body size and high fecundity of marine species are exceptional. In general, high fecundity is considered to occur because of high mortality during the early life stages. Yet, mortality of sea turtles to one year of age has been considered to be significantly lower than that of the less fecund freshwater turtles. Estimates of mortality however were based largely on beach-based studies as few empirical data on hatchling survival after entry into the sea have been available.

This study quantified survivorship of hatchlings after entry into the sea and during reef crossing at Heron and North-West Islands, two coral cays at the southern end of the Great Barrier Reef. Predation rates were quantified by two independent methods.

The first method involved following individual hatchlings (n=1740) tethered by a 10 m monofilament nylon line, as they swam from the water's edge towards the reef crest. Predation rates under particular combinations of environmental variables (tide, time of day, and moon phase) were measured in 84 separate, 10 minute trials, with 20 hatchlings in each. Predation rates varied from 0 to 85% with a mean of 31% (S. E. ± 2.5%).

A series of nested logistic regression models was used to examine the effect of the environmental variables. Tide and moon phase had a significant effect on predation rate: Predation was lowest during the combination of new moon and high tide and was highest during low tide around the full moon.

The second method estimated hatchling mortality by quantifying, from a collection of 232 reef fishes, the proportion whose foreguts contained turtle hatchlings. Of the 89 fishes which had identifiable stomach contents, hatchlings were found in the guts of six specimens of *Lutjanus carponotatus* and one of *Epinephelus spp.* Extrapolating from data obtained in an unrelated study on the biomass of these species per unit area of reef flat, I estimated that these two species together consumed approximately 3800 (95% confidence interval 1593-7220) hatchlings, or 84% (42 - 100%) of the hatchlings that had entered the water during the study period. Around full moon, the same lunar phase during which the fish were collected by spearing, predation rates obtained by the tethering experiments varied, depending on the state of the tide, between 30-70%.

Although predation rates were significantly influenced by environmental variables, no correlation could be found between the timing of emergence from the nest and periods of reduced risk of predation in the water. Frequency distribution of emergence events were similar between nights that differed markedly in the times of high and low tides (Kolmogorov-Smirnov two sample test statistic = 0.20, p = 0.68).

Three possible models predicting the timing of emergence were generated and tested against the observed pattern. Hatchlings did not emerge uniformly throughout the diel cycle (Uniform emergence model, $X^2 = 59.986$, df = 6, $p < 0.001$) but emerged primarily in the early evening. The timing of emergence was found to be associated with changes in sand temperature gradients within the top ten centimeters of the sand column (Thermal gradient model, $X^2 = 4.239$, df = 3, $p \approx 0.25$) and not, as previously believed, by a given temperature of the surface of the sand (Threshold model, $X^2 = 12.736$, df = 4, $p < 0.025$) . I concluded that nocturnal emergence is more likely an adaptation to reduce mortality caused by physiological stress of the day time heat than a predator avoidance mechanism. These findings were supported by experimental manipulation of temperature gradients within the top 10 cm of the sand column in an artificial hatchery.

Behavioral and morphological adaptations increasing survivorship after the hatchlings enter the water were identified: 1) qualitative observations suggest that rapid early dispersal of hatchlings increases their probability of survival; 2) experimental trials showed that predation was significantly greater upon hatchlings painted black on the ventral surface than on those displaying the natural, countershaded pattern (McNemar's symmetry test , $X^2 = 6.231$, df = 1, $p = 0.013$).

Using a population model based on the Lefkovitch stage class matrix, the intrinsic growth rate of the eastern Australian green turtle population was found to be more sensitive to changes in survivorship in the pelagic and juvenile stages than to changes in any other stages of the life cycle. This is primarily due to the relatively low annual survivorship and the

associated long duration of those two stages. Change in hatchling survivorship in the shallow water reefal habitats was also found to have a significant effect on the intrinsic growth rate of the population and was similar in effect to the doubling of fecundity. Restricting the release of hatchlings to periods of high tides would result in an approximately 2 % increase in annual population growth rate.

Sea turtle biologists consider that hatchlings spend as short a time as possible in nearshore waters because of the high predation pressure in those habitats. The results of this study lend substantial support to that view. However, one species, *Natator depressus*, the only species of sea turtle without a pelagic phase in its life cycle, has apparently overcome the problem of predation in shallow water coastal habitats by producing larger, but fewer, hatchlings. No other sea turtle has taken up this evolutionary option and the costs and benefits of a life cycle involving a pelagic phase remain subject to speculation.

QUOTATION.

"I should not perhaps have got started talking this way about turtle eggs, because there is no end to it, really. But I feel strongly that everybody ought to know that the size of a complement of turtle eggs is no mere accident and not simply the payload that a lady turtle is able to swim with. It is a number packed with ecology and evolution. There are so many factors involved in setting it, in fact, that I think it may be worthwhile to try to make an inventory of them, to see how they work, and how they get so interwound with each other that thinking about them makes you finally feel that almost everything the race of turtle does, or that happens to it, is to some degree reflected in the number of eggs that the female drops into the hole she digs in the sand."

(The eloquent words of the late Archie Carr, in his classic chapter titled "A Hundred Turtle Eggs" In : So Excellent a Fishe, Anchor Natural History Books, 1973)

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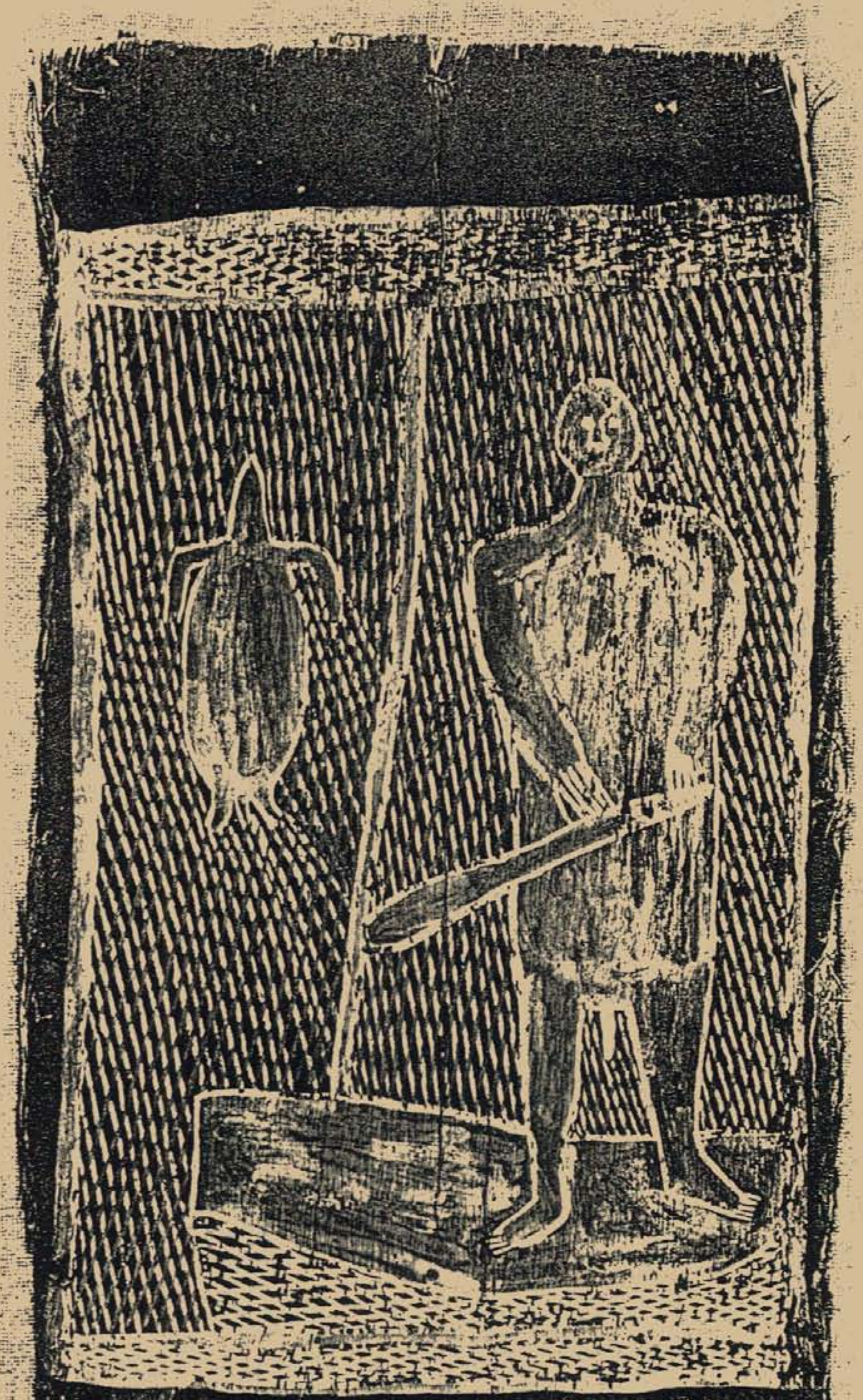


CHAPTER 1

GENERAL INTRODUCTION

The Man, Turi-Turi
Bark painting by Bananga (Yirrkalla)
National Gallery of South Australia

Turi-Turi was an expert at catching turtles. One day, when far out to sea, a heavy storm broke his bark canoe and he was drowned. The painting depicts Turi-Turi standing in his canoe, paddle in hand. The turtle he was chasing is on the left and the waves that destroyed his vessel are represented by the white band on the lower edge.

1 GENERAL INTRODUCTION

Students of the physical sciences have long recognized that in order to understand how systems work one must describe and understand the properties of and relationships between each of their components. By observing the behaviour of inanimate objects Newton established a set of laws which enabled an adequate understanding of the physical world around us.

Similarly, observation of the natural world and the patterns found within, allowed Darwin and Wallace to formulate the Theory of Evolution, a central tenet of modern biology. At the very basis of evolutionary theory is the variability in fitness between individuals. By definition, fit organisms make a greater proportional contribution to future generations than their relatively unfit counterparts (Stearns 1976, Begon *et al.* 1990). All aspects of an organism's morphology, physiology and behaviour effect its rate of reproduction and survival, and thus contribute to its fitness. Life history studies follow a holistic approach and attempt to take into consideration all relevant aspects of an organism's biology in order to understand the ecology of species and whole communities.

Life history theory was well established as early as 1954 and by the 1970's hypotheses relating to observed trends in life history traits were abundant (Stearns 1976). One concept, which has been particularly influential in the development of life history theory is "r - and K - selection", which broadly distinguished two main types of organisms.

Typical "r" selected species are characterized by: an unpredictable environment, uncertain adult survival, early age at first reproduction, semelparity, variable population size, small but many offspring, no parental care and a short generation time. "K" selected species, on the other hand, are typified by: a constant or predictable environment, uncertain juvenile survival, delayed reproduction, iteroparity, a long generation time and a constant population size at or near carrying capacity.

The r/K scheme is most severely limited by its failure to recognize that environmental fluctuations are a feature of all environments and these fluctuations may affect organisms differently in different life stages. Eventually, models were developed that differentiate between habitats in which the major effect of environmental fluctuations is on adult mortality and those in which juvenile mortality is affected most. In the latter case adults may choose to hedge their bets and not release all their offspring at one time into the same environment: Highly variable juvenile mortality results in delayed maturity, iteroparity, fewer offspring per reproductive episode and longer life. Environmental instability that affects adult survival results in increased reproductive effort, more offspring, shorter generation time and semelparity (Stearns 1976). However both the r/K and bet hedging models "predict the evolution of the same combination of life history traits, but for different reasons" (Stearns 1977). As yet no predictions of significantly different combinations of traits have been proposed.

the K- selected features of the adults and juveniles. In contrast, I suggest that mortality of the eggs and hatchlings is high and variable, a pattern which would explain the suite of r- selected life history characteristics found during these life stages. While similar differences between adults and eggs and hatchlings can be found in all species of the tesudines, they appear more pronounced in marine than in freshwater and terrestrial species.

Relevant empirical data on the mortality of hatchlings is imperative for the development of these ideas. But while sea turtles spend most of their lives at sea, our knowledge is predominantly based on observations of the females, their eggs and hatchlings on the nesting beach. Recent tagging studies have been extended to the feeding grounds of some populations and are now providing estimates of growth rates, age at maturity and reproductive rates (Limpus and Walter 1980, Balazs 1982, Limpus 1990). However, while tagging studies provide estimates of survivorship on the feeding grounds, survivorship in the early, aquatic life stages still remain largely a matter of speculation based on estimates of terrestrial mortality and theoretical considerations (Richardson and Richardson 1982, Frazer 1986, Iverson 1991).

In an extensive review of 52 studies, Stearns (1977) revealed that only 17 provided convincing evidence for the coexistence of life history traits as predicted by the accepted models of life history theory. In 16 cases the combinations differed from the accepted scheme; no conclusions could be drawn because of unreliable research methods in the remaining 19. This finding highlights the fact that life history theory is still incomplete and limited in its powers of prediction and explanation.

Sea turtles are an especially interesting group which does not fit any of the predicted combinations of life history traits. Sea turtles combine some characteristics typical of K- selected species. They are large bodied, long lived, iteroparous reptiles with a very long pre-reproductive period. They also have some characteristics typical of r-selected species. They lay large clutches of relatively small eggs and parental care is absent (Hendrickson 1980, Limpus and Walter 1980, Balazs 1982, Wilbur and Morin 1988, Elgar and Heaphy 1989). This apparent dichotomy holds whether one considers sea turtles against other organisms in general or within the context of testudines *per se.* In some respects sea turtles are the most K- selected of all the testudines (*i.e.* their large size) while in others they are the most r- selected with the largest clutches of relatively the smallest eggs and the highest annual reproductive output (Hendrickson 1980, Elgar and Heaphy 1989).

I hypothesize that this particular set of life history traits might be the result of different mortality schedules experienced by adult and hatchling turtles. I propose that once they settle into their coastal feeding grounds, mortality is relatively low and fairly constant - hence

The mortality of hatchlings after entry into the sea is assumed to be high, but until now, it has not been quantified. Mortality schedules are known to significantly affect a number of other life history parameters, in particular the size and number of offspring. Hence, quantifying hatchling mortality is important for several reasons:

1) to provide empirical data that can be used in life tables thus enhancing the understanding of the population dynamics of marine turtle populations;

2) to examine the similarities and differences in first year survivorship between freshwater, terrestrial and marine turtles;

3) to furnish insights into why sea turtles follow the general strategy of many marine organisms, characterized by a pelagic juvenile phase followed by recruitment into shallow water reefal or coastal habitats.

Predation is probably one of the main causes of mortality in the early life stages and as such, predation is expected to influence several behavioral and morphological characteristics of prey organisms. However, the principle of predator avoidance is often evoked by biologists without the support of quantitative observations. Students of sea turtle biology are no exception: Spatially and temporally concentrated nesting, nocturnal emergence from the nest, the frenzied activity in the first day or so after emergence, pelagic dispersal and countershading of hatchlings have all, at one time or another, been interpreted in terms of predator avoidance. This thesis will investigate the validity of such assertions by correlating patterns of predation and behavioral and morphological characteristics of hatchlings.

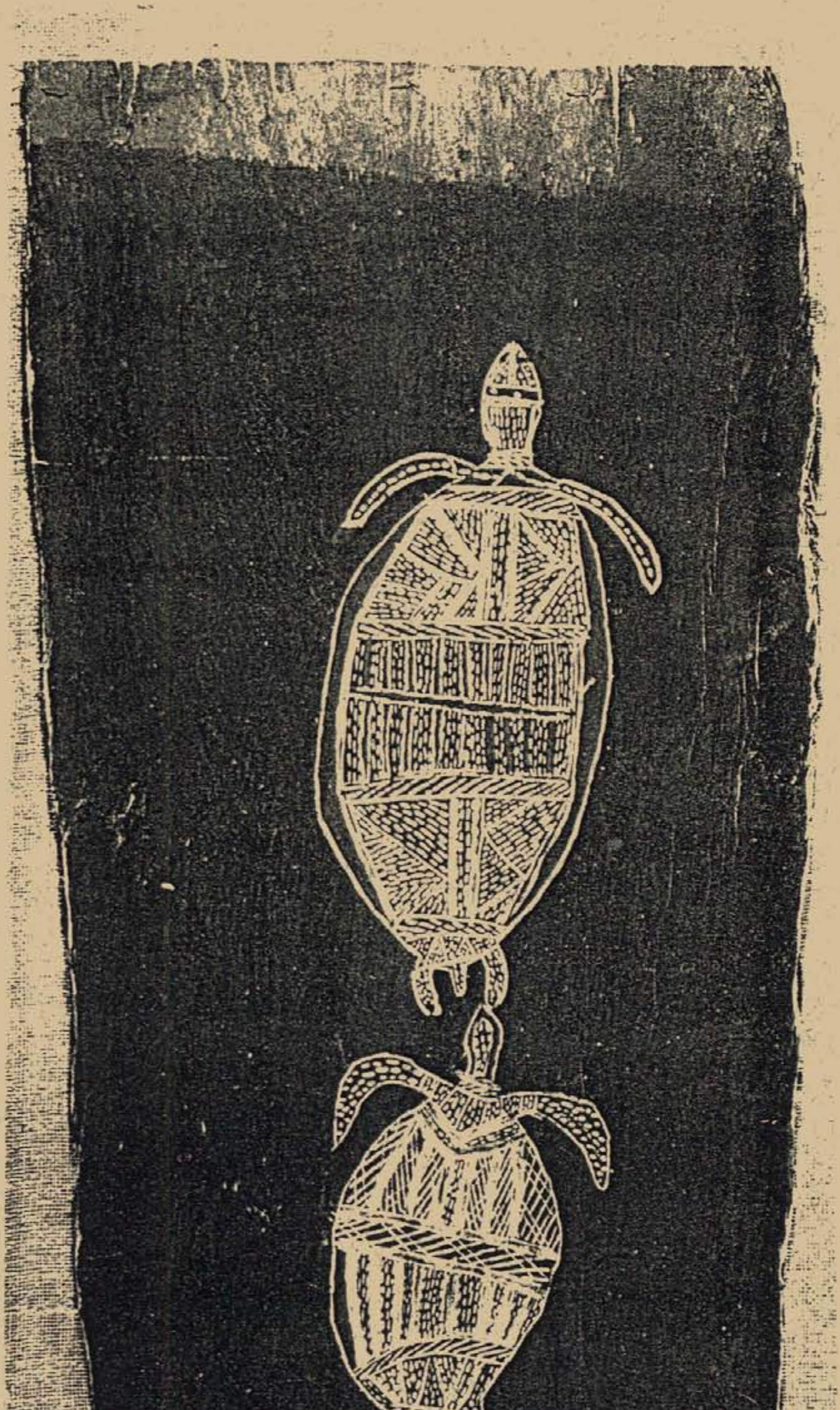
The specific aim of my study was to measure mortality of hatchling sea turtles after entry into the sea and assess if the mortality schedule of sea turtles is likely to account for the differences in life histories between the marine turtles and the turtles of freshwater and terrestrial habitats. To achieve this aim, this thesis: (i) identifies differences in life histories within the Testudineae, (ii) quantifies aquatic predation of sea turtle hatchlings and (iii) reconciles the results of these two lines of inquiry with my hypothesis that the combination of life history traits exhibited by sea turtles is a result of stage specific differences in mortality.

In Chapter 2, I examine the relevant literature and compare testudine life histories. The identification and verification of major differences between taxa allow a focused search for corresponding differences in the habitat-organism interface which may have led to the evolution of the observed differences in life history parameters.

Chapter 3 describes experiments that I conducted to measure hatchling mortality in shallow water coral reef habitats and which provide an estimate of survivorship in the first hour or so of the sea turtles' aquatic life. The influence of certain environmental variables on the predation rate was also investigated. In Chapter 4, I examine some behavioral and morphological characteristics of green turtle hatchlings which can be seen as adaptive in reducing early mortality.

This study provided insights about the influence of environmental factors on the rate of aquatic predation on green turtle hatchlings. This knowledge provides some previously unrecognized options for management . By using stage based population models, the potential of these options is explored in Chapter 5.

In the concluding remarks in Chapter 6 the main findings of this thesis are bruoght into focus and the relationships between predation, survivorship and fecundity are considered. The evolutionary background to these parameters is also discussed.



CHAPTER 2

A REVIEW OF THE LITERATURE

Turtles

Bark painting by Tatalara (Groote Eylandt)

National Gallery of South Australia

At the time of creation the mythical green turtle, Imoraka , and his wife made their camp on the southern coast of Groote Eylandt. Later their bodies were transformed into two low rocks on the sea shore.

Each season, when the female turtles come ashore to lay their eggs, the local people visit the two stones and chant the turtle songs over them. This ritual is to cause the turtles to lay many eggs.

2 A REVIEW OF THE LITERATURE.

2.1 INTRODUCTION TO THE TESTUDINES.

The characteristic that makes turtles (Order Testudines or Chelonia) one of the more easily defined groups of vertebrates is the presence of a hard shell. It consists of a convex dorsal part, the carapace, and an almost flat ventral part, the plastron. The two are connected by a bridge on each side. This rigid bony structure is unique among vertebrates in its degree of involvement with, and modification of, several major skeletal elements such as the shoulder girdle, the ribs and the vertebrae (Pritchard 1979, Burke 1991).

Gaffney (1984) provides an historical overview of chelonian systematics. Keys for the identification of the approximately 220 species of extant turtles, terrapins and tortoises are given by Carr (1952) and Pritchard (1979). Because the usage of these common names is loosely defined, I shall avoid using them. Throughout this review I shall use the word "turtle" to mean Testudines in general, and qualify this with reference to habitat (marine, freshwater or terrestrial) as required.

Among tetrapods, turtles are considered to be the epitome of delayed reproduction, longevity and iteroparity (Wilbur and Morin 1988). They have adapted to many different habitats and while they all lay amniotic eggs in subterranean nests, they display great variation in phenotypic traits such as body size, egg size, fecundity and age at first reproduction. Some turtles are less than 10 cm in straight linear length of the carapace, lay one or two eggs in a clutch, and may mature at approximately 4 years of age. Other species attain a large body size measuring over 70 cm in carapace length, lay over 100 eggs per clutch and may require 40 years or more to reach sexual maturity (Limpus and Walter 1980, Balazs 1982, Wilbur and Morin 1988).

What is the adaptive significance of this variability in these life histories? Can examination of these parameters enhance our understanding of the ecological strategies of sea turtles, in particular that of the green turtle *Chelonia mydas*, the subject of this dissertation?

2.1.1 AN OVERVIEW OF THE EVOLUTIONARY HISTORY OF THE TESTUDINES.

To understand the significance of life history characteristics, it is necessary to study trade-offs between growth, investment in reproduction and survival. It is also fundamental to recognize that many features of extant organisms evolved under different conditions from those that they experience today. Turtles are considered to be the most ancient of extant land vertebrates. The fossil record gives little information as to their origins and hence their early evolutionary history is somewhat uncertain. Unknown turtle ancestors presumably evolved from the original cotylosaurs or "stem reptiles" (Pritchard 1979, Obst 1986) or possibly originated from the saurians, one of the earliest forms of terrestrial vertebrates (Obst 1986). It is probable that the turtle lineage was already distinct by the early Permian, 200 milion years ago (Pritchard 1979, Gaffney and Meeker 1983). The earliest turtle fossils, members of the family *Proganochelidae* (*Proganochelys quenstedi* and the closely related *Triassochelys dux*) appear suddenly in the fossil record during the Triassic (225 million years ago). These animals, displaying the distinctive trunk morphology by which we recognize the order, are already true chelonians, not chelonian ancestors (Obst 1986, Burke 1991).

Speculations abound as to how the *Proganochelydae* evolved from the primitive reptile stem. It is certain that they did not evolve from any group which had already developed a lateral or dorsal temporal opening of the skull, nor from forms in which the palate was fused to the braincase. Thus, separation occurred not later than the early Permian (Carroll 1969). Ancestors have been sought amongst various fossil groups, including the plesiosaurs (Owen 1849, Baur 1887), the placodonts (Broom 1924), the pariesaurs (Gregory 1946) and the labyrinthodont, *Gerrothorax* (Vallen 1942, cited by Burke 1991). Watson (1914) presented *Eunotosaurus africanus* as the missing link between the Testudines and their cotylosaurian ancestors. In *Eutonosaurus,* however, no dermal bones are associated with the axial skeleton, the abdominal ribs are absent and the pectoral girdle is external to the ribs. It is now thought unlikely that *Eunotosaurus* was in the mainstream of testudinate evolution (Pritchard 1979, Burke 1991). Recent work based on cranial similarities between *Proganochelys* and *Eucaptorhinus*, a Permian captorhinomorph, suggests that the testudines evolved from a tetrapod with standard post-cranial morphology (Gaffney and Meekar 1983, Burke 1991). To date no fossils with intermediate morphologies between *Proganochelys* and the Captorhinomorpha have been discovered and the evolutionary history of the unique turtle body plan remains obscure.

The distinctive, shelled body form has imposed several limitations on the evolution of turtles (Hendrickson 1980). With the development of the shell, locomotory options were greatly limited. The limbs remained the only possible propulsive organs. Also lost was the option to give birth to large live young because the bony shell allowed no internal expansion for developing embryo(s) (Hendrickson 1980). Testudines do not give birth to a large number of live young, unlike several species of snakes, both marine and terrestrial. Consequently, testudines remain tied to the land for egg laying. Presumably as a result of the limitations to future development imposed by the shell, testudines remained conservative and have changed little since the Triassic (Zangerl 1969, Hendrickson 1980).

2.2. INTRODUCTION TO THE MARINE TURTLES.

2.2.1 EVOLUTION, MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATION TO THE MARINE ENVIRONMENT.

It is believed that the earliest turtles were marsh and swamp dwellers which subsequently radiated into truly terrestrial and aquatic, (including marine) habitats (Romer 1956, Pritchard 1979). Invasion of the marine environment occurred repeatedly, involving different testudine lineages. In Cretaceous times, there were four groups of sea turtles two of which, the Dermochelydae and the Cheloniidae, have extant representatives (Zangerl 1980). Successful invasion of the marine habitat required significant morphological and physiological modifications of the basic testudine condition.

Notable modifications, mostly reductionist in nature, occurred in the shell structure. Both the bony plates of the carapace and the extent of ossification of the plastral elements were greatly reduced (Romer 1956, Zangerl 1980). The plastron and the bridge became flexible to facilitate diving to relatively great depths. The ability to retract the head into the shell was lost, and instead the limbs, together with the short blunt head and neck, are faired smoothly into the shell structure. Maximum shell depth and width is well forwards and appears to coincide with the center of gravity, which is important in maintaining vertical and lateral stability in the water (Davenport *et al.* 1984).

The development of wing-like hypertrophied forelimbs coupled with an efficient swimming action (Davenport *et al.* 1984) and streamlined, hydrodynamically efficient body results in the superior speed and endurance of marine turtles. The hind flippers of all recent cheloniids are relatively small and evidence suggests that the living species are the only cheloniids that have their hind limbs modified as steering rudders (Zangerl 1980). Further merits of the special limb and body design features of marine turtles are discussed in detail by Davenport *et al.* (1984). Other adaptations to an aquatic way of life occur in the skull structure of all species of marine turtle which display a tendency toward the formation of a secondary palate thus separating, to varying degrees, the nasal passages from the buccal cavity (Romer 1956).

A major physiological adaptation to the truly marine existence is the remarkable ability of sea turtle hatchlings to maintain blood plasma homeostasis by drinking sea water. This ability, which is facilitated by salt secreting lachrymal glands (Bennett *at al.* 1986) is notably absent in all crocodilians, including the marine species *Crocodylus porosus*, although salt secreting glands in their tongues have been described (Bennett *et al.* 1986).

By the Cretaceous (100 million years ago), cheloniid turtles displayed all the major anatomical and structural adaptations to the oceanic environment that are features of present-day sea turtles (Pritchard 1979, Zangerl 1980, Obst 1986). From then on, the history of sea turtles is one of periodic radiations and pelagic specialization from a central primitive stock whose present day representatives are considered to be *Caretta* and *Lepidochelys* (Zangerl 1980).

2.2.2 MODERN SEA TURTLES: AN OVERVIEW.

2.2.2.1 Taxonomy.

Seven species of extant sea turtles are currently recognized (Frair 1979, 1982, Zangerl 1980, Limpus *et al.* 1988). They are grouped into six genera within two families. The family Cheloniidae includes the green turtle, *Chelonia mydas*; the loggerhead, *Caretta caretta*; the hawksbill, *Eretmochelys imbricata*; the flatback, *Natator depressus;* the olive ridley, *Lepidochelys olivacea;* and Kemp's ridley, *L. kempi*. The family Dermochelidae contains one species, the large leatherback turtle, *Dermochelys coriacea*.

2.2.2.2 Background information about the species.

The green turtle (*C. mydas*), an herbivore (Garnett *et al.* 1985, Lanyon *et al.* 1989), is a circumtropical species found between the northern and southern 20°C isotherms (Hirth 1971, Pritchard 1979, King 1982). Its nesting is largely restricted to a few geographically discrete rookery regions (Hirth 1971, Bustard 1972, Balazs 1980, King 1982).

The other species are all carnivores. Loggerheads (*C. caretta*) have been described as "antitropical" in distribution (Pritchard 1979), with most major rookery areas situated outside the tropics (Bustard 1972, Pritchard 1979, Ross 1982). The loggerhead diet consists mainly of hard shelled animals such as mollusks and crustaceans. Their ability to cope with this diet is facilitated by their massive head, with jaws and palate acting as crushing plates (Moodie 1979, Thompson 1980). At least in some parts of their range loggerheads bury themselves in thick mud and hibernate during the cold season (Carr *et al.* 1980).

By comparison with green and loggerhead turtles relatively little is known about the other five species of the Cheloniidae. The geographical distribution of hawksbills (*E. imbricata*) is similar to that of green turtles (Pritchard 1979, King 1982). Their preferred habitats are reefs, shoals and estuaries, where they feed on a wide range of benthic animals (Carr and Stancyk 1975). Unlike green turtles, hawksbills nest mostly individually, dispersed over many kilometers of remote beach.

Olive ridleys (*L. olivacea*) are found in the tropical coastal areas of the Indian, Pacific, and Atlantic oceans. Their diet consists mainly of crustaceans. They nest in often spectacularly large aggregations which, in Latin America are often referred to as "arribada". (Pritchard 1979, Ross 1982). By contrast, the geographical range of Kemp's ridley is limited to the Gulf of Mexico and the Atlantic coast of the USA. Nesting occurs in large diurnal arribadas in a single rookery region on the Atlantic coast of Mexico. The diet of Kemps ridley (*L. kempi*) is probably similar to that of *L. olivacea* (Mrosovsky 1983).

Another sea turtle with a restricted range is the flatback which feeds mainly on soft-bodied benthic animals (Limpus *et al.* 1988). Flatback feeding grounds extend along the warm temperate and tropical waters of the Australian continental shelf, and its only breeding areas are in Australia (Limpus *et al.* 1983 b, 1988).

The leatherback is the largest species of extant turtle. It is easily distinguishable from the other sea turtles by the lack of keratinised scutes over the shell and skin. Structural rigidity of the carapace is achieved by the development of five longitudinal ridges. The leatherback is regarded as a truly pelagic animal maintaining itself on a diet of jellyfish (Mrosovsky 1983), and other soft bodied animals (Limpus 1984). A thick fat layer and a counter-current heat exchange system in the flippers of this turtle allow it to forage in cool deep waters of lower latitudes, well outside the tropics (Mrosovsky 1980, Limpus 1984). Major nesting grounds are found along thePacific coast of Mexico, the tropical Atlantic coast of Latin America, Trengganu in Malaysia, Natal, Papua-New Guinea and Sri Lanka.

2.3 TESTUDINE LIFE HISTORIES, WITH SPECIAL REFERENCE TO THE MARINE TURTLES.

2.3.1 INTRODUCTION.

The natural history of turtles has been reviewed previously by Bustard (1972, 1979), Auffenberg and Iverson (1979), Bury (1979) and Wilbur and Morin (1988). The testudine line is conservative in some regards. The general patterns of testudine structure and function (see section 2.1 above) has imposed constraints to further development. All turtles are oviparous, lay their eggs on land and appear to incur high mortality during the early life stages (Iverson 1991). Reproduction is generally delayed until individuals are close to their asymptotic size. Adult survivorship is high, with a presumably long reproductive life (Wilbur and Morin 1988). Superimposed on these basic similarities, however, is a remarkable diversity of adaptations to the many different environments in which turtles live.

Since the pioneering work of Archie Carr over three decades ago, much has been learnt to fill the many gaps in our understanding of sea turtle life histories. The females and the hatchlings of these turtles are relatively easy to observe on land. Several hundreds of thousands of sea turtles have been tagged world wide while nesting and, more recently, while on their feeding grounds (Limpus and Walter 1980, Limpus and Reed 1985). Despite the problems of tag loss (Hughes 1982, Mrosovsky 1983, Limpus 1992a), tagging programs have provided estimates of breeding frequency and annual fecundity; information on the migratory paths and geographical range of females breeding at a given rookery; and longevity beyond the time when first tagged. With certain assumptions, the data generated by tagging programs have been used to describe population dynamics (Marquez *et al.* 1982a, b; Richardson and Richardson 1982, Frazer 1986). The relationship between the geographical and genetic population structure of loggerhead and green turtles derived by tagging studies have been verified and extended by the application of modern electrophoretic techniques (Gyuris and Limpus 1988, Meylan *et al.* 1990, Bowen *et al.* 1992 J. Norman and C. Moritz pers. com.). Eggs and hatchlings have been counted and measured throughout the ranges of sea turtles. Some good estimates on survivorship of eggs are now available (Fowler 1979). Sex ratios of wild populations have been studied using modern endocrinological (Owens 1982, Wibbles *et al.* 1990) and surgical (Limpus and Reed 1985) techniques.

By reptilian standards, all sea turtles are large bodied animals that are highly adapted for efficient long distance travel in the sea (Davenport *et al.* 1984). In comparison with other turtles, they are also noted for their unusually high fecundity (egg production) (Moll 1979, Pritchard 1979, Hendrickson 1980, Heatwole and Taylor 1987). With the exception of the large Amazon river turtle, *Podocnemis expansa,* no other turtles attain such a large body size and lay as large a clutch as do marine turtles.

Natural selection, an inevitable consequence of heritable differences in fitness, acts on individuals to maximize the number of surviving offspring. Organisms are required to optimize the partitioning of their resources between the demands of growth, maintenance, and reproduction. Increased reproductive effort may yield certain benefits, but there are costs such as decreased probability of parental survival. Selection favors the optimization of these costs and benefits (Stearns 1977). Furthermore, selection will divide the total reproductive effort into production of offspring of an optimal size and number thereby maximizing a female's fitness in terms of returns per unit of resource invested (Charnov and Krebs 1973, Lloyd 1987, Winkler and Wallin 1987, Fleming and Gross 1990).

In developing a general understanding of the adaptive strategies of sea turtles, much can be learnt by comparing the life history parameters of marine, freshwater and terrestrial species. While the great variety of adaptations to a myriad of habitats make the notion of stereotyped "terrestrial", "freshwater" or "marine" species difficult, such a comparison allows one to focus on aspects of the habitat-phenotype relationships of sea turtles and facilitates the interpretation of their large body size and apparently high fecundity.

Generally, high fecundity implies a strongly concave survivorship curve with high mortality during the early life stages (Hendrickson 1980, Graham and Branch 1985, Leis 1991). Low survivorship of juveniles may result primarily from either starvation or predation. The main focus of this thesis is to investigate the impact of predation during the early life stages on life history evolution and population dynamics of marine turtles. Life histories are primarily concerned with the interaction between reproductive rates and survival (Millar and Hickling 1991). I shall consider the role of predation in the context of relevant components of the organism-environment interface, which interact in the shaping of life histories.

2.3.2 REPRODUCTIVE RATES.

2.3.2.1 Frequency of reproduction.

Reproductive cycles of turtles have only recently been studied rigorously and it is now apparent that female turtles do not necessarily breed at regular intervals but become reproductively active only when they have accumulated the necessary energy reserves (Kennett and Georges 1990, Wilbur and Morin 1988, Kwan 1991). Further, for most species, the females' reproductive output in any given breeding season is divided into several clutches of eggs. Terrestrial and freshwater turtles typically lay one to four clutches in a breeding season (Elgar and Heaphy 1989). Most green turtles lay between three and seven clutches of eggs (Hirth 1971) although some workers report that a high proportion of females deposit only one clutch (Ehrhart 1982). Hendrickson (1958) reported as many as 11 clutches per female in Sarawak. Because of the great variability within sea turtles as a group, it is difficult to make a unifying statement about the number of clutches laid per female (Ehrhart 1982).

The widespread tendency for turtle species to lay multiple clutches in a season may be considered as a typical example of bet hedging: There may be significant selective advantages in dividing eggs into several smaller clutches; such as minimizing the probability of all eggs laid in a season being destroyed and achieving a desirable sex ratio amongst the hatchlings by exposing different clutches to different temperature regimes throughout the breeding season. Selection for several smaller clutches is however opposed by the need to minimize the amount of energy per egg laid expended during nest construction and the cost of maintenance during the internesting periods. Working with loggerhead turtles, Hays and Speakman (1991) showed that the energetic cost of nest construction may be a significant proportion of a female's total energy investment in each egg. Hence, for marine turtles and possibly other species where the relative cost of nest construction is high, and where the probability of a nest being destroyed is independent of clutch size, turtles should divide their reproductive output into fewer, larger clutches. However, their study ignored intra- and interannual variation in currents and the vagaries of weather which may affect survivorship of hatchlings at sea (Brown 1990) and the possible variability in mortality of the hatchlings as they cross shallow water coastal habitats. Hence sea turtles may be under relatively stronger selective pressure than terrestrial and freshwater turtles to divide their eggs into larger numbers of clutches.

It appears that for each species of turtle, be it marine, freshwater or terrestrial, the number of clutches per breeding individual (and hence the total number of eggs laid) as well as the proportion of mature females that breed in any season is influenced by a number of environmental parameters, most of which relate to the quantity and quality of food available (Wood and Wood 1980, Wilbur and Morin 1988, Limpus and Nicholls 1988). Some genetic factors may also be involved (Wilbur and Morin 1988).

2.3.2.2 The number and size of offspring.

2.3.2.2.1 Eggs.

The females of all species of turtle deposit their eggs on land, usually in nests dug into various substrates ranging from loose sand to clay. Sea turtles dig their nests in moderately well sorted beach sand of low organic content (Mortimer 1990). Several species of the *Chelidae* and *Kinosternidae* depart from the usual pattern of nest construction and lay eggs on the ground and cover them by leaf litter (Packard and Packard 1988). No post-ovipositional parental care occurs in turtles (Carr 1973, Bustard and Greenham 1969, Bustard 1972, Hendrickson 1980, Shine 1988).

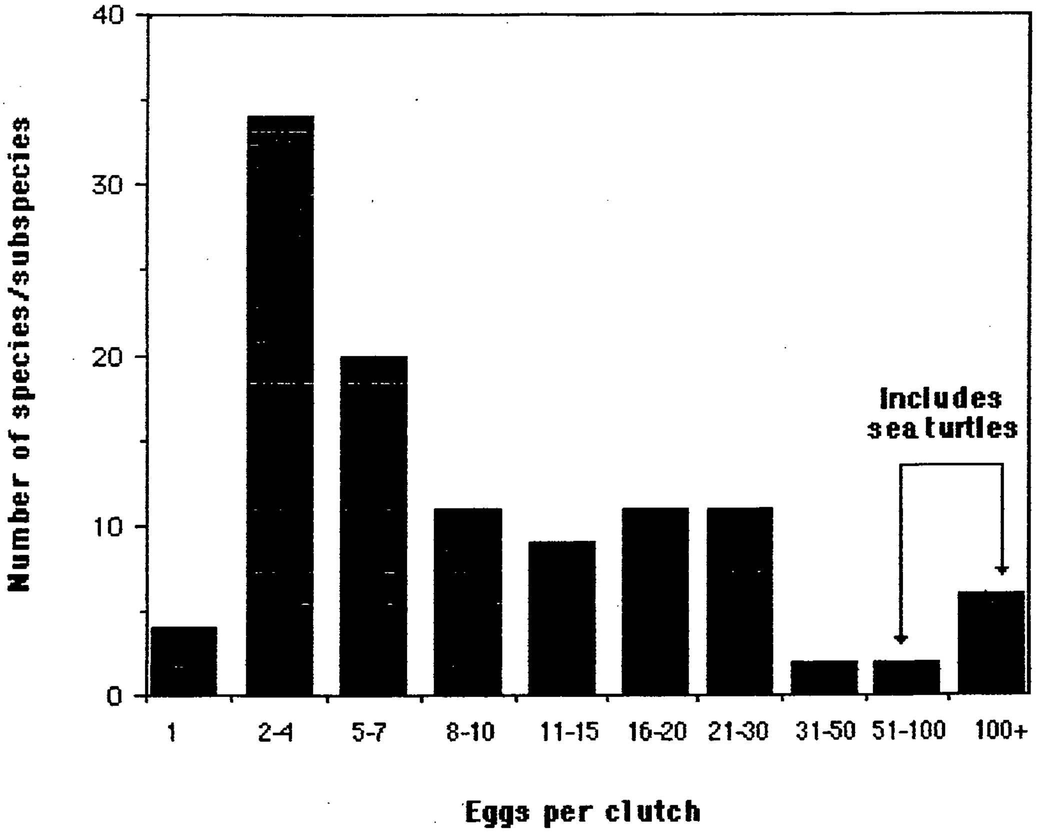
The physiological ecology of testudine eggs has recently been reviewed by Packard and Packard (1988). Most turtles, including cheloniids, dermochelyids, testudinids and several freshwater genera lack heteromorphic sex chromosomes and sexual differentiation is affected by the temperature of incubation (Packard and Packard

1988). The adaptive value of temperature-dependent (TSD) versus genetic sex determination (GSD) remains unexplained (Ewert and Nelson 1991). Earlier efforts to understand TSD in reptiles postulated that some reptiles lack the genetic variation that would allow the evolution of GSD (Bull 1980, 1983, Mrosovsky 1980), or that developmental temperature would be linked to differential fitness (Charnov and Bull 1977). Further explanations have been advanced by Ewert and Nelson (1991) and it now appears unlikely that TSD is simply a vestige of an early sex determining system unrelated to current conditions.

Among testudines, incubation periods vary markedly as does the time the hatchlings spend in the nest following completion of development. As sea turtles nest on unstable sandbars and beaches, they typically have short incubation periods (Ewert 1979) and emerge without delay (Mrosovsky 1968, Bustard 1972, Carr 1973, Miller and Limpus 1981, Christens 1990). The period of embryogenesis in *C. mydas* ranges between 47-94 days depending on the incubation temperature (Miller 1985) whereas most North American freshwater turtles have mean incubation periods of at least 60 days (Gibbons and Nelson 1978). The hatchlings of many freshwater species may overwinter in the nest. The adaptive significance of this variation in the timing of emergence is discussed by Gibbons and Nelson (1978) and is best understood in terms of survival probabilities of the hatchlings. Overwintering hatchlings await environmental cues, that indicate the high probability of favourable conditions such as winter cold followed by spring warm-up in the temperate regions or the onset of heavy rainfall in the tropics.

The relationship between the size and the number of eggs in a clutch has received considerable attention (Moll 1979, Ehrhart 1982, Wilbur and Morin 1988, Elgar and Heaphy 1989). Clutch sizes in turtles range from one egg in some emidids and testudinids (Elgar and Heaphy 1989) to 192 in *E. imbricata* (Limpus *et al.* 1983 a). Most turtles, however, lay less than 30 eggs per clutch (Moll 1979 and figure 2.1). Recent studies have identified a significant covariation between habitat and relative egg weight and relative clutch size (i.e. egg weight and clutch size corrected for body size effects). Terrestrial turtles lay larger and fewer eggs than freshwater species and marine turtles lay the relatively smallest eggs in the largest clutches (Elgar and Heaphy 1989). A significant negative correlation between relative clutch size and relative egg weight suggests a trade-off between these two variables. However, a positive correlation between relative clutch size and relative clutch weight implies that such trade-off is incomplete, that is, species that lay comparatively larger clutches may not fully compensate by producing proportionally smaller eggs (Elgar and Heaphy 1989).

Figure 2.1 Histogram showing the mean or usual clutch size of 109 species and subspecies of turtles (after Moll 1979).



The trade-off between egg size and clutch size in testudines is further complicated by the fact that many species lay several clutches in a breeding season thus relaxing the constraints imposed by the size of the female's body cavity (Moll 1979). This important aspect in the evolution of the size-number compromise has received only cursory mention by previous authors. Information has been collected on the size and number of clutches (laid in single breeding seasons). However, due to the paucity of long term studies, little information is available on the annual variation of these statistics or, most significantly, on reproductive life span. Consequently, no reliable measures of expected annual fecundity are available for most species, although well founded estimates of these parameters have been produced for a population of loggerhead turtles (Richardson and Richardson 1982, Frazer 1983, 1984, 1987, Crouse *et al.* 1987). The estimated annual fecundity of loggerheads at Little Cumberland Island is in excess of 100 eggs and other species of sea turtles yield similarly high values when calculations are based on the number of eggs laid per season, divided by the mean or modal interseasonal nesting interval (Table 2.1). Frazer (1984) cautions against the use of this method for estimating per capita annual egg production since the results can only be viewed as a crude first order approximation. Inaccuracies in such estimates may result from one or more of the following: 1) incorrect estimation of the number of clutches laid per female; 2) variation in the remigration intervals or 3) highly skewed data on clutch size.

Table 2.1 Estimates of annual fecundity among sea turtles (data from Harrisson 1956, Hendrickson 1958, Hirth 1980, Marquez *et al.* 1982 a,b, Brooke and Garnett 1983, Frazer 1984, Frazer and Richardson 1985.)

Species	Location	CS	NC	RI	AF
C.mydas	Tortuguero	110	2.8	3	103
	Surinam	138	2.9	2	200
	Heron Is. Aus	110	4.5	4	124
	Hawaii	104	1.8	2	94
	Mexico, Pacific	65	4	1.8	144
	Sarawak	105	6-7	3	227
N. depressus	Mon Repos	50.2	3	3	50
C. caretta	Sth. Africa	114	4.5	2	257
	Georgia,USA	120	2.5	2-3	120
E. imbricata	Tortuguero	161	≥2	3	≥107
	Seychelles	182	4	3	247
	Seychelles	160	3	2.5	192
L. olivacea	Surinam	116	1.4	1	162
	Mexico, Pacific	100	3	2	150
	Mexico, Pacific	95	3	1.3	219
L. kempii	Gulf of Mexico	105.5	1.3	1-2	78
D. coriacea	Trengganu	83.5	2.2	2	92

CS=mean clutch size, NC=mean number of clutches per breeding season,

RI=modal renesting interval in years, AF=estimated annual fecundity.

Wilbur and Morin (1988) and Elgar and Heaphy (1989) tabulated data on life history variables including clutch size and number of clutches per season for an extensive list of turtle species (Appendix 1). Annual fecundity of terrestrial and freshwater turtles is well below that calculated for the marine species even if all females of terrestrial and freshwater turtles are assumed to breed in each nesting season which, however, is apparently often not the case. (Tinkle *et al.* 1981, Gibbons 1983, Wilbur and Morin 1988, Kennett and Georges 1990). In the absence of data on survivorship or reproductive life span, comparisons of lifetime reproductive output between and within species remain speculative. Notwithstanding our limited knowledge, it appears that the lifetime reproductive output of sea turtles is very high, which distinguishes them from most other turtles (Hendrickson 1980, Pritchard 1979, Moll 1979, Hirth 1980).

To help explain the high variability in clutch size and frequency of nesting among species, Wilbur and Morin (1988) reviewed the literature on geographic variation within widely distributed species. They found that among freshwater turtles, variation in latitude and climate often correlated with several aspects of reproductive rates such as clutch size, the number of clutches per season and age at maturity. In the United States, females of the southern populations of *Sternotherus odoratus* mature earlier at a smaller body size and produce more clutches of eggs per year than females in the northern populations. Also in the United States, similar differences are found between the southern and northern populations of *Chrysemys picta*. Whether such differences are the result of long-term natural selection or phenotypic plasticity remains undetermined. Similar generalizations can not be drawn for even the most often studied species of marine turtle, *C. mydas*. The estimated annual fecundity of female *C. mydas* ranges between 94 and 227 eggs (Table 2.1). Reproductive rates of sea turtles may be influenced not only by latitude, ambient temperature, forage quality, etc., but also by the distance traveled between nesting and feeding grounds (Bjorndal 1982,1985). Also, the breeding population of most rookeries is drawn from a variety of feeding grounds, located at different distances from the nesting beach and offering different forage quality (Limpus *et al.* 1992). Consequently, measures of reproductive rates taken at a particular rookery will reflect this multiplicity of factors and hence evolutionary processes will be considerably more difficult to decipher.

Comparisons between the different sea turtle species are also difficult, due to the magnitude of within-species variation as evidenced by *C. mydas* above. The paucity of long term studies for the other species do not allow adequate description of intra- and inter-specific variation. However, one species, *N. depressus,* whith body size somewhat smaller than *C. mydas* and about the same size as *C. Caretta,* has a clutch size less than half of the clutch size of other marine turtles while the eggs and hatchlings are significantly larger (Walker and Parmenter 1990) (also see section 2.3.2.2.2 below).

2.3.2.2.2 Hatchlings.

Hatchling sea turtles typically emerge from their nests at night (Hendrickson 1958, Bustard 1967, Nellis and Small 1983, Witherington *et al.* 1990). Two advantages of nocturnal emergence have been suggested: 1) avoidance of physiological stress caused by high daytime temperatures and 2) protection of the hatchlings from terrestrial, airborne (Hendrickson 1958, Mrosovsky and Shettleworth 1968, Bustard 1972) and possibly aquatic predators. This study will investigate whether the timing of emergence is likely to have evolved to minimize predation.

Little is known about the aquatic, early post-hatchling phase of the life history of any turtle. After emergence, hatchlings of freshwater species enter the habitat that is occupied by the adults where the hatchlings presumably exploit cryptic microhabitats (J. Parmenter pers. comm.). Hatchlings of terrestrial species disperse slowly from the area of hatching, the rate being largely determined by the availability of local food resources (Auffenberg and Iverson 1979). Sea turtle hatchlings rapidly make their way to the sea where they are lost to human observers until, several years later, they are sighted again in their shallow water feeding grounds as small juveniles. Although poorly understood, the post-hatchling period, or "the lost years", of sea turtles is thought to be spent in an open ocean environment (Carr 1973, Witham 1980, Limpus *et al.* 1984, Carr 1986). As an exception, *N. depressus* appears not to have a pelagic phase in its life cycle and hatchlings are found living sympatrically with the adults (Walker and

Parmenter 1990). The absence of oceanic dispersal would readily explain why this species has a highly restricted geographical distribution. The large size of hatchling *N. depressus* is believed to offer some protection from the numerous inshore predators as well as offering several physiological advantages which facilitate diving (Walker and Parmenter 1990, Walker 1991).

2.3.2.2.3 Evolutionary considerations.

There is evidence to suggest that, in general, selection acts primarily, although not exclusively, on the size rather than the number of offspring (Lloyd 1987, Ford and Seigel 1989). The curve relating the fitness of each offspring to the amount of parental investment it receives is sigmoidal. The optimum offspring size can be specified conceptually as a point along the curve at which the proportional benefits of increasing the size and the number of offspring are equal (Brockelman 1975, Lloyd 1987). The theoretical rationale for selection based on offspring size rather than number is provided by Price and Schluter (1991) who explain that genetic parameters of life history traits such as fecundity will have lower heritability than those of the underlying morphological, physiological and behavioral traits. The shape of the offspring-fitness curve is dictated by a number of parameters such as the nature of the physical environment, food availability, predation, competition and susceptibility to disease. Currently our knowledge of the ecology of turtle populations is inadequate to understand fully the offspring size-number compromise of particular species. Nests and hatchlings of many freshwater and terrestrial species for instance, are notoriously difficult to find in their natural habitats. Rates of nest disturbance are often difficult to measure because undisturbed nests may often not be found (Tinkle *et al.* 1981, Parmenter 1985). Introduced predators or natural predators whose numbers are enhanced by man are often amongst the major nest predators of both freshwater and marine turtles (Auffenberg and Iverson 1979, Fowler 1979, Stancyk 1982, Parmenter 1985, Wilbur and Morin 1988). Current predation rates on nests are therefore likely to be different to those under which reproductive patterns have evolved. This presents further difficulties in understanding the role of predation in the evolution of life histories.

2.3.2.3 Growth and maturity.

The growth of juveniles to adults of both freshwater and marine turtles is satisfactorily described by von Bertalanffy models (Bjorndal and Bolten 1988, Frazer *et al.* 1990). Major changes in growth rates occur at hatching, at sexual maturity and upon reaching asymptotic size. Not only do growth rates change throughout an individual's life but they also change throughout the year reflecting environmental conditions such as temperature, moisture regimes and food availability (Balazs 1980,1982, Georges 1985, Congdon *et al.* 1987, Heatwole and Taylor 1987, Kennett and Georges 1990, Iverson *et al.* 1991). Consequently, maturation times may differ significantly between members of the one population and between populations that are using different foraging areas (Bradshaw 1971, Balazs 1982, Zug *et* *al.* 1986, Bjorndal and Bolten 1988, Congdon *et al.* 1987, Limpus 1992 b).

Most hatchling turtles are carnivores, presumably to facilitate the early rapid growth which may be important if the armored shell is to become effective as protection against predators (Greene 1988, Wilbur and Morin 1988). However, the actual growth rates of wild post-hatchling turtles are not known. Most juveniles grow slowly and growth may slow markedly or stop altogether on reaching maturity.

Turtles usually take several years to reach maturity: ten years or more is not an uncommon maturation time (Heatwole and Taylor 1987). Until recently, it was believed that most species mature at a specific size rather than a specific age (Moll 1979). Long term, rigorous studies are now revealing that not all individuals commence breeding upon reaching the size of the smallest breeding adults (Carr and Goodman 1970, Limpus 1992 b). It is now evident that age, size, nutritional status and probably genetic factors determine when an individual reproduces for the first time (Gibbons *et al.* 1981, Luckenbach 1982, Parmenter 1985, Limpus 1992 b). Slow growth rates plus the large body size of sea turtles results in protracted periods of 30 years or more to reach sexual maturity (Limpus and Walter 1980, Balazs 1982, Frazer and Ehrhart 1985, Limpus 1992 b) The growth rates and ages at maturity of the larger-bodied terrestrial and freshwater species are similar to those of the marine turtles, with no real differences in growth physiology between species occupying different broad habitat types (Zug *et al.* 1986). The relationship between a turtle species' size and mean age at maturity is not linear and hence the size alone is a poor predictor of any species' mean age at maturity. For example, the small American desert tortoises of the genus *Gopherus* mature in the wild at a carapace length of 23-26 cm, between 15 and 20 years of age (Bury 1982). By contrast *Geochelone gigantea*, another terrestrial turtle, measures 75 cm in carapace length when mature at 25 years of age (Wilbur and Morin 1988).

There is also large variability in growth rates between similar sized individuals living sympatrically which makes age estimates based on size of individual turtles quite unreliable (Bjorndal and Bolten 1988, Limpus 1992b) To date, no technique has been developed to age turtles (Castanet and Cheylan 1979, Zug *et al.* 1986, Klinger and Musick 1992). Despite their critical importance, gaps in our information on growth rates, age at maturity and longevity remain as major obstacles to the understanding of testudine life histories.

Nutrient and/or energy limitation has been repeatedly cited as the main reason for the very slow growth rate and late maturation of turtles in general (Bury 1982, Kennett and Georges 1990, Cogger, pers. comm.). The accelerated growth rates and earlier maturity observed in captive as against wild turtles are ascribed to year-round continuous high-quality feeding of captive animals (Wood and Wood 1980, Luckenbach 1982). Nutrient limitation has been repeatedly cited as the main reason for the very slow growth rate and late maturation of the herbivorous green turtle (Balazs 1982, Bjorndal

1982). Captive green turtles fed on high protein commercial diets grow much more rapidly than do wild green turtles on herbivorous diets (Bjorndal 1985). Growth rates of the benthic feeding carnivorous loggerhead and hawksbill turtles appear to be significantly faster than that for the herbivorous green turtle and consequently those species probably mature earlier (Mendonca 1981, Bjorndal and Bolten 1988).

In general, fitness is maximized by maturing as early as possible. However, in some circumstances, delaying reproduction may be a more advantageous strategy. Age specific fecundity and age specific survivorship are parameters that strongly influence age at maturity. Bell (1976) showed that in species in which fecundity increases with age and in which immature animals survive as well as adults do, it may be advantageous to delay maturity. There is some evidence to show that turtles fulfill these criteria (Gibbons 1968, Wilbur 1975, Tinkle *et al.* 1981, Frazer 1986). Wilbur and Morin (1988) argued, more simplisticly, that age at maturity may be set by the time it takes to reach given body size at which the trade off between predation and reproduction favors the switching of resources from growth to reproduction. However, if annual survivorship after the first year or so of life is not increased with increasing body size, then age and body size at maturity may more likely be determined by the size and number of offspring required for the species to maintain itself.

2.3.3 REPRODUCTIVE MIGRATIONS.

All sea turtles undertake periodic migrations from their feeding grounds to breed at often distant rookeries (Carr 1980, Meylan 1982, Mortimer 1982, Limpus *et al.* 1992). Long range movements associated with reproduction or in search of more favourable habitats by several freshwater species have also been reported (Gibbons 1986, Kennett and Georges 1990) but such behaviour appears to be atypical for terrestrial turtles (Auffenberg and Iverson 1979, Gibbons 1986). A direct comparison between the migratory achievements of freshwater and marine species is difficult as most studies record the terrestrial component only of movements which are associated with the breeding of freshwater species. However, the migration distances of sea turtles are typically many times those of freshwater species, even if the larger body size of marine turtles is taken into account (Table 2.2).

Table 2.2. Recorded long distance breeding migrations of several freshwater and marine turtles. Where body size (straight linear or curved length of the carapace) was not given in the publication of the migration record, I used size given for the species inTable I of Wilbur and Morin (1988). (* Movement over land. † Species with many migration records. Only the shortest and longest distance record are shown.)

Species	Typical body length (m)	Distance traveled (x10^3 m)	Size/distance ratio (x10^3)	Source (see below)
Freshwater species:				
Pseudemys scripta	0.2	0.4 *	2	a
		1.6 *	8	a
Trionyx muticus	0.12	4	33	a
Malaclemys terrapin	0.2	0.15*	~1	a
Emydoidea blandingii	0.15	0.1 *	6	b
		0.144 *	~1	b
Terrapene carolina	0.13	0.45*	3	c
Chrysemys picta	0.13	0.09 *	~1	d
Chelydra serpentina	0.25	0.183 *	~1	e
		0.1*	8	e
Marine species:				
C. caretta †	0.95	279	294	f
		2548	2686	f
C. mydas †	1.07	2	~2	f
		3000	28038	g
L. olivacea †	0.68	400	59	g
		1900	27944	g
E. imbricata †	0.63	385	464	h
		1650	1988	h

(a) Gibbons1986 , (b) Ross & Anderson 1990, (c) Williams &Parker 1987,
(d) Cristens & Bider 1987, (e) Congdon *et al.* 1987 , (f) Limpus *et al.* 1992,
(g) Meylan 1982, (h) Parmenter 1983.

Both male and female sea turtles leave their feeding grounds and migrate to traditional rookery regions where insemination of each female by several males takes place in relatively protected waters near the nesting beach (Booth and Peters 1972, Comuzzie and Owens 1990). By contrast, the males of many freshwater and terrestrial species may enlarge their areas of activity during the breeding season to take in the activity range of several females (Auffenberg and Iverson 1979, Obst 1986) as mating occurs within the females' activity areas. The peak of the breeding period varies but significantly correlates with latitudinal and between-year variation of several environmental parameters such as rainfall and ambient temperatures. In most species, breeding occurs during spring or summer although autumn and year-round nesting also occur (Moll 1979,Tinkle *et al.* 1981, Christens and Bider 1987, Echtberger and Ehrhart 1987, Iverson *et al.* 1991).

2.3.4 SURVIVORSHIP.

Survivorship is affected by various causes of mortality such as disease, predation or lack of food. Assessment of the relative importance of the various causes of mortality is difficult in the absence of empirical data. It is assumed that the vulnerability of turtles to predation decreases with size (Wilbur and Morin 1988, Iverson 1991) and therefore survivorship would be positively correlated with size (Frazer *et al.* 1991). Some researchers have suggested that hatchling turtles exhibit the relatively high annual survivorship, characteristic of adults immediately upon entering the aquatic habitat (Gibbons 1968, Wilbur 1975, Tinkle *et al.* 1981). It is agreed however, that survivorship of the eggs and hatchlings of terrestrial and freshwater turtles on land is very low (Auffenberg and Iverson 1979, Parmenter 1985, Wilbur and Morin 1988). Survivorship in the early life stages of marine turtles is estimated to be particularly low (Hirth 1971, Richardson and Richardson 1982, Crouse *et al.* 1987, but see Iverson 1991), and possibly much lower than that of other turtles (Ehrenfeld 1979).

2.3.4.1 Survivorship of eggs and hatchlings.

Considerable data have been accumulated on egg mortality, however, much of this is qualitative (Wilbur and Morin 1988, Tinkle *et al.* 1981, Stancyk 1982). Egg mortality appears to be primarily the result of predator activity. Predators may consume all or a portion of the eggs in a clutch but uneaten eggs may die in the disturbed nests. A wide range of mammalian, avian and saurian predators preys on turtle nests and newly hatched turtles (Stancyk 1982, Greene 1988, Wilbur and Morin 1988, Frazer *et al.* 1991). Invertebrate predators include crustaceans and insects. Various microorganisms can possibly cause additional egg mortality (Ewert 1979, Solomon and Baird 1980, Stancyk 1982, Wyneken *et al.* 1988, Gyuris, unpublished). Less frequently eggs fail to develop or embryos die at various stages of development. Soil and beach erosion, and fresh or salt water inundation may result in the destruction of a significant percentage of a season's egg production (Limpus 1978, Fowler 1979, Hopkins *et al.* 1979, Eckert 1987, Packard and Packard 1988). Adverse physical conditions in the nest are probably the cause of most of the otherwise unexplained embryo mortalities (for an overview see Packard and Packard 1988). Colonial nesters, when nesting in high density, may inadvertently dig up and destroy a proportion of previously laid eggs (Hendrickson 1958, Bustard and Tognetti 1969). However the overall effect of this is probably slight. At Raine Island, in the northern Great Barrier Reef, even in years of high density nesting when the distance between nesting turtles is generally less than ten meters, less than 1% of all clutches laid were dug into by other turtles and in most cases the number of eggs destroyed per clutch was less than 30 (pers. obs.). Fertility of eggs may exceed 95% although the hatching and emergence success of hatchlings may be somewhat lower than this percentage even in undisturbed nests (Hirth 1980, Miller 1985, Parmenter 1985, Whitmore and Dutton 1985, Wyneken *et al.* 1988, Harry and Limpus 1989).

The survivorship of eggs and hatchlings in the nest is low for many species of turtles (Wilbur and Morin 1988, Iverson 1991). The particularly high rate of nest predation on freshwater species (Table 2.3) led Wilbur (1975) to assume that survivorship of hatchlings that reached the water was high, similar to that of juveniles and adults. This assumption, however, was questioned later by Tinkle *et al.* (1981). Predation on the eggs of terrestrial turtles is assumed also to occur at high rates (Auffenberg and Iverson 1979, Deimer 1986).

The available information on non-human predators and predation rates on sea turtles has been reviewed by Stancyk (1982). Additional data are provided by Mrosovsky (1971), Frith (1975), Limpus *et al.* (1983a and b), Nellis and Small (1983), Hopkins *et al.* (1979), Whitmore and Dutton (1985), and Limpus and Parmenter (1986). The rate of predation on sea turtle nests is considerably easier to quantify than for freshwater and terrestrial species because of the relative ease of finding the nests. Even so, much of the literature on predation is qualitative or anecdotal, often limited to a list of predators of eggs or hatchlings. The limited amounts of quantitative data reveal that patterns of nest success/failure vary considerably between times of the year, among rookeries and among years (Fowler 1979, Hopkins *et al.* 1979, Limpus *et al.* 1983b). Egg loss caused by predators may be in excess of 90% in some rookeries (Hopkins *et al.*1979), whereas other nesting areas are relatively free from natural predators (Balazs 1980, pers. obs.) (Table 2.4). Natural predators of eggs and hatchlings on the beach are rarely implicated as causes of heavy losses, whereas the effect of terrestrial predators introduced by man into sea turtle nesting habitats, or whose numbers are enhanced by human activities, may be substantial (Fowler 1979, Hopkins *et al.* 1979).

Table 2.3 Examples of the rates of nest predation found among freshwater turtles.

Species	% of nests destroyed	Location	Predator(s)	Source
Chelydra serpentina	30-100	Michigan	raccoon, red fox	Congdon *et al.* 1987
	63	Sth. Dakota	-	Hammer 1969
Emydoidea blandingii	100	Wisconsin	skunk	Ross & Anderson 1990
	78	Michigan	raccoon	Congdon *et al.* 1983
Chrysesmys picta	21	Michigan	-	Tinkle *et al.* 1981
	44	Quebec	raccoon, skunk	Christens & Bider 1987
Chelodina longicollis	48	Sth. Australia	-	Chessman 1978
	100	Sth. Australia	-	Parmenter 1985

Table 2.4 Predation rates on and predators of sea turtle eggs.

Percentage destroyed of nests	of eggs	Location	Predator(s)	Source
50	-	Tortuguero	mammals(i), birds	Fowler, 1979
49-87	-	Florida	raccoons	Davis & Whiting, 1977
-	64	Galapagos	Scarab beetles and feral hogs(i)	Fowler, 1979
-	0	Hawaii	-	Balazs, 1980
	<5	Cays, sth. GBR	crabs	pers. obs.
100	-	Lacey Is. Aus.	varanids	Limpus, 1980
-	0	Cays, nth. GBR	-	Limpus, 1980
60	-	Fog Bay, Aus.	varanids	Guinea, pers.com.
-	12(ii)	Suriname	crabs	Whitmore & Dutton,1985
83	-	Campbell Is. Aus.	varanids	Limpus *et al.* 1983c
-	0-38	Crab Is. Aus.	birds and crabs	Limpus *et al.* 1983b
-	80	Sth. Carolina	raccoons(i), crabs	Hopkins *et al.* 1979

(i) Human activity influenced predation.

(ii) of eggs per nests destroyed

Recently, Iverson (1991) considered that survivorship from egg to hatching was significantly higher among terrestrial and marine turtles than among freshwater turtles. But he also noted that "several factors may be operating to bias the available survivorship data on marine turtles" such as: 1) the possible discouragement of predators by regular beach patrols; 2) nesting density on the nesting beaches of many declining populations would be much reduced compared to former levels and predation rates may have changed accordingly and 3) the choice of study sites may be biased toward islands where population sizes and densities of predators would be lower. Even with these biases, I consider Iverson's (1991) comparison of survivorship from egg to 1 year of age to be premature considering the paucity of data and the bias in selecting available data for inclusion in his analysis. For marine turtles the 'eggs to 1 year of age' survivorship value, used in the analyses, is based on only two similar data points (estimated annualized survivorship = 0.59 and 0.58), both derived by Marquez *et al.* (1982 a and b, respectively). Not included was the estimate of Frazer (1986) who calculated annualized survivorship as 0.10-0.30, on the basis of a population model of a stable age-class distribution. The only estimate of annual survivorship of freshwater turtles from egg to 1 year of age used is 0.185 (Wilbur 1975).

While there are numerous references to predation on emerged hatchlings (Hendrickson 1958, Frazier 1971, Hirth 1971, Mrosovsky 1971, Bustard 1972,1979, Witham 1974, Frith 1975, Diamond 1976, Balazs 1980), quantitative data are scarce. I am aware of only two studies which measured hatchling mortality following emergence.

Predation on hatchlings of *N. depressus* as they cross the beach ranged between 2.8 and 38%, depending on the time of the year (Limpus *et al.* 1983b). Bird predation by rufous night herons (*Nyctitorax caledonicus*) accounted for most mortality and was highest during April through May whereas most nesting occurred during December. Seasonally intense predation by these birds has been observed at other sea turtle rookeries (C J Limpus and V Baker pers. com.). Mortality of hatchling *C. caretta* was less than 2% during beach crossing at dawn (Limpus 1973). There appear to be no parallel data for freshwater and terrestrial species.

Although the duration of the inshore, shallow water phase in the life of marine turtle hatchlings is relatively short (generally spanning a few hours), the greatest natural predation pressure probably takes place there (Hendrickson 1958, Hirth 1971, Bustard 1972, Limpus 1978, Stancyk 1982). Most estimates of mortality in this stage are either qualitative, anecdotal or based on theoretical considerations (Hendrickson 1958, Hirth 1971, Bustard 1972, Witham 1974, Frith 1975, Frick 1976, Balazs 1980, Richardson and Richardson 1982, Witherington and Salmon 1992). This study provides the first actual measurements of survivorship among hatchlings of the marine turtle *C. mydas* during the first hour or so of their aquatic life.

2.3.4.2 Survivorship of juveniles to adults.

As predicted by bet hedging models of life history theory, long term adult survival is of particular value in variable environments characterized by uncertain reproductive success (*i.e.* low probability of matings, high juvenile mortality, or uncertainty of food supplies to provide energy for reproduction) in which repeated reproduction (iteroparity) can increase fitness (Bell 1976, Tuljapurkar 1990). This broad strategy has generally been expected to apply to turtles. Although turtles are reputed to be among the longest-lived vertebrates it is becoming apparent that most do not live to very old ages in many habitats (Frazer *et al.* 1990).

Some of the long term tagging studies, spanning a decade or more, are now starting to produce detailed estimates of age-specific survivorship and longevity. Frazer *et al.* (1990) provided a table of estimated age specific survivorship values for a population of *C. picta* in Michigan. Annual survivorship increased with age among juveniles and adult males from 0.21 at age 1 to 0.8 at age 11. In contrast, survivorship among females appeared to decrease with age. However, the authors cautioned that such a finding may be an artifact of behavioural differences between the sexes. Although several individuals lived beyond their 20th year, few would be expected to survive for more than a decade. Frazer (1987) also estimated annual survivorship values of 0.695 for juvenile and 0.81 for adult female *C. caretta* in the southern United States. Under current assumptions (i.e. population declining at the rate of 3% per year), only one in 1000 adult females is expected to survive for more than 32 years beyond their recruitment into the breeding population. Adult female survivorship of *C. mydas* at Tortuguero, an extensively exploited population, is relatively low, with most members of a cohort of novice breeders tagged while nesting not surviving for more than a further sixteen years (Bjorndal 1980). Survivorship estimates are not yet available from the long term and continuing tagging studies of Limpus on the relatively unperturbed populations of eastern Australian *C. mydas* and *C. caretta* .

Great variation in longevity exists between individual turtles in some populations. Estimating reproductive life expectancy is complicated not only by the paucity of data but often by the lack of comparable reporting of such data. More recent studies use the standard measure of survivorship, allowing for a comparison between populations and species. Few individuals in the Michigan populations of the freshwater tutle *C. picta* (above) are expected to live for more than 4-6 years of reproductive life (Frazer *et al.* 1990) and less than 10% of loggerhead turtles in the southern United States (above) are expected to remain in the nesting population for more than 14 years (Richardson and Richardson 1982). Adult life expectancy is 4 years for *Terrapene ornata* (Wilbur and Morin 1988). In a population of the freshwater turtle*Terrapene carolina* in Maryland 11-15% of adults are expected to be alive after 30 years (Stickel 1978) whereas in Missouri there is a "population turnover period" of 14 years (Schwartz and Schwartz 1974). In a more recent publication (Schwartz and Schwartz 1991), 6% of the same population in Missouri is reported to have survived for more than 25 years. Williams and Parker (1987) found over 25% of adults still alive 23-25 years after initial marking. The annual survivorship value of 0.94 for *T. carolina* in Maryland and Indiana is higher than that in *C. picta* (0.85, Wilbur 1975 and 0.76 Tinkle *et al.* 1981) and *Pseudemys scripta* (0.79, Gibbons and Semlitsch 1982) or in the terrestrial testudinid, *Sceptochelys agassizi* (0.82-0.96, Turner *et al.* 1984). In a study of desert tortoises, *Gopherus agassizii*, 5 % -29 % of animals survived to age 25 or older (Germano 1992).

Estimates of survivorship in the juvenile, subadult and adult stages of turtles are few. In a review of the literature, Iverson (1991) found no significant difference in survivorship among the juvenile to adult age classes of freshwater and terrestrial turtles. In contrast, survivorship was shown to be significantly lower in adult (female) marine turtles. Unfortunately, it was not possible to determine if the lower survival rate is a natural characteristic of female sea turtles or reflects anthropogenic effects. Certainly both populations of sea turtle for which adult survivorship values were used in Iverson's analyses are known to be subjected to high level of both direct and indirect anthropogenic mortality (i.e. green turtles of the Caribbean and loggerhead turtles of the southern USA).

The paucity of data and the high degree of variation in adult life expectancy both within and between species makes it difficult to draw general conclusions about possible correlations between habitat and reproductive life span. It may be safely stated that the reproductive life span of sea turtles fits within the range of that found among freshwater and possibly terrestrial species.

2.4 DISCUSSION.

The available information supports Hendrickson's (1980) assertion that the large body size and high fecundity of marine turtles distinguish them from most freshwater and terrestrial testudines. Many other life history parameters, such as survivorship, growth and age to maturity, are similar between marine, terrestrial and freshwater turtles. What are the adaptive values of the two distinguishing features? Did selection for size cause changes in fecundity and vice versa, or did these two characters coevolve as a result of selective forces that affected both size and fecundity? It is frequently argued that life history variation can be best understood by interpreting it in relation to body size since that is the integrated outcome of many internal constraints and external selection pressures (Stearns 1984, Barbault 1988). In examining the relationship between body size and the evolution of mammalian life histories, Millar and Hickling (1991) conclude that observed patterns of life history parameters and associated body size are most likely the result of environmental factors affecting both size and life histories, since selection for one does not appear to necessarily result in changes of the other. What are the environmental factors that influenced the evolution of marine testudines toward this particular suite of characters, so different from most other turtles?

Invasion of the marine habitat by the ancestral swamp and marsh dwelling testudines occurred gradually (Obst 1986, Iverson 1991). Sea turtle ancestors probably nested and fed in areas that were in close proximity of each other. The distance between the two areas probably increased by degrees, as the result of seafloor spreading and changes in population densities, climate and topography (Carr and Coleman 1974, Hirth 1978, Moll 1983).

Most tropical and some temperate shallow water areas of continental shelves provide an abundant and diverse flora and fauna that are exploited by modern sea turtles. In order to take advantage of these vast foraging areas, marine turtles have particular problems to overcome. Like all other turtles, they are tied to land for the laying of cleidoic eggs. At the same time the conditions that result in the creation of suitable nesting beaches appear rarely to coincide with feeding pastures. Consequently the feeding range of most populations of marine turtles is far more extensive than their comparatively limited breeding grounds (Carr 1980, Mortimer 1982, Moll 1983, Limpus *et al.* 1992). Today, most adults engage in energetically costly long distance breeding migrations (Bjorndal 1982, 1985, Limpus *et al.* 1992). The waters adjacent to most nesting beaches may not only lack the food resources that can sustain the growth and development of large numbers of hatchlings but they possibly fail to provide protection from the many predators in coastal areas (Walker and Parmenter 1990, Walker 1991). Thus, the hatchlings had to be able to exploit a suitable developmental habitat away from the natal shores.

For most freshwater and terrestrial turtles, the adult feeding and breeding habitats are not separated by such relatively great distances. The hatchlings can find food and suitable microhabitats which offer protection from predators near their place of hatching. Thus there is no need for adult migration and long distance dispersal of hatchlings. I propose that this single, but apparently fundamental difference in hatchling dispersal can account for the large size and high fecundity observed in marine turtles when compared with freshwater and terrestrial species. As an exception to the general pattern of the marine species' life histories, *N. depressus* produces fewer but larger young which do not disperse pelagically. In this regard this marine species is similar to the freshwater and terrestrial species.

2.4.1 BODY SIZE.

Body size is usually interpreted firstly as a trade-off between immediate reproductive gain and accumulated energy into growth to increase survivorship and/or future reproductive success and secondly, as a function of the energy the organism can acquire from its environment (Barboult 1988). In addition, one must take into account other ecological parameters such as the distance between the feeding and breeding grounds for most sea turtles.

Both sexes of marine turtles make long range breeding migrations. During a breeding season females stay away from their foraging grounds for periods of several months, during which time food is severely limited or unavailable. Adult female green turtles allocate 10-24% of their annual energy budget for reproduction, and the cost of egg production makes up less than half of the total reproductive energy budget (Bjorndal 1982,1985). Similar data are not available for the other sea turtle species. Under these circumstances, the relatively large body size of marine turtles may have adaptive value. Body size has a profound effect on various physiological parameters such as energetic and thermoregulatory efficiency and metabolic rate (Reiss 1989). A larger body mass allows a reduction in metabolic demand per unit mass. With a long distance, energetically costly migration involved, possibly the best strategy is to accumulate, over several years, relatively large resources for reproduction and thus spread the cost of migration over many eggs. A larger body allows the accumulation of larger energy stores and hence the production of a larger complement of eggs.

The quantity or availability of resources and other, physical and biotic aspects of the environment (such as the scale and degree of heterogeneity of the habitat, and interspecific competition) may affect the evolution of body size in a variety of ways. A population of turtles, where each individual is the size of a sea turtle, would find it impossible to survive in a habitat that can be successfully exploited by the smaller bodied freshwater species. Conversely, in the marine habitats occupied by present day sea turtles large size is permissible and in fact may be selected for.

The limited data available on size specific survivorship within turtle species indicate that survivorship increases with size and thus probably with age. There is also some evidence to suggest that larger or older animals are more fecund than their smaller, possibly younger counterparts (Hirth 1980, Frazer 1984, Hays and Speakman 1991). Hence delaying maturity until large body size is reached not only reduces vulnerability to predation, but at the same time increases future reproductive potential. It is probable that the body size of various turtle species reflects, at least in part, the size of predators of the communities in which these turtles live. The proportionally large body size of marine turtles would balance the large marine predators of the open oceans, reefal and inshore habitats (Witzell 1987).

2.4.2 FECUNDITY.

Of all turtles, marine turtles have the largest clutches of eggs, and lay several clutches per breeding season. They do not reproduce in each season but nor do many freshwater turtles. The reproductive life span characteristic of different species and populations varies greatly and does not seem to be correlated with habitat. Thus, it may be safely concluded that marine turtles are generally the most fecund of all testudines, necessitated by their unique life history during the early life stages.

Environmental uncertainty faced by emerged hatchlings is minimized by many turtle species by delaying emergence so it coincides with favourable conditions for the young (Gibbons and Nelson 1978). Sea turtles are left with no such option. Their unstable nesting habitat must have presented a strong selection pressure to reduce incubation time and for immediate emergence after hatching. Current measurements of survivorship during the early life stages (from oviposition through incubation and hatching until the hatchlings reach suitable developmental habitat) may not be directly comparable between freshwater, terrestrial and marine turtles. All studies have ignored the fact that, unlike freshwater turtles, marine turtle hatchlings remain vulnerable to predation while in nearshore or coral reef habitats and before reaching their open ocean developmental habitat. The high fecundity of marine turtles may be a response to the possibly high predation rate in the nearshore environments, which past studies have not been able to elucidate.

Unlike freshwater turtles, neonate sea turtles (with the exception of *N. depressus*) swim far away from their natal shores to the open ocean. Young sea turtles spend several years drifting with long shore currents and oceanic eddies and gyres that carry rich patches of invertebrate plankton on which the hatchlings feed (Fletemeyer 1978, Carr 1980, 1986, Carr and Meylan 1980, Witham 1980). In the Caribbean at least, suitable hatchling habitats are associated with floating rafts of sargassum weed. The little work that has been done to date suggests that sea turtle hatchlings stay in or near such rafts (Fletemeyer 1978, Carr and Meylan 1980, Carr 1986). No parallel observations have been made in the Pacific although there is indirect evidence to indicate that hatchlings emerging at the east Australian mainland and Great Barrier Reef rookeries are carried in a southerly direction along the coast then turn east to pass north of New Zealand before they end up in the Coral Sea (Limpus, pers. comm.). The need for the evolution of this oceanic dispersal and development is not well understood. *N. depressus* however, which is endemic to tropical Australian waters, does not have a pelagic dispersal phase. It would be interesting and possibly instructive to speculate on relationships between the evolution of this species and sea level changes that caused the periodic isolation of the Gulf of Carpentaria from the ocean (Decker and Correge 1991), thus creating the vast Lake Carpentaria.

Ocean currents and associated phenomena are dynamic entities both in time and space (Owen 1981, Le Fevre 1986, Brown 1990, Leis 1991) and little is known about the spatial and temporal distribution of aggregations of plankton within them which may be suitable for the hatchlings to eat (Carr 1980, 1986, Leis 1991). While there is a considerable body of knowledge about the behaviour, especially the orientation behaviour, of hatchlings in near shore habitats (Frick 1976, Salmon and Wyneken 1987, Wyneken *et al.* 1990, Lohman 1991) there are few observations from open waters (Carr 1986). It is not known, for example, whether hatchlings behave as passive particles within currents or if they adopt a behavior pattern that would increase the probability of intercepting and staying within a suitable plankton patch. In the absence of knowledge about the distribution of plankton within currents and the dispersal behaviour of hatchlings, it is impossible to estimate the proportion of hatchlings which encounter a suitable developmental habitat before their post-hatching yolk supply is used up. Hatchlings maintained in captivity without food visibly start to lose condition after 4 -7 days (pers obs). Thus in the derivation of the optimal size-number compromise for most sea turtle hatchlings, the size component is probably strongly linked with the need to satisfy the energetic requirements of the swim that takes the hatchling into a current system that can provide habitat for survival and growth. High fecundity is a likely adaptation to meet this environmental uncertainty. A possible reduction in predation on larger hatchlings may not offset the reduced probability of a sufficient number of hatchlings reaching and surviving in the pelagic habitat.

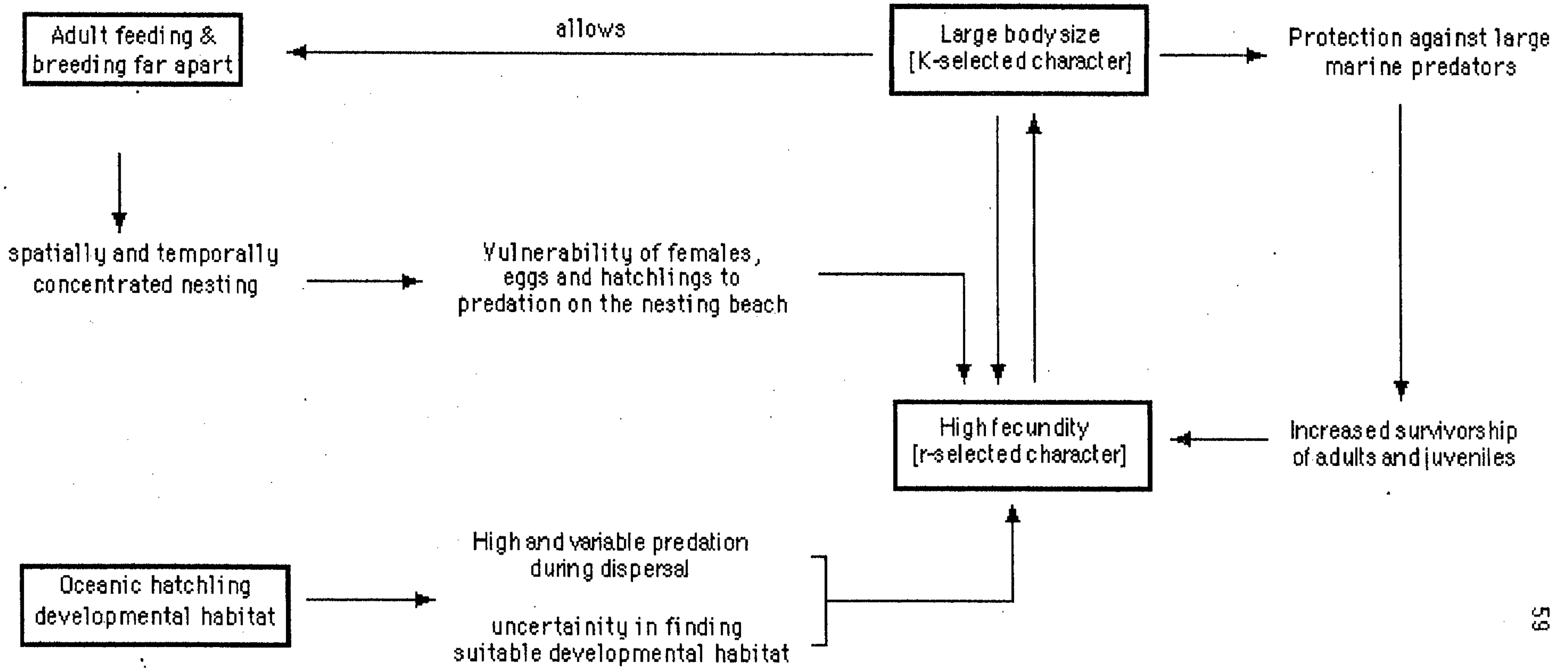
Modeling studies seem to have ignored the fact that hatchling mortality may differ markedly between beach, shallow water inshore and reefal habitats, and deep water oceanic environments (Frazer 1983 as reworked in Crouse *et al.* 1987). The stage based life table of

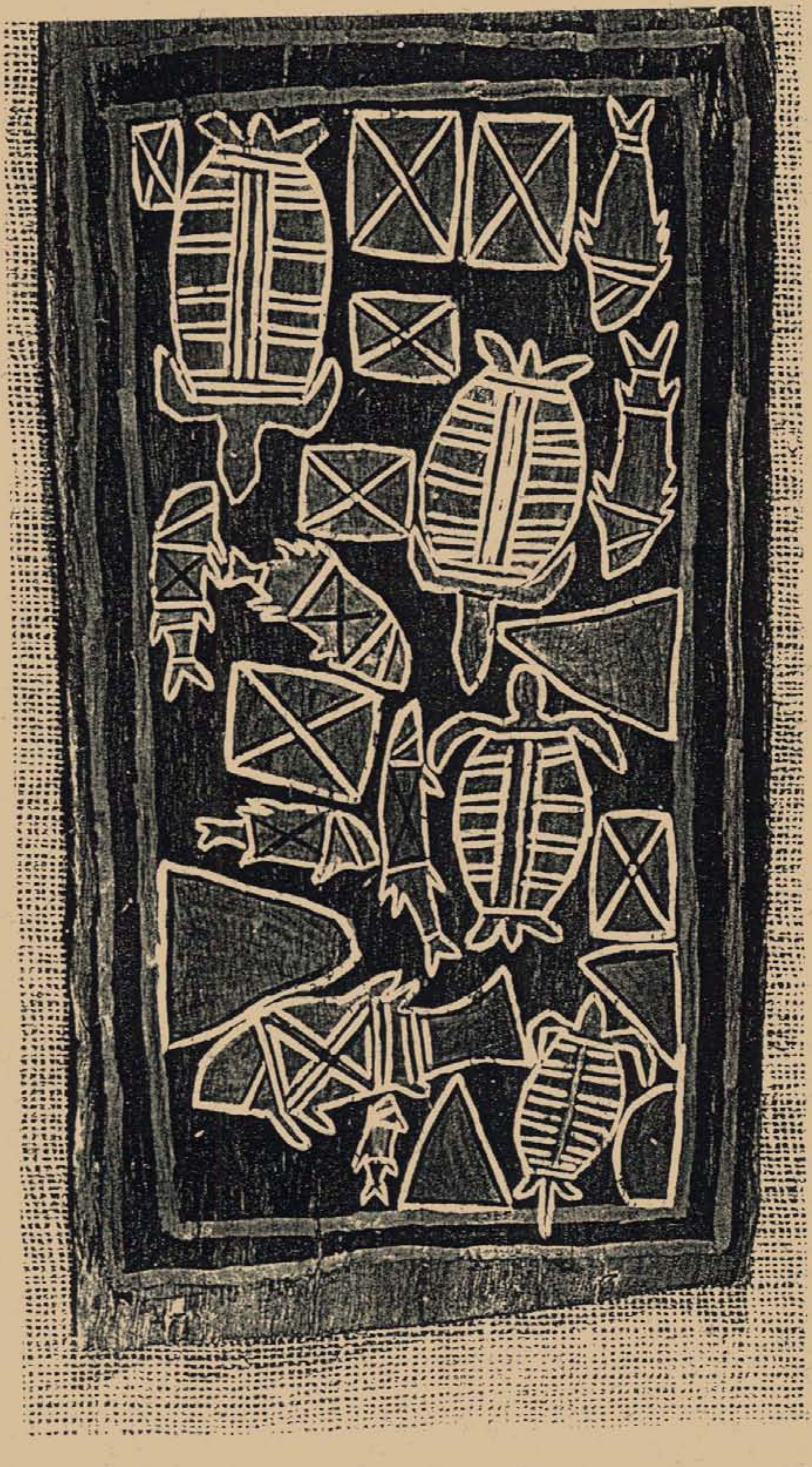
Crouse *et al.* (1987: table 3) provides an estimate of the composite annual survivorship for eggs and hatchlings. Such a composite value may be reliable and may make useful predictions of a population's reactions to changed circumstances. However, it does not provide insight into how the requirement for a pelagic developmental stage has influenced the compromise position of the offspring-size/number relationship for sea turtles.

2.5 SYNOPSIS.

Sea turtles are large and unusually fecund marine reptiles. They have a long evolutionary history and have changed little since the Cretaceous. With the exception of *D. coriacea*, they are exploiting the abundant resources found along the productive, shallow water areas of continental shelves, habitats in which heterogeneity is only evident over a large scale. As a result of their basic testudine body plan, they are tied to laying eggs on land. Adults make long distance reproductive migrations. After emerging from their subterranean nests, all but flatback hatchlings disperse into oceanic habitats where they feed for an undetermined period (at least several years) before settling into their shallow water feeding areas. Eggs and hatchlings on the beach are subject to varying degrees of predation. The hatchlings are probably also subject to high and possibly variable levels of predation during their early aquatic existence. Further significant and variable mortality may occur as a result of environmental uncertainty associated with various oceanographic phenomena essential for the hatchlings' survival. Survivorship of immatures and adults is comparatively high. As for most other turtles, growth is slow. Reproduction is delayed until asymptotic size is reached. The high mortality in the early life stages is offset by high fecundity. Of all testudines, marine turtles lay relatively the smallest eggs in the largest clutches. Minimum egg, and therefore hatchling size are indirectly dictated by predation and the energetic requirements of the young. An increase in adult body size may have been the only option available to increase fecundity. At the same time, large body size afforded these animals protection against large marine predators and facilitated the exploitation of extended feeding grounds. Thus, the adaptive significance of body size is multifactorial. The observed pattern of large body size and high fecundity of the marine turtles is the result of environmental factors jointly affecting both body size and fecundity. These ideas are summarized by figure 2.2.

Figure 2.2 A conceptual diagram summarising the relationships between body size and fecundity of sea turtles.





CHAPTER 3

PREDATION ON HATCHLINGS OF THE GREEN TURTLE IN CORAL REEF HABITATS.

The Garabi Islands.
Bark painting by Mauwalan (Yirrkalla)
National Gallery of South Australia.

Garabi is a string of small islands off the western coast of the Gulf of Carpentaria. During the time of creation these islands were the homes of a number of mythical men and women. Today these people, now transformed into sea creatures, still visit their old homes.
The painting shows the Garabi islands as a series of geometric shapes around which these creatures, the turtles, queen fish and rock cod still live.

3 PREDATION ON HATCHLINGS OF THE GREEN TURTLE IN CORAL REEF HABITATS.

3.1 GENERAL INTRODUCTION.

Their unusually large clutch size distinguishes marine turtles from most other reptiles, including other testudines. This high fecundity is usually attributed to high mortality during the early life stages (i.e. eggs and hatchlings). The natural mortality of eggs and hatchlings of sea turtles in the terrestrial environment is highly variable. However, it is considered to be significantly lower than that of the less fecund freshwater turtles (Iverson 1991) (also see chapter 2, section 2.3.4.1).

Although aquatic predation on hatchling sea turtles is presumed to be high, most estimates of mortality are anecdotal or based on theoretical considerations (Hendrickson 1958; Hirth 1971; Bustard 1972; Witham 1974; Frith 1975; Balazs 1980; Richardson and Richardson 1982). Witherington and Salmon (1992) recently attempted to measure predation on hatchlings of the loggerhead turtle (*Caretta caretta*), but their conclusions were limited by the small sample sizes and non-uniform methodology. Approximately 7% of the 74 hatchlings they observed were taken by fish. Their experiments, however, were not controlled for habitat, tidal movements, lunar phases or the length of time the hatchlings spent under observation.

Several aspects of hatchling behaviour, such as nocturnal emergence from the nest and the hatchling frenzy, are considered to have evolved in response to predation (Hendrickson 1958; Bustard 1972; Wyneken and Salmon 1992). The advantages of these behaviors have not been tested by experiments which allow predation rates under different environmental conditions to be compared directly.

Quantifying predation rates on hatchlings in the sea presents special problems. A predation event must be confirmed either by visual observation of the event or by other, indirect, means. Observation techniques should not interfere with predator-prey interactions. The prey should not be restricted, impaired or otherwise affected in ways which would change the probability of its being caught. The observation technique used should not affect the behaviour of predators. Devising a method that satisfies these criteria is difficult in coastal waters which are often of very poor visibility.

I attempted to estimate hatchling predation using two independent experiments. Tethering has been used successfully to assess predation rates of a variety of predator-prey systems in several different habitats (Shulman 1985; Barshaw and Able 1990) and it appeared suitable for use with sea turtle hatchlings. A second estimate of hatchling mortality was obtained by examining the foregut contents of predatory fishes.

3.2 MEASURING PREDATION RATES DIRECTLY: THE TETHER METHOD.

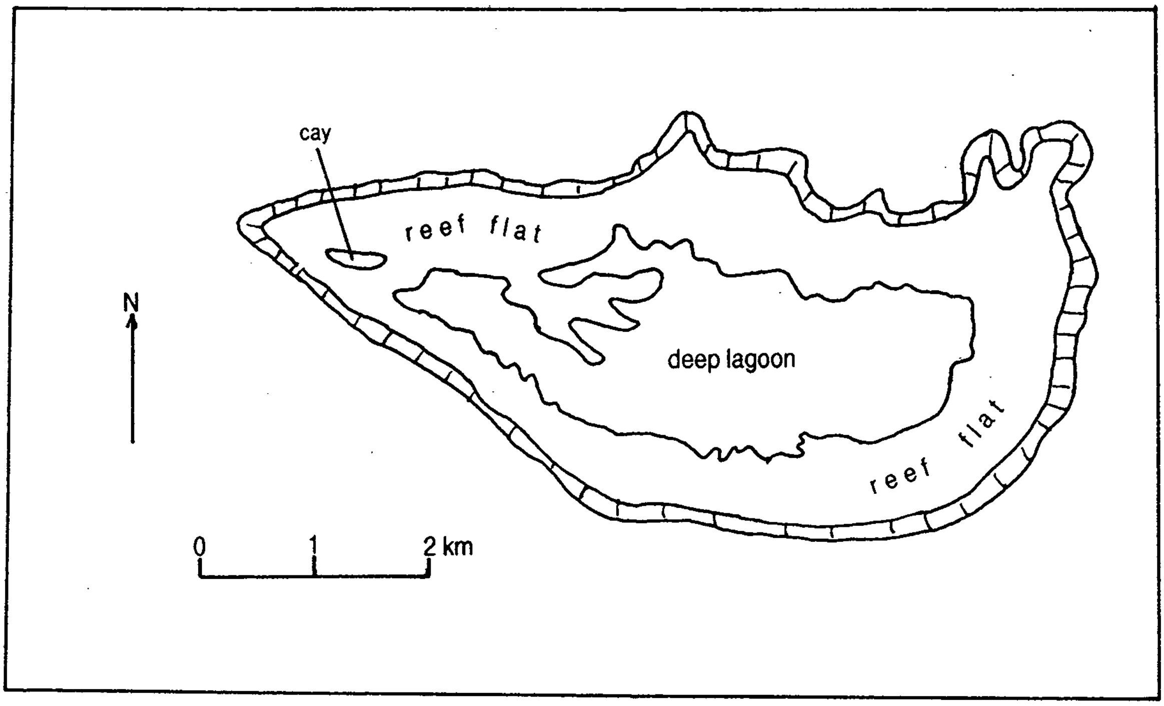
This aspect of my study addresses the need for empirical data on hatchling survival after entry into the sea by: 1) developing a method for measuring aquatic predation; 2) estimating predation rates of hatchling turtles in the first hour or so of their aquatic life; and 3) investigating whether environmental variables have a significant effect on predation rates.

3.2.1 MATERIALS AND METHODS.

3.2.1.1 Study site.

Heron Island Reef, at the southern end of the Great Barrier Reef, is an elongate lagoonal platform reef approximately 11 km long and 5 km wide at its eastern end (Figure 3.1). A vegetated sand cay, Heron Island, is situated on the western end of the reef. The tidal range varies between 2 m (springs) to 1 m (neaps). On spring tides large proportions of the reef crest and reef flat are exposed at low water, isolating a large lagoon which occupies much of the eastern reef. Water depth in this lagoon ranges between 0.5 and 7 m at low tide. The approximate areas of the three major habitats are: reef crest and reef slope ≈ 5.5 km^2, reef flat ≈ 14.3 km^2 and lagoon ≈ 8.4 km^2 (Limpus and Reed 1985). Because of the greater spatial heterogeneity in the lagoon, measurements of predation were limited to the more uniform reef flat and reef slope habitats.

Figure 3.1 Heron Island and reef. (Hatched area indicates reef slope.)



Heron Island provides nesting habitat for green turtles which dig their nests in the vegetated sand dunes. Each night from January through April green turtle hatchlings emerge from these nests and swim over the reef flat to deep water. The peak of emergence occurs in February. The emerged young cross 10-30 m of dune and beach area before entering the sea.

As with all other green turtle rookeries, the number of females using Heron Island's beaches for egg laying may vary by several orders of magnitude from season to season (Limpus and Nicholls 1988). During the three years of my study (1987/8 1988/9 and 1990/1991 seasons), however, the numbers of nesting turtles at the Heron Island rookery were similar totaling approximately 500-1000 females for the season, with 80-120 turtles nesting nightly at the peak of the season. (Limpus 1989). As there were no cyclones or other major environmental perturbations during this period, I assumed that the numbers of hatchlings were also similar between these nesting seasons. The three year's data were thus analyzed as a single set.

3.1.2 Collection of hatchlings.

Hatchlings were collected shortly after emergence as they crossed the beach on their way to the sea. All animals were stored in Styrofoam boxes and used in experiments shortly after emergence and always within 24 hrs of emergence.

3.2.1.3 Observations of free-swimming hatchlings.

Free-swimming hatchlings (n=57) were followed by snorkel divers during mid- to late afternoons, at the maximum distance consistent with underwater visibility (generally about 5 m). These observations took place over the reef flat during the rising or falling tides when the water depth varied between approximately 1-1.5 m. Turtles were followed until they were eaten, lost from view or reached deep water over the reef crest. Predator-prey interactions were observed and the outcome recorded. Movements of 24 hatchlings over the reef flat were tracked from the beach using a hand held compass and taking compass bearings on divers following individual hatchlings in the water.

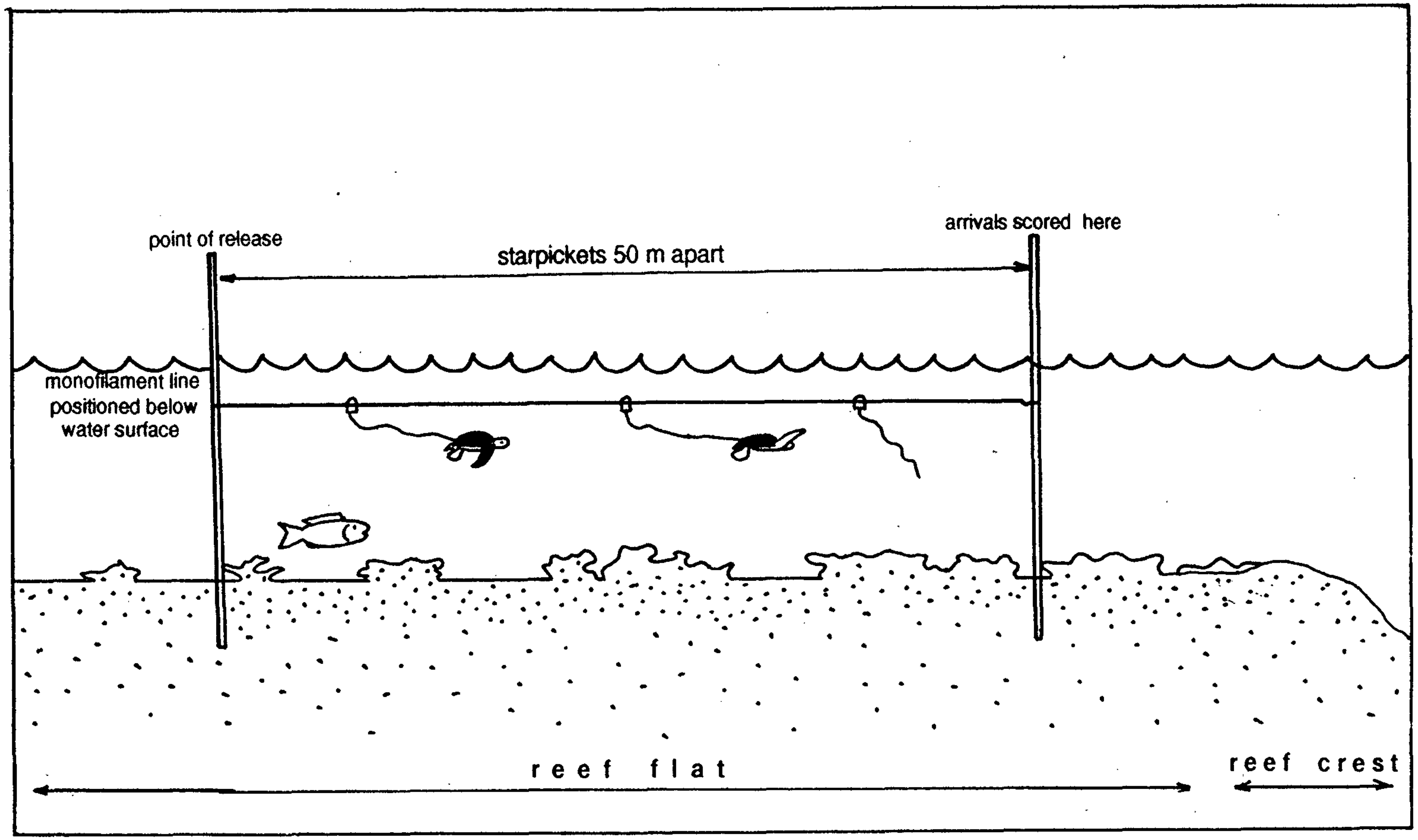
3.2.1.4 Measuring predation using tethered hatchlings.

3.2.1.4.1 Preliminary trials.

Two methods to measure predation on tethered hatchlings were tested. The first method involved establishing permanent 50 m transects over the reef flat perpendicular to the beach. The alignment of these transects followed the general direction of the hatchlings swimming across the reef flat. Powerised perlon monofilament line ("Fisherman" brand, 32 lb) was strung between starpickets driven into the coral. Hatchlings were tethered by a fine, 50 cm long monofilament, nylon line (Platypus® 27N 0.25 mm 6 lb and Super Schneider® 0.20 mm 4 lb), which was secured through the distal edge of a post central scute (Figure 3.2). This prevented the hatchling disengaging itself, but allowed the tug of a predator to release the hatchling. The free end of the tether was attached to a light weight brass interlock snap clip ("Steelite" brand, size 1) which was clipped to the transect line. (Figure 3.3). In this way hatchlings were made to swim along the transect and surviving hatchlings could be recovered at the seaward end. A measure of predation was given by the proportion of 20 tethered hatchlings that survived the 50 m swim along the transect.

Figure 3.2. Position of monofilament line passed through one post-central scute and tied in a knot on the dorsal surface.

Figure 3.3 Transect line with hatchlings attached. (Drawing not to scale.)



This method had severe shortcomings that made it unsuitable for measuring predation. The transect line often accumulated large clumps of drifting algae which obstructed the path of the snap clips and consequently the movement of the hatchlings. Hatchlings often struggled against the tethers and their movement along the transect was very slow. Presumably attracted by the hatchlings, the number of predators in the area increased noticeably very shortly following the commencement of a trial.

These problems were eliminated by the second method (see below) which was used successfully to measure predation on hatchlings in shallow water reefal habitats.

3.2.1.4.2 Measuring predation.

Most trials were performed on the northern reef flat and the adjacent reef slope because the prevailing south-easterly wind often made other sites unsuitable. Each individual hatchling was tethered by a 10 m long fine, monofilament, nylon line (attached to the hatchlings as before), and followed individual for ten minutes as they swam from the water's edge towards the reef crest and the deep water beyond. Observers holding the free end of the line could feel a predation event. The hatchlings' swimming ability was unimpaired by this tether except for some reduction in speed (see below). Predation rates were quantified by recording the number of hatchlings eaten in a group of 20 hatchlings during the ten minute observation periods.

Because hatchlings tended to swim directly against any tension, the lines were kept slack in order to minimize effects on the direction of swimming. To facilitate night observations a 1.5 ml plastic vial filled with 1 ml of luminous Cyalume® fluid was attached approximately 4 m behind the hatchlings, allowing the observers to follow the chosen path of the hatchling. These vials were never attacked by fish. The vials filled with exhausted Cyalume® were left attached in the daytime trials for consistency. Observers either walked or swam 8-10 m behind the experimental hatchlings. During extremely low spring tides, when the reef flat was completely exposed, predation trials were run on the rising or falling tide when water depth was sufficient to allow the hatchlings to swim without having to crawl over much exposed coral. When following hatchlings during high tide at night, most observers used surf ski paddle boards as protection against larger sharks. Hatchlings that were not taken by fish by the end of the ten minute observation period were released from the line by the observer and allowed to swim away.

A variation of this general technique was used to investigate predation over the reef slope. Hatchlings were attached to a 20 m monofilament line without Cyalume® (20 m was chosen to approximate the width of the reef slope). Hatchlings were released and observed by a person standing on the reef crest at low tide or by a person in a dinghy anchored at the crest when the tide was high.

These experiments were used to investigate the effects of three environmental variables on the rate of predation of hatchling green turtles. The variables were tide (high and low tides as calculated from tide tables issued by the Queensland Marine Board), time of day (day and night) and lunar period. Days between the four moon phases (new moon = phase 1, first quarter = phase 2, full moon = phase 3, last quarter = phase 4) were categorized on the basis of the moon phase closest to the day on which an experiment took place.

All the predation experiments over the reef slope were performed during a 6 day period (12-18 Feb. 1990). Moon phase could not be included as a variable in that part of the study. However, because the windward and leeward reef slopes show a marked difference in the species abundance and composition of fishes (Goldman and Talbot 1976), location was included as one of the independent variables.

Predation rates under particular combinations of these environmental variables were measured by following 20 individual hatchlings for ten minutes each. The resulting group of 20 observations is referred to as a trial. A series of nested logistic regression models was used to examine the effects of the independent variables on predation rates (i. e. the proportion of hatchlings preyed upon in each trial) by backward elimination (Anon. 1990). The usual analysis of deviance (X^2 test), was replaced by the F-ratio test, based on the mean deviance, because the data were over dispersed.

The general form of these tests was as follows:

$$F = \frac{\dfrac{\mathbf{RSS}_{\text{simple model}} - \mathbf{RSS}_{\text{more complex model}}}{\mathbf{df}_{\text{simple model}} - \mathbf{df}_{\text{more complex model}}}}{\mathbf{RSS}_{\text{more complex model}} / \mathbf{df}_{\text{more complex model}}}$$

(Where **RSS** = residual sum of squares and **df** = degrees of freedom.)

If the models are not significantly different, the more complex model does not explain the data significantly better than the simpler model and the simpler model is preferred. If the models are significantly different, this indicates that the term that was removed from the more complex model to obtain the more simple model was having a significant effect and therefore must be included in the model. Because changes in deviance obtained by the successive removal of terms from the model are conditional on the terms remaining in the model, the construction of an analysis of deviance table which assigns a unique change in deviance to each term of the model is not possible. However, the relative significance of terms is indicated by the magnitude of change in deviance that results when a particular term is removed from the model.

3.2.2 VALIDATION OF TECHNIQUES.

3.2.2.1 Effects of the monofilament line.

To establish the optimum tether length, predation rates were measured using 5 m, 10 m, and 15 m lines. The 60 hatchlings used in this experiment were all from the same clutch. All three tether lengths were tested simultaneously with 20 hatchlings used for each length.

Tether length had a significant effect on predation rates. Increasing the distance between the hatchling and the observer from 5 m to 10 m resulted in increased predation rates. Predators showed interest in the hatchlings on the 5 m lines, but only one attack was made. Results obtained for the 10 m and 15 m lines were identical with 6 of the 20 hatchlings in each group preyed upon. Because the 15 m line often tangled on handling and because of the extra drag it presented to the hatchlings, the length of line used in all the predation experiments over the reef flat was standardized at 10 m.

The swimming speed of tethered hatchlings (n=9) was compared with free-swimming (n=9) hatchlings to provide a basis for calculating overall predation rates during the hatchlings' swim across reefal habitats. The widths of habitats to be crossed were estimated using an aerial photograph of Heron Island Reef. The time required by free-swimming hatchlings to traverse a given distance was calculated.

Free-swimming hatchlings moved significantly faster than their tethered counterparts (28 *vs* 16 m/min; t-test, T = 7.49, df = 16, p = 0.0001). Salmon and Wyneken (1987) obtained similar swimming speeds for free swimming loggerhead turtle hatchlings. The speed of the tethered hatchlings approximated that of the loggerhead turtle hatchlings towing floats in the predation experiments of Witherington and Salmon (1992)

3.2.2.2 Observer bias.

Numerous observers assisted in the field project, usually on a replacement basis. The investigation of observer bias was thus limited to two periods where individual observers overlapped long enough to be compared. The proportion of hatchlings preyed upon within each trial was calculated separately for each observer. The average proportion for each observer was then compared by the Friedman two-way non-parametric ANOVA (Siegel 1956) using 'trials' as a blocking factor. The analysis was conducted separately for each period as the two sets of observers were different. No significant difference was detected between individual observers (Team 1; Friedman statistic = 1.895, df=3, p = 0.5945 and Team 2; Friedman statistic = 2.643, df=2, p =0.2668 for the two periods). It was therefore assumed that, considering the relative simplicity of the task, other observers performed equally well after their initial training.

3.2.3 RESULTS.

3.2.3.1 Observations of the behaviour of free-swimming hatchlings and their aquatic predators.

No group behaviour was observed among free-swimming hatchlings. Compass tracking of free-swimming hatchlings (n=25) indicated that they swam directly away from the island's beaches towards the reef crest (Figure 3.4), a finding consistent with that of previous workers (Frick 1976, Salmon and Wyneken 1987). Because the circumference of the reef crest is much greater than that of the island (Figure 3.1) the density of hatchlings decreases as they swim away from the beach. This effect is especially pronounced on the eastern reef flat and lagoon.

Fish predation on the free-swimming hatchlings was high (93.6%). Of the 57 free swimming hatchlings that were followed by snorkel divers, 44 were eaten by fish (Table 3.1). Only three (6.4%) survived to reach the reef crest and the remaining ten were lost from the sight of the observer. Most attacks were sudden rushes by demersal predators. Hatchlings were often attacked unsuccessfully before a predator finally succeeded. Of the 44 successful predation events, 28 were preceded by attempted predation by fish too small or too weak to be successful. No hatchling took evasive action to avoid predation.

The most commonly observed predators were fishes of the family Serranidae (Epinephelidae) followed by Lutjanidae and Labridae. Small sharks, lethrinids and eels were occasionally observed to prey on hatchlings (Table 3.1). Long toms (Belonidae), often attempted to prey on hatchlings but were never successful. No data were obtained on the identities of the nocturnal predators.

Figure 3.4 Dispersal pattern of hatchlings from beach. ('N' denotes night time releases)

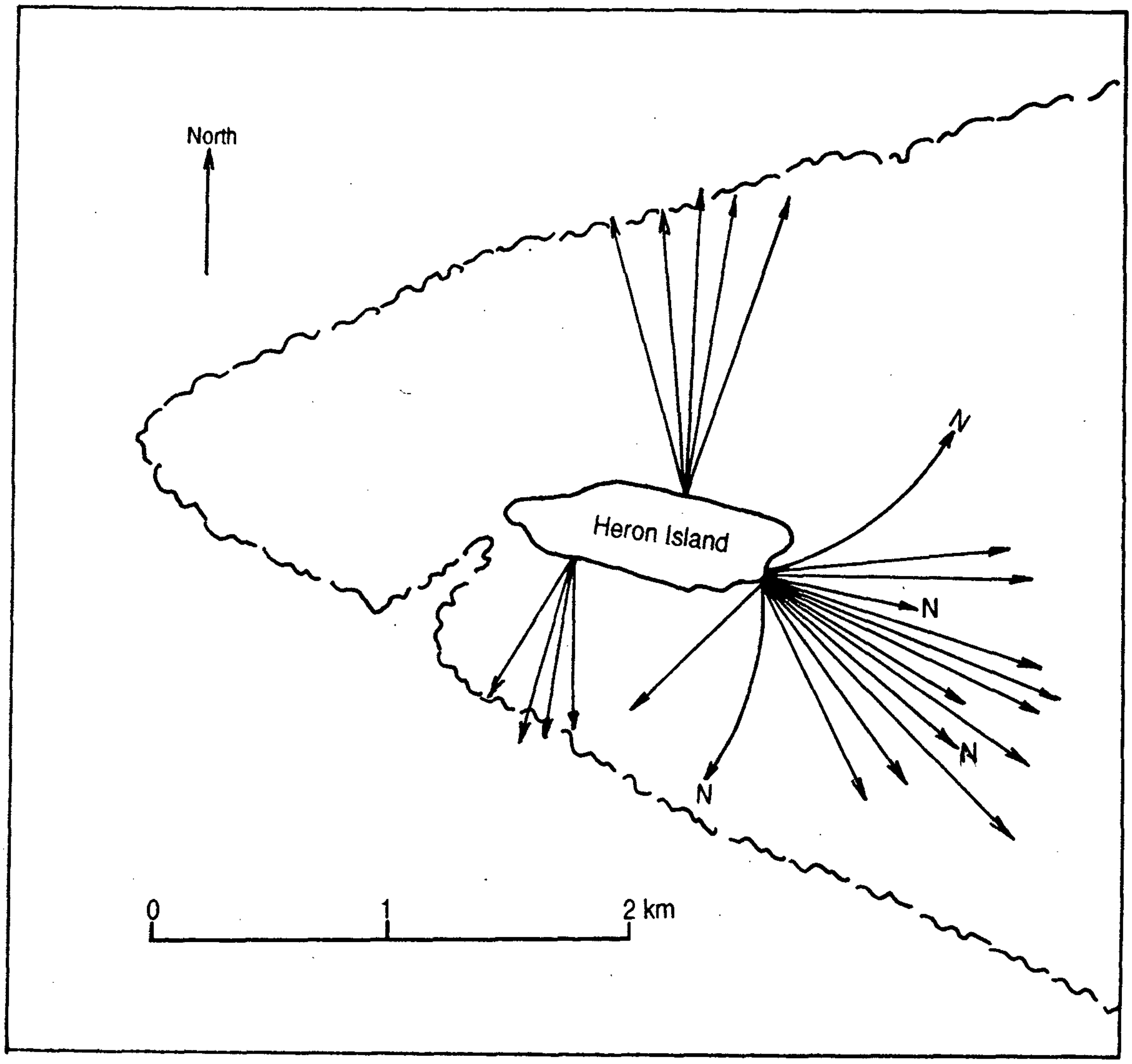


Table 3.1. The fate of 57 free-swimming *C. mydas* hatchlings which were followed by snorkel divers during the daytime (mid- to late afternoons) over the eastern reef flat. († Members of this genus were not identified to species due to the inexperience of assisting personnel)

DATE	OUTCOME			PREDATORS	
TIME	eaten	survived	lost from sight		
9 Jan. 1987	5		1	3	*Epinephelus* (var. sp.)†
1650 hrs				1	Black tip reef shark
				1	*Lutjanus carponotatus*
10 Jan. 1987	31		4	24	*Epinephelus* (var. sp.)†
1700 hrs				1	*Cromileptes altivelis*
				1	Scarid
				1	*L. carponotatus*
				2	Serranid
				1	Muraenid eel
				1	*Choerodon cyanodus*
12 Jan. 1987	2			1	*Epinephelus* sp.†
1700 hrs				1	Black tip reef shark
3 Feb. 1990*	5		3	2	*C. cyanodus*
1600 hrs				1	*L. mahsena*
				1	*L. carponotatus*
				1	*Epinephelus sp.*†
4 Feb. 1990*	1	3	2	1	*L. carponotatus*
TOTAL	44	3	10		

* In 1990, hatchlings were followed off the northern reef flat which is considerably narrower than the reef flat off the eastern end of the island (used in the 1987 observations). Three of these hatchlings survived to reach the reef crest and open water.

3.2.3.2 Predation rates and environmental variables influencing predation.

A total of 84 predation trials were performed over reef flat habitats around Heron Island in three separate breeding seasons (23 March - 5 April 1987; 4 January - 3 April 1988; and 2 -18 February 1990). Of the 1740 tethered hatchlings followed, 9 were attacked by seagulls (*Larus novahollandiae*) at the water's edge. Other animals were substituted for these individuals.

Predation rate varied among trials from 0 to 85% with a mean of 31% (standard error ± 2.5%). A summary table of predation trials is given in Appendix 2.

The simplest logistic regression model that explained the variation in predation contained tide and moon phase as independent variables. Moon phase was entered into the model as (1) the quarter about the new moon, moon phase 1, and (2) all other times, moon phase 2-4 (i.e. full moon and first and last quarters). This division was based on visual examination of the data which showed no differences among moon phases 2-4 (Figure 3.5). For similar reasons, tides were entered into the model as high and low with no distinction made between spring and neap periods (Figure 3.6). The deviance was significant when either tide or moon phase was removed from the model, indicating that both factors were important in determining predation rates (Table 3.2).

Figure 3.5 Overall predation rates (proportion taken by fish) of tethered hatchling green turtles in (n) trials each of 20 hatchlings over reef flat during various moon phases.

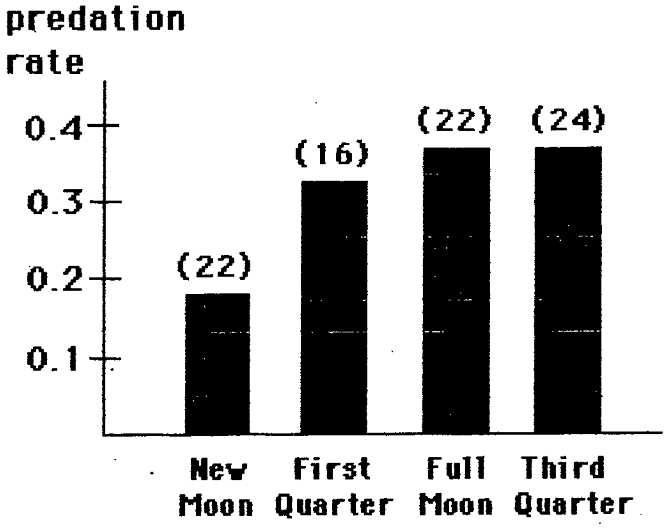
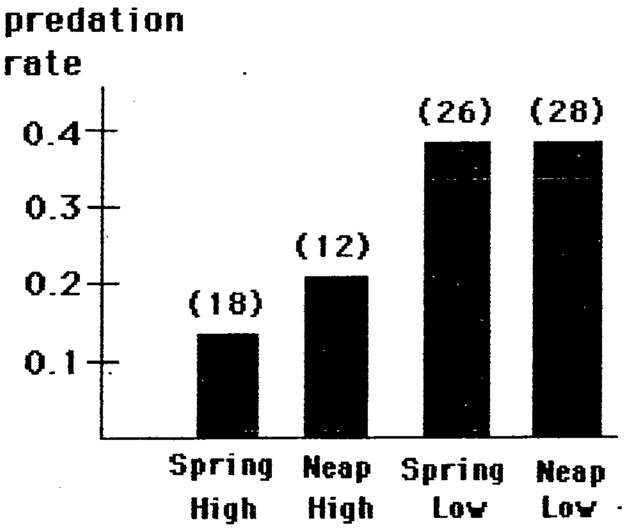


Figure 3.6 Overall predation rates (proportion taken by fish) of tethered hatchling green turtles in (n) trials each of 20 hatchlings over the reef flat during various tides.



The observed and calculated probabilities of survival under the various tidal and lunar conditions are given in table 3.3 and figure 3.7. The model fits the data well. Survival rate was the lowest under conditions of moon phase 2, 3 and 4/low tide and the highest during new moon/high tide.

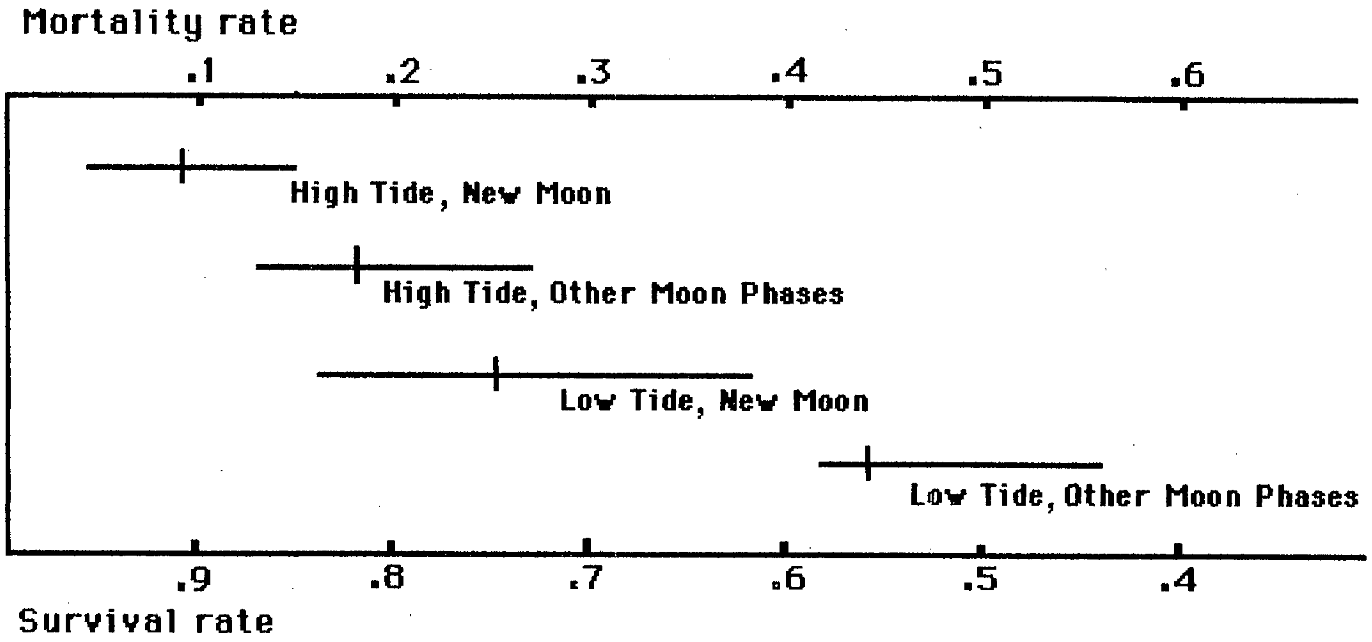
Table 3.2 Summary of logistic regression analysis of predation trials over the reef flat showing deviance and degrees of freedom that are displayed in the coefficient table. The columns **F, (df)** and **p** list results and probabilities of the F-ratio tests based on comparisons of successively simpler models. (Note that not all the succesive steps involved in the backward elimination steps are shown. 'Model 1' is the initial model followed by the simplest model (5) that adequately describes the data.)

Predictor Variables included in model	**Deviance**	**df**	**F (df)**	**p**
Analysis 1: predation trials in reef flat habitat; entire data set				
Model 1 time of day tide moon phase time of day+tide moon phase+tide time of day+moon phase	257.1	71	n.a.	n.a.
Model 5 tide moon phase	295.4	81	0.4326 (2,79)	0.6559
Model 6 tide	334.7	82	10.7763 (1,81)	0.0015
	(i.e. moon phase has a significant effect)			
Model 7 moon phase	401.4	82	28.6781 (1,81)	0.0000
	(i.e. tide has a significant effect)			

Table 3.3 Survival rates (observed and **estimated**) of hatchling turtles after 10 minutes swim over reef flat under various environmental conditions. (95% confidence intervals for the estimated values are shown in parentheses).

	High tide	Low tide	Marginal total
New moon	$\frac{171}{180}$ = 0.95 (obs.) **0.91** (est.) (0.85-0.95)	$\frac{187}{260}$ = 0.72 **0.75** (0.62-0.84)	0.81 **0.83**
Full moon, first &last quarters	$\frac{336}{420}$ = 0.80 **0.82** (0.73-0.87)	$\frac{466}{820}$ = 0.57 **0.56** (0.44-0.58)	0.65 **0.69**
Marginal total	0.85 **0.87**	0.61 **0.65**	0.77 **0.76**

Figure 3.7 Mean and 95% confidence intervals for expected mortality /survival rates of hatchlings swimming for ten minutes over the reef flat at Heron Island Reef.



The data were analyzed further to test whether predation is affected by moon light availability rather than other lunar effects. Using data for the night time trials only with moon (up or down) and tides (high, low) as predictor variables, I investigated whether the presence/absence of the moon in the night sky had a significant effect on predation. In addition, the effect of lunar periodicity on predation during the day, when illumination level did not change with changes in the phase of the moon, was also investigated . Although the effect of tide was significant during both the day and night trials, the availability of moonlight was not significant in determining predation rates at night (Table 3.4, analysis 2). The effect of moon phase on daytime predation was marginal ($p = 0.07$, Table 3.5, analysis 3). These results support the conclusion that moon phase rather than moonlight availability has a significant effect on predation.

Table 3.4 Summary of logistic regression analysis of predation trials over the reef flat showing deviance and degrees of freedom that are displayed in the coefficient table. The columns **F, (df)** and **p** list results and probabilities of the F-ratio tests based on comparisons of successively simpler models.

Predictor Variables included in model	**Deviance**	**df**	**F (df)**	**p**
Analysis 2: night time only predation trials in reef flat habitat				
Model 1				
tide				
presence of moon	181.9	36		
Model 2				
presence of moon	221.2	37	7.7702 (1,36)	0.0084
	(i.e. effect of tide is significant)			
Model 3				
tide only	190.1	37	1.6213 (1,36)	0.2111
	(i.e presence of moonlight is not significant)			
analysis 3: day time only predation trials in reef flat habitat				
Model1				
tide				
moon phase	123.1	4		
Model 2				
moon phase	207.9	43	28.9025 (1,42)	0.0000
	(i.e. effect of tide is significant)			
Model 3				
tide	133.4	43	3.4083 (1,42)	0.0719
	(i.e. effect of moon phase is not significant at 0.05 level)			

Logistic regression analysis of 13 predation trials over the reef slopes (Appendix 3) did not identify any independent variables or any of their interactions that accounted for the observed variability (Table 3.5). The rate of predation ranged between 0-25% with a mean of 7% (standard error ± 2.4) over the set distance of 20 m, which took between one to two minutes for the hatchlings to swim. However a considerable proportion of the hatchlings were preyed upon (approximately 40%) while they were being retrieved in order to disengage them from their 20 m lines. This type of predation was not observed over the reef flat.

Table 3.5 Summary of logistic regression analysis of predation trials over the reef slope showing deviance and degrees of freedom that are displayed in the coefficient table. The columns **F, (df)** and **p** list results and probabilities of the F-ratio tests based on comparisons of the successively simpler modelsdisplayed in this table.

Predictor Variables included in model	Deviance	df	F (df)	P
Model 1 time of day tide site time of day+tide site+tide time of day+site	16.23	6	n.a	n.a.
Model 2 time of day tide site	25.79	9	1.767(2,6)	0.249
	(i.e interactions are not significant)			
Model 3 time of day tide	28.34	10	0.886 (1,9)	0.371
	(i.e. effect of site not significant)			
Model 4 time of day	29.02	11	0.239 (1,10)	0.635
	(i.e. effect of tide not significant)			
Model 5 tide	28.48	11	0.049 (1,10)	0.829
	(i.e. effect of time of day not significant)			

3.2.3.3 Estimate of total predation over the reef flat.

Assuming that predation rates are constant across the reef flat and that predation rates of tethered hatchlings are the same as those of free-swimming hatchlings, the proportion of turtle hatchlings that survive the swim across the reef flat to reach deep water can be estimated using the standard exponential survivorship function (Ricker 1975):

$$N_t = N_0 * e^{-Z*t} \quad \text{or} \quad N_t = N_0 * S^t$$

Where N_0 is the number at the start of a run and N_t is the expected number at time "t". The symbol "Z" refers to the instantaneous rate of mortality and "S" the rate or proportion of survival in a unit of time (Ricker 1975).

The instantaneous mortality rate is calculated from the experimental data by the function:

$$Z = -\text{Log}_e S = -\text{Log}_e \frac{N_1}{N_0}$$

where N_1 is the number surviving at the end of one unit of time, in this case 10 minutes.

I used the probability of survival derived from the logistic regression analyses to estimate the value of "S" for the various environmental factors of interest.

Assuming that it takes 30 minutes for the average free-swimming hatchling to cross the approximately 1 km wide section of the northern reef flat at Heron Island, only 18% of them would be expected to survive and reach deep water during low tide at the first quarter of the moon. By contrast 55% are expected to survive if they enter the water during the same lunar period but at high tide. These two survival rates are significantly different, their 95% confidence ranges being 16-20% and 39-65% respectively.

3.2.4 DISCUSSION.

3.2.4.1 Justification of the method.

Observations of free swimming hatchlings were not considered suitable to quantify predation rates for several reasons. This observation technique was likely to interfere with predator-prey interactions resulting from the proximity of the prey and the observer. No observations of free swimming hatchlings could be made during the night, which is the time most relevant to this study, without the interference of underwater lights. Thus the observations of free swimming hatchlings were principally used to identify predators of the hatchlings and to observe predation events.

Measures of predation rates obtained by the two methods (i.e. free swimming and tethered hatchlings) are not directly comparable. All observations of free swimming hatchlings were done in relatively shallow water and observation times were not standardized. However, the high predation rates on the free swimming hatchlings provide some verification that tethering was not likely to result in an obvious overestimation of predation rates.

I assumed that predation rates (per unit of time, not distance) of tethered hatchlings closely approximated those of free-swimming individuals. The tether, when kept slack, imposed no impediment to the swimming ability of the hatchlings, other than some reduction in speed. However even the relatively high speed of the free-swimming hatchlings did not seem to offer protection against the much greater swimming speed and maneuverability of predators, as evidenced by the observations of interactions between untethered hatchlings and their fish predators during the snorkel dives; 44 of the 47 hatchlings succesfully followed over varied periods (but most often less than 20 minutes) during the afternoons were eaten by fish (i.e. 93.6%). Furthermore the predation rate on tethered hatchlings was low over the reef slopes. Many of these hatchlings, however, were taken by predators when their swimming became poorly coordinated while being retrieved by the observer indicating that predators were present in the area. Taken together these observations suggest that tethering *per se* does not increase the probability of predation.

3.2.4.2 Effects of environmental variables.

The lower predation rates on sea turtle hatchlings during high compared with low tides are consistent with our limited knowledge of fish behaviour. The majority of shallow water reef fishes show a strong avoidance to swimming far above the protection of the substrate as they themselves would then be exposed to predation (Shulman 1985, Hobson 1991). This especially applies to individual predators such as the Serranids, and may also apply, albeit to a lesser extent, to schooling predators such as the Lutjanids. With increasing water depth, a hatchling will be further from the bottom and thus less accessible and less detectable (McFarland 1991) to the bottom dwelling predators.

Variation in predation associated with the phases of the moon is somewhat more difficult to account for in terms of our knowledge of fish feeding behaviour. Amongst other sensory inputs, visual cues are considered to be an important aid to fish in locating and seizing prey (McFarland 1991). During new moon the nights are dark, therefore fish predators might be either less active or less successful than on nights during the other moon phases. This explanation however does not account for the fact that on many nights other than during the new moon there are several hours when the moon is not up. The availability of moon light did not affect predation rates during night trials (Table 3.5). Further, it would appear that moon phase can not be dismissed as a factor affecting predation during daylight hours (Table 3.5). It is therefore most likely that lunar periodicity, rather than degree of illumination, is the significant factor influencing predator behaviour. In support of this contention there are numerous accounts of associations between moon phase and behaviour of fish and other reef animals (Johannes 1981).

3.2.4.3 Hatchling behaviour and predation rates.

Two advantages of hatchlings emerging from the nest at night have been proposed: (1) it eliminates exposure to diurnal predators and (2) it removes exposure to the potentially lethal daytime heat of the beach. Two quantitative studies of terrestrial predation on turtle hatchlings have been published to date. Less than 2 % of loggerhead, *Caretta caretta* hatchlings are preyed upon while crossing the beach at dawn at Mon Repos, a mainland beach in southern Queensland (Limpus 1973). At Crab Island, off the northern coast of Australia, between 3 and 38 percent of emerged flatback, *Natator depressus,* hatchlings are preyed upon while crossing the beach (Limpus *et al.* 1983 b). In addition there are a few anecdotal accounts of heavy bird predation on hatchlings that emerge during the day (e.g.. Mrosovsky 1971, Stancyk 1982, Fowler 1979). In the absence of comparative studies of nocturnal vs. diurnal predation it is impossible to conclude whether nocturnal emergence offers the hatchlings significant protection from predation as they cross the beach. The greatest predation of hatchlings probably takes place after they have entered the water (Hendrickson 1958; Bustard 1972; Limpus 1978; and this study). Reef fishes show pronounced diel rhythms of activity with different composition of species feeding during the day and the night (Collette and Talbot 1972, Smith *et al.* 1972) This diel periodicity is also reflected in the presence and the feeding activity of the various carnivorous species in different reefal habitats. Yet surprisingly, in this study of aquatic predation, the day/night factor did not emerge as a significant independent variable. Crossing the reef flat at night as opposed to during daytime conferred no appreciable protection from aquatic predators, suggesting that nocturnal emergence from the nest is a behavioral response to minimize; 1) terrestrial predation during beach crossing; 2) exposure to the heat of the day; and 3) aquatic predation in habitats other than that studied here.

3.3 MEASURING PREDATION INDIRECTLY: EXAMINATION OF FISH STOMACH CONTENTS.

There are incidental reports of several species of fish consuming turtle hatchlings. These accounts give no information as to the relative importance of the various predators. My observations of the free-swimming hatchlings suggest which species are the most frequent predators during daylight (see table 3.1). But because hatchlings predominantly emerge from their nests and swim over the reef flat by night, these observations may not be a reliable index of the significance of the various species of predators.

In addition to obtaining an independent measure of predation to be compared with those obtained using tethered hatchlings, this study aimed to: (i) determine the species which were the most frequent predators of hatchling turtles crossing the reef flat, and (ii) estimate the importance of hatchlings in the diet of those fishes.

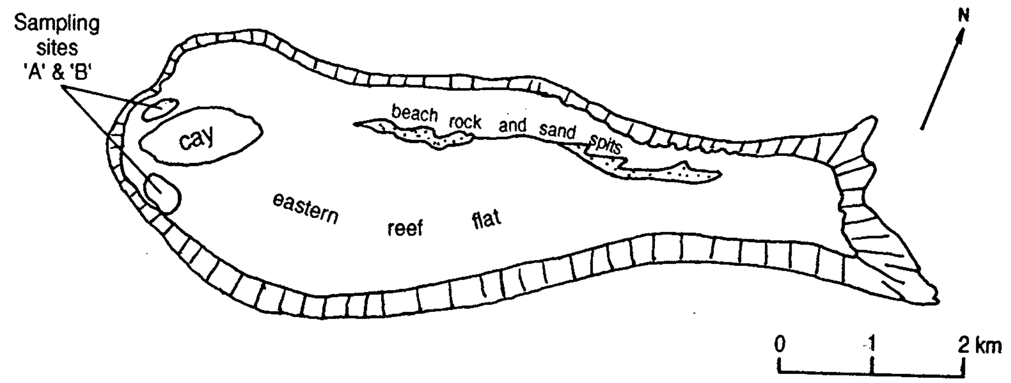
3.3.1 MATERIALS AND METHODS.

3.3.1.1 Study site.

North-West Island (23°17' south, 151°41' east) is the northernmost of the Capricorn Group of islands in the southern section of the Great Barrier Reef (Figure 3.8). The island, similar to Heron Island, is associated with an elongate platform reef covering an area of 38 km^2.

The cay, largest in the Capricorn-Bunker group, is amongst the most significant green turtle rookeries in the region (Limpus *et al.* 1984). This reef was chosen primarily because zoning by the Great Barrier Reef Marine Park Authority (GBRMPA) allowed the scientific collection of fishes from reef areas adjacent to the island. Removal of fishes from the reef at Heron Island was not allowed .

Figure 3.8 North-West Island and reef. Sampling sites are indicated. (Bars on the outer edge of the reef indicate the position of the reef slope.)



3.3.1.2 Collection and processing of specimens..

North-West Island was visited between 17 and 24 January 1989 by a team of experienced spear fishermen. During this time high tides occurred approximately between 1800 and 2300 hrs and full moon was on the 22nd January. During this period the predicted heights of high water ranged between 3 and 4.2 m.

Known carnivorous fishes of a size capable of consuming turtle hatchlings were collected by spearing in areas of the reef flat and reef slope in front of the beach where hatchlings were known to emerge from nests. Fish were speared during the morning in order to obtain a sample that indicated the incidence of forage items consumed the previous night. A gill net, 50 m x 2 m drop with mesh of 75 mm, was deployed on two nights to collect nocturnally active fish patrolling the inner reef flat. Collected fish were mostly identified to species (with only a few exceptions to genus) and weighed. The alimentary canal of each fish was removed, individually labeled and preserved in 10% sea water formalin. Several weeks later the foregut contents of each fish were identified and weighed. Contents were classified into the following categories: crustacea, fish, turtle hatchling, mollusk, fish and crustacea, fish and cephalopod, crustacea and gastropod, crustacea and cephalopod, and unidentified.

3.3.1.3 Analysis and interpretation of results.

The number of nesting turtles and emerged nests were counted by walking along the perimeter of the island each day at dawn and noting the fresh tracks made by adult females and hatchlings during the night.

Areas of the reef were estimated using a digital planimeter (Planix, Tamaya & Co.) and an aerial photograph of North West Island Reef (Kevron Aerial Surveys, Perth, W.A.). Because the inherent problems of estimating standing stocks based on underwater visual counts of fishes are increased many fold using poorly trained observers (GBRMPA 1978), I decided to use the data of Goldman (1973) collected on nearby One Tree Reef. In that study, fish from different habitats were collected using explosive charges and the data were expressed as biomass of each species found over a unit area in a given habitat. No estimate of species-by-species reef fish abundance is available for any of the other reefs in the Capricorn-Bunker region. Thus, for the purpose of this study it is assumed that the biomass of the various predators is similar among the reefs within the region.

3.3.2 RESULTS.

Fish were speared over a combined estimated area of approximately 44 ha (1.3% of North West Island reef). A total of 232 fish, representing at least 32 species, was collected. *Lutjanus carponotatus* was the most numerous species collected (n=74), followed by *Epinephelus megachir* (n=43) and *Plectropomus leopardus* (n=40) (Table 3.6). Gill netting proved to be of extremely limited use with only one potential predator, a black whaler shark (*Carcharinus melanopterus*) captured. The stomach of this shark was empty.

Table 3.6 Fish collected by selective spearfishing at North-West Island between 17 and 24 January 1989.

Species	(n)	Biomass(kg)
Lutjanus carponotatus	75	39
Epinephelus megachir	43	14
Plectropomus leopardus	40	48
Plectropomus (var. spp.)	13	117
Lethrinus (var.spp.)	9	
Plectorynchus flavomaculatus	8	
Epinephelus sp	8	
Cephalophis (var. spp.)	7	
Choerodon (var. spp.)	7	
Lutjanus (var. spp.)	3	
Other species	19	
Σ	232	218

3.3.2.1 Fish stomach contents.

Of the 232 guts examined 28 were damaged by the spear and were discarded; 115 specimens had empty stomachs (contents weighing <1g). Most stomachs contained crustaceans (56.4%) or fish (28.2%). Several species of fishes had a mixed diet of fish, crustacea, cephalopods and/or gastropods (Table 3.7). Turtle hatchlings (*Chelonia mydas*) were found in the stomachs of six *L. carponotatus* and one *E. megachir* . The number of *L. carponotatus* from which turtle hatchlings were recovered approximated those containing any other food item (Table 3.7). *E. megachir* was feeding almost exclusively on crustaceans with a minor contribution of fish, turtle and gastropods. Only one specimen contained turtle hatchlings (Table 3.7). With one exception, the 40 *P. leopardus* stomachs examined, contained only fish. The condition and the weight of hatchlings recovered from fish stomachs are summarized in Table 3.8.

Table 3.7 Details of the foregut contents of fish sampled at North-West Island.

Contents	**All fish sampled**	***L. c.***	***E. m.***	***P. l.***
Crustaceans (empty)	62 (18)[1]*	5	23	0
Fish (empty)	31 (6)*	6	1	14
C. mydas hatchlings	7	6	1	0
Gastropods	1	1	0	0
Fish and crustaceans	6	4	1	0
Crustaceans and gastropods	1	0	1	1
Crustaceans and cephalopods	1	0	0	0
Fish and cephalopods	1	1	0	0
Unidentified (empty)	94 (91)*	0 (43)*	0 (14)*	22 (21)*
Damaged gut	28	9	2	3
Σ	232	74	43	40

L.c. = L. carponotatus, E. m. = E. megachir, P. l. = P leopardus

[1]* 18 of the 62 had <1 g crustaceans. Others asterisked are similar.

Table 3.8 Summary of the number of nightly nest emergences, number of fish caught daily, and particulars of turtles in fish guts. All fish containing hatchlings were caught over the reef flat. Seven turtle hatchlings were freshly ingested while one was partially (*) and two were almost completely (**) decomposed. No food item other than turtle was contained in the guts containing turtle hatchlings.

Date	**No. of nest emergences**	**Species of fish**	**No. and weight of hatchlings in guts**	**No. fishes caught**
17.01.89	?	None with hatchlings		23 (1 *Em*, 3*Lc*)
18.01.89	?	*E. m.*	two, 51.02 g	35 (11 *Em*, 7 *Lc*)
19.01.89	3	*L. c.*	one, 15.10 g*	53 (7 *Em*, 21 *Lc*)
20.01.89	4	*L. c.*	two, 47.55 g	42 (9 *Em*, 19 *Lc*)
20.01.89		*L. c.*	one, 26.80 g	
20.01.89		*L. c.*	one, 2.51 g**	
20.01.89		*L. c.*	one, 6.16 g**	
21.01.89	6	*L. c.*	two, 49.11 g	39 (14*Em*, 12 *Lc*)
22.01.89	2	No Spearing		
23.01.89	11	None with hatchlings		22 (0 *Em*, 5 *Lc*)
24.01.89	7	None with hatchlings		17 (1 *Em*, 12 *Lc*)

Em = E. megachir, Lc = L. carponotatus

3.3.2.2 Number of hatchlings crossing the reef.

The 1988/89 green turtle nesting season along the Great Barrier Reef was amongst the poorer nesting seasons recorded for the region (C. J. Limpus pers. com.) On North West Island, the number of green turtles ashore during our stay varied between 26 and 44 per night. Hatchlings emerged from only a few nests each night. (Table 3.8). During the eight nights preceding the collection of fishes hatchlings emerged from an estimated 44 nests. The mean clutch size for green turtles nesting at Heron Island, another of the Capricorn-Bunker rookeries, is 115.25 (S.E.= 3.943) (Limpus 1984) and emergence success is approaching 90% (pers. obs.). Therefore approximately 4500 (i.e. 44 x 115.25 x 0.9 = 4564) hatchlings were expected to have entered the sea during the study period.

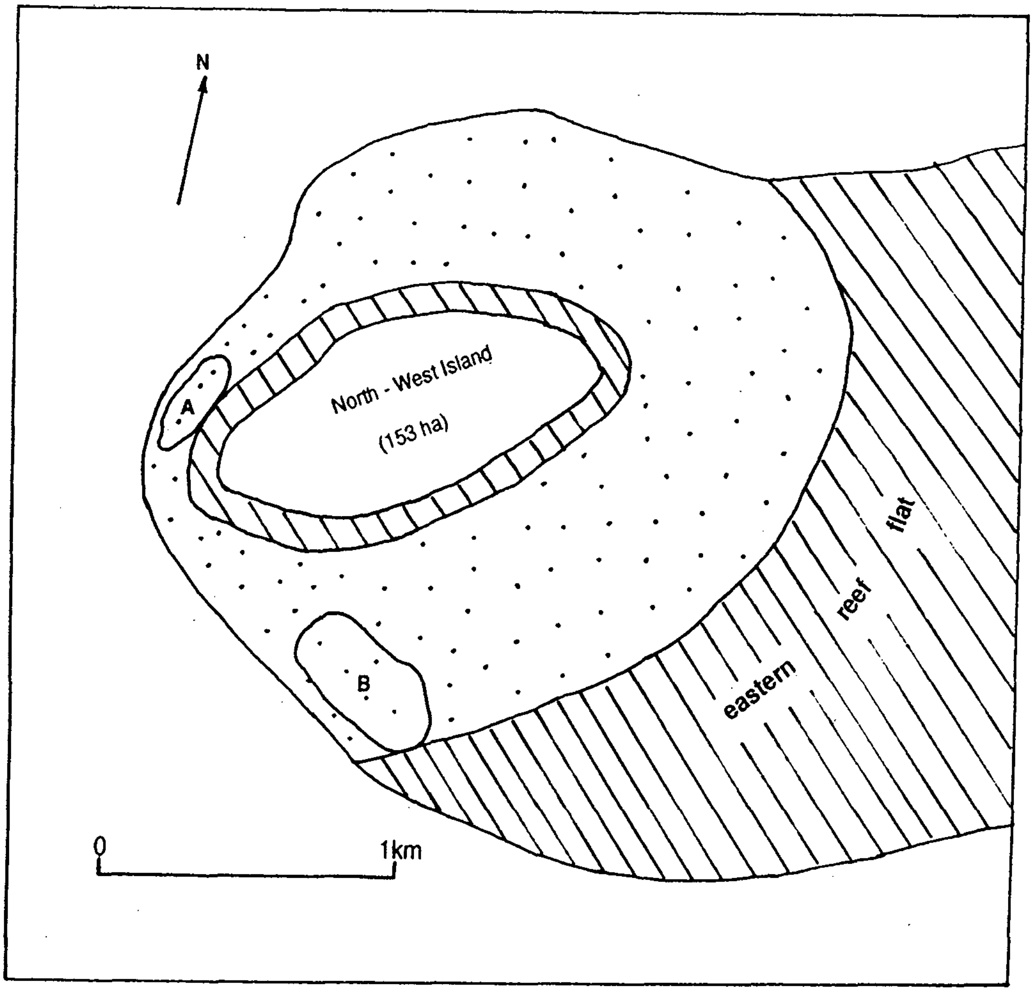
3.3.2.3 Estimate of total predation over the reef flat.

Estimates of standing stock of fish were based on previous work at the neighbouring One Tree Island Reef by Goldman (1973). As information about the incidence of predation on turtle hatchlings was obtained only from *L. carponotatus* and *Epinephelus spp.*, all calculations are based on the estimated standing stock of these fishes over the reef flat and the proportion of these fish containing turtle hatchlings.

Assuming that the probability of a hatchling being preyed upon is constant across the reef flat, the probability of any fish consuming a hatchling is inversely but not linearly proportional to the distance from the beach. This is a consequence of the non-uniform distribution of hatchlings over the reef flat partly as a result of a radial dispersion pattern (see above, Section 2.3.1). In addition and perhaps even more significantly, the density of hatchlings is affected by continued attrition, caused by predation, as they swim over the reef flat. Thus, the proportion of stomachs containing hatchlings may vary considerably depending on the sampling site. In the absence of information about the location of the last feed of fishes sampled, it was assumed that fish were feeding in the area of their capture. (This assumption may not be valid, especially for the highly mobile *L. carponotatus*).

Fish were collected in sectors of the reef flat ranging from 100 to 750 m from the beach (Figure 3.9). The sampled sectors had a combined area of 44 ha which represents 5.9 % of a 650 m wide band of reef flat around the island (Figure 3.9). Of the 106 *L. carponotatus* and *Epinephelus* spp. examined 7 fish had consumed a total of 10 turtle hatchlings. Assuming that the probability of any of these predators containing turtle hatchling remains is 0.066 (i.e. 7/106). The 95% confidence range can be estimated (using binomial probabilities) and is between 4.2-14.4 hatchlings consumed by an equivalent sample of *L. carponotatus* and *Epinephelus* spp. The combined biomass of these two species in the spearfishing sample was 53 kg while the standing stock of these two species over an area corresponding to the size of the sampled area of 44 ha was calculated to be 1185 kg. This biomass of fish would be expected to consume 223 (proportionally adjusted 95 % confidence range = 94-426) hatchlings. Assuming that this predation rate applied to the whole of the reef flat area which was sampled (Figure 3.9) approximately 3800 hatchlings (proportionally adjusted 95 % confidence range = 1593-7220) or 84% (42-100%) of those that have entered the water would be consumed within the band of reef flat defined above.

Figure 3.9 North-West Island Reef, showing area within which predation on hatchlings is estimated (stippled).The hatched area was not sampled and the estimated predation rate does not include predation occurring in the hatched areas.



The consumption of turtle hatchlings in the band of reef flat (area stippled in Figure 3.9) can be viewed as the minimum estimate of the number of hatchlings preyed upon by *L. carponotatus* and *Epinephelus spp.* over North-West Island Reef during the study period. It does not include hatchlings preyed upon in the zone immediately adjacent to the beach (approximately 62 ha of reef flat), nor those that are consumed while traversing the large expanse of the eastern reef flat (areas hatched in Figure 3.9) or those consumed by other species of fish.

3.3.3 DISCUSSION.

3.3.3.1 Most frequent predators of hatchling *C. mydas.*

The literature on fish predators of hatchling sea turtles is depauparate. Stancyk (1982) listed 15 fish predators of marine turtle hatchlings, eight of which were identified to species level. Additional species are listed in Appendix 4.

Sampling of reef fish populations is made difficult by the many factors that affect their spatial and temporal distribution. Habitat and food requirements, intra- and inter-specific interactions and social habits all result in greatly variable distributions. In addition, physical changes in the environment such as the time of day, moon phase and state of the tide also affect the distribution and activity of reef fishes (Hobson 1965 1972, Russell *et al.* 1978). The sampling strategy in this study was designed to at least partly compensate for the diel movement of fishes between the reef flat and reef slopes by collecting fish from both habitats.

As a collection technique, spear fishing suffers from many drawbacks that are commonly encountered when using visual census methods (GBRMPA 1978). However, in this study, the selective bias of this method was, in fact, a desirable attribute since it allowed selective sampling of appropriate target species. The composition of the present sample is likely to be influenced by the absolute frequency of species on the reef and the non-cryptic behaviour and ease of sighting and spearing of various species. Accordingly, *L. carponotatus* was the most numerous species in the sample. Not only is it very abundant on the southern Great Barrier Reef but it is easy to see during the day when it often aggregates in groups. By contrast, *E. megachir* and *P. leopardus* are both solitary, often sheltering amongst coral and consequently more difficult to find.

Time of year and the availability of forage items greatly influence the gut contents of sampled fish (Randall and Brock 1960, Goldman and Talbot 1976). Turtle hatchlings occur only on very few reefs and their availability to predators is seasonal. Because most carnivorous fishes are highly opportunistic (Goldman and Talbot 1976), it is reasonable to expect that, when in season, turtle hatchlings are utilized as food.

3.3.3.2 The importance of hatchlings in fish diets.

In this study, turtle hatchlings, fish and crustaceans were found in the guts of *L. carponotatus* with approximately equal frequency. Lutjanids are generally reported as nocturnal feeders, but they may also take prey during the day on occasion (Sano et al. 1984, Randall *et al.* 1990). I have several anecdotal records of green turtle hatchlings in the guts of *L. carponotatus* caught by fisherman on the reef at Heron Island including one report of two hatchlings in the gut of one specimen. This fish was caught in the morning following the emergence of hatchlings from the first nest emergence of the season in January 1986. The data generated by this study together with anecdotal observations over several years indicate that hatchlings form a significant part of the diet of *L. carponotatus* on reefs bordering sea turtle rookeries during the hatchling emergence season.

The spearfishing study suggests that turtle hatchlings make a relatively minor contribution to the diet of *E. megachir.* This is in contrast to direct observations of predation events. During snorkel dives in daylight, *Epinephelus* sp. were the most frequently observed predators. (Lutjanids are known not to feed during the day.) Several records of line-caught specimens containing hatchlings have also been reported to me. During February 1990, while collecting specimens for an unrelated study, Dr. M. Capra reported that out of 10 *Epinephelus* sp. caught by line fishing at Heron Island reef, five regurgitated *C. mydas* hatchlings on being landed in the dinghy. Three of the 12 *L. carponotatus* landed during the same time also regurgitated turtle hatchlings. But as the fish he caught were not sacrificed, the true proportion of *Epinephelus* and *L. carponotatus* that were feeding on hatchlings is not known.

None of the seven specimens of *Choerodon* spp. in the present sample contained turtle hatchlings, although *Choerodon* spp. were frequently observed preying on the turtles in the experiments involving tethered hatchlings. Larger Labrids, such as *C. cyanodus*, are much less frequently seen by divers than are *L. carponotatus* and *Epinephelus* spp (GBRMPA 1978). They are most often found in the reef crest and reef slope habitats. During low tides, they were seen in larger tidal pools where they were frequently observed preying on turtle hatchlings. This fish would approach slowly, and thoroughly investigate the prey before deciding to attack. Many of these fish were observed from a distance of 8-10 m to take a hatchling, maim it and then release it only to capture and release it again before finally swallowing it. Little is known of the nocturnal feeding habits of *Choerodon spp.* on the Great Barrier Reef. Labrids are reported to be inactive and shelter at night (Hobson 1965; Randall *et al.* 1990). However *Choerodon* sp. can be caught at night by line fishermen (Goldman pers. com.). *C. cyanodus* is wary of the presence of divers, which makes it a relatively difficult species to capture by speargun.

Under normal circumstances hatchling emergence is primarily nocturnal. Given that Lutjanids and Serranids are the dominant group of larger nocturnal predators, it is likely that turtle hatchlings make an important contribution to the diet of many of those fishes. My data are insufficient to examine the effect of relative prey abundance on prey selection by the various fish predators of hatchlings of *C. mydas*. However it may be possible that predators using different search modes (for example *L. carponotatus* *versus Epinephelus spp.*) require different relative densities of an alternate prey, in this case turtle hatchlings, before they make significant use of it. Similar switching behaviour in predatory fish (guppies, *Poecillia reticulatus*) and invertebrate predators (damselfly naiads) have been discussed respectively by Murdoch *et al.* (1975) and Akre and Johnson (1979).

3.3.3.3 Effects of fish predation on hatchling survival.

Estimating total consumption of hatchlings by fishes is made difficult by several factors. Some of these relate to the actual sampling of reef fish populations and others arise from the non-uniform distribution of hatchlings over the reef flat. Despite the problems of sampling and assessment, discussed above, this study demonstrates that coral reef fishes consume a significant proportion of turtle hatchlings as they swim over the reef flat.

3.4 GENERAL CONCLUSIONS.

3.4.1 AGREEMENT BETWEEN THE ESTIMATED RATES OF PREDATION DERIVED BY THE TWO METHODS.

The study of predation rates involving tethered hatchlings concluded that predation rates were very high and that hatchling survival rates were correlated with environmental parameters such as tides and moon phases. Around full moon, the lunar phase during which fish were collected by spearing, predation rates varied depending on the state of the tide, but were between 0.18 and 0.44/10 minutes spent on the reef flat by hatchlings. Thus, after 20 minutes, (the approximate time taken by a hatchling to swim 650 m) approximately 30 -70% of hatchlings that enter the sea are not expected to survive. By comparison the study of fish stomach contents estimated that 84% (42 - 100%) of hatchlings are taken by fish while crossing a reef flat of the same width. While these results cannot be compared statistically they both confirm that a large proportion of hatchlings are lost to predators soon after entry into the water.

3.4.2 BETWEEN YEAR VARIATION IN PREDATION RATES.

The number of green turtles nesting in any one year varies widely (Limpus and Nicholls 1988) and the number of hatchlings entering the sea each night reflects this year to year fluctuation. The number of hatchlings entering the water in the 1989 hatching season (spearfishing study) was much smaller than the number during the 1987, 1988 and 1990 seasons (study of tethered hatchlings). It remains to be determined whether the highly variable number of turtle hatchlings in different years significantly affects predation rates in nearshore environments.

3.4.3 GEOGRAPHICAL VARIATION IN PREDATION RATES.

No attempt was made to investigate the larger scale spatial and temporal variation of aquatic predation of hatchlings, although it is almost certain that significant variations exist. As noted by Limpus (1978) and Mortimer (1982), the intensity of predation in the water may be influenced by the type of offshore habitat the hatchlings must cross. Predation on loggerhead turtle hatchlings was comparatively low on the east coast of Florida (Witherington and Salmon 1992). However the results of Witherington and Salmon (1992) are not directly comparable to the results obtained by the present study because of a marked difference in observation periods between the two studies. Most green turtle nesting in eastern Australia occurs on coral cays which are surrounded by reefal habitats comparable to the reefs of Heron and North-West Islands (Limpus 1978). The results of this study suggest that aquatic predation of the hatchlings in the first hour or so after leaving the beach has a potentially significant impact on the dynamics of the local population(s). Published descriptions of turtle rookeries seldom give details of the type of aquatic habitat immediately adjacent to the nesting beach, but nesting beaches are not necessarily bordered by coral reefs (e.g.. Tortuguero, Meylan 1982, and Ascension Island, Mortimer 1982).

3.4.4 THE EVOLUTIONARY SIGNIFICANCE OF PREDATION ON HATCHLINGS.

At eastern Australian rookeries, aquatic predation on green turtle hatchlings is high and there is pronounced temporal and spatial variation over a range of scales (above). The production of a large number of eggs which are divided into several clutches is a likely adaptation to compensate for the observed high and variable predation rate. These features of the reproductive strategy of sea turtles are consistent with the predictions of 'bet-hedging' models and, to some extent, with the 'r- and K- selection' theory. Variable environments affecting survivorship in the early life stages select for dividing a season's reproductive effort into several smaller clutches rather than fewer, larger ones. High mortality in the early life stages *per se,* on the other hand, is compensated by a large number of relatively small offspring and no parental care.

CHAPTER 4

PREY DEFENCE MECHANISMS OF GREEN TURTLE HATCHLINGS.

Rualko and the Turtle.
Bark painting by Unknown artist (Yirrkalla)
National Gallery of South Australia

Rualko, a mythical man who lived on the eggs of turtles and sea birds, camped on the western shores of the Gulf of Carpentaria. The long herringbone design in the middle of the painting is a turtle track. The footmarks of Rualko as he walked to the nest to rob it are on the right hand side of the turtle track, and those made on his return, are on the left. He also collected the eggs of the four sea gulls shown on the painting.

4 PREY DEFENCE MECHANISMS OF GREEN TURTLE HATCHLINGS.

4.1 GENERAL INTRODUCTION.

It has been suggested that an important criterion in the selection of major nesting sites by sea turtles has been isolation from the diverse terrestrial vertebrate predators which are present on larger land masses (Carr 1973, Iverson 1991). Most of the key green turtle rookeries in eastern Australia are located on isolated coral cays (Raine Island, Moulter Cay, No. 7 and No. 8 Sandbanks and the Capricorn-Bunker rookeries).

In Chapter 3 I concluded that a very large proportion of hatchlings is taken as prey by reef fishes as the hatchlings leave their natal beach. As air breathing quadrupedal animals, sea turtles are not able to access the extensive repertoire of predator avoidance mechanisms developed by fishes (Hixon 1991, Hobson 1991) such as schooling and increased swimming speed. Adult turtles obtain protection from predators through their large size, sleeping in the shelter of underwater caves and ledges, and voluntary stranding on land at low tide. Hatchlings do not have access to any of these options of predator avoidance. They are constrained by their small size, limited diving ability and slow swimming speed.

In this chapter I examine possible mechanisms whereby green turtle hatchlings minimize the risk of predation in the sea including: 1) behavioral adaptations such as the timing of emergence and hence the timing of their swim across the shallow water habitats; and 2) morphological adaptations, in particular the effectiveness of countershading.

4.2 BEHAVIORAL DEFENCES: THE TIMING OF EMERGENCE.

4.2.1 INTRODUCTION.

Sea turtles typically lay their clutches of about 100 eggs in subterranean nests in sand dunes above the high water mark (Carr 1973; Ehrhart 1982; Limpus *et al.* 1984). The eggs incubate 50-80 cm below the sand surface for 7-11 weeks (Miller and Limpus 1981). After hatching, the young must dig to the surface. This process, which may take several days, is greatly facilitated by the co-ordinated activities of the members of the clutch (Carr 1973; Balazs and Ross 1974). Hatchlings may dig upwards from their nest chamber at any time during the 24 hr period (Bustard 1972; Balazs and Ross 1974). However, when approaching the surface during daylight the hatchlings generally stop digging, presumably in response to high sand temperatures (Bustard 1967, 1972; Mrosovsky 1968, 1980; Mrosovsky and Shettleworth 1968).

Emergence characteristically occurs at night (Hendrickson 1958; Bustard 1967; Mrosovsky 1968; Witherington *et al.* 1990). Behaviour of the uppermost hatchlings appears to influence the behaviour of other members of the clutch below (Bustard 1967). All the hatchlings in a clutch typically emerge within minutes of one another, although in some instances small groups or individual hatchlings may emerge some time before or after the main group (Hirth 1971; Witherington *et al.* 1990). Upon reaching the sand surface, the hatchlings cross the beach rapidly and enter the water. They then maintain intensive swimming activity for several hours or days (Carr 1986; Salmon and Wyneken 1987)

Investigation of the effect of environmental parameters on aquatic predation rates (Chapter 3) revealed no significant difference in predation rates between day and night. Similarly, Witherington and Salmon (1992) found no suggestion of diel variation in predation rates in the near shore waters of Florida. These results suggest that nocturnal emergence amongst sea turtle hatchlings evolved as a means to reduce mortality due to physiological stress and possibly diurnal predation during beach crossing.

Two environmental parameters which influence predation rates on hatchling turtles were identified in the previous chapter. Predation was inversely related to water depth (tide) and predation was lowest during the new moon. No studies have attempted to investigate possible associations between this variation in predation rate and the temporal pattern of emergence.

Temperature has often been suggested as the main mechanism for controlling emergence. Inhibition of activity by temperatures above 28.5°C (Mrosovsky 1968, 1980, Mrosovsky and Shettleworth 1968), 30°C (Bustard 1967; Heath and McGinnis 1980), 33°C (Hendrickson 1958) and 30-33°C (Bustard 1972; O'Hara 1980) has been demonstrated in both hatchling and post-hatchling sea turtles. However, these thresholds have not been verified in the field.

Sand temperature gradients may be used in the nest site selection process by adult loggerhead turtles (Stoneburner and Richardson 1981). The possibility of hatchlings responding to negative thermotaxis has been raised (Mrosovsky 1980), but until now has not been investigated.

Section 4.2 of this chapter quantifies the temporal pattern of hatchling emergence, associated sand temperature profiles and tidal regimes at the nesting beach at Heron Island. Three models predicting the timing of hatchling emergence are constructed and compared with the observed pattern of emergence. The first model assumes that hatchlings emerge uniformly throughout the day. The other models are based on threshold temperatures or on thermal gradients in the sand. The relative advantages of the latter two models in reducing mortality are discussed.

4.2.2 MATERIALS AND METHODS.

4.2.2.1 Study site.

Heron Island, an elongate coral cay, has an approximate east-west longitudinal axis. The island is 1.6 km in circumference and is surrounded by a sandy beach some 15-30 m wide at low tide. Most turtle nests are located in the vegetated dunes where they are at least partially shaded by trees (*Pandanus sp., Casuarina equisetifolia, Scaevola saricea, Tournefortia argentia* and, less frequently, *Pisonia grandis*).

4.2.2.2 Counting of emerged hatchlings.

In the first two weeks of February in 1988 and 1990, the numbers of hatchling turtles that emerged from nests were recorded along approximately 200 m of beach, about 12% of the beach used by the turtles for nesting. A low barrier fence of plastic mesh (commercially sold as "gutterguard") was erected above the high water mark to intercept emerging hatchlings on their way to the sea. At approximately 30 m intervals, buckets were buried in the sand on the dune side of the fence to serve as pit traps. The ends of the fence were curved back in an arc, 30 cm in diameter, to prevent hatchlings escaping (Figure 4.1). The fence was sufficiently soft and resilient to permit adult turtles to proceed up the beach to their nesting sites. The fences were patrolled hourly.

Occasional damage caused by adult turtles was repaired and the hatchlings trapped in the buckets were counted and then released on the seaward side of the fence and allowed to make their way to the water.

Figure 4.1 Fence line with pit traps in position on the northern beach of Heron Island, February 1990.

Patrols were maintained for the entire 24 hours on four days, and on six days they were made between 1600 and 0700 hrs only, as few hatchlings emerged during daylight.

At the conclusion of each day's hatchling counts, the number of emergence events for each hour was estimated on the basis of (i) the number of hatchlings counted, (ii) location of groups of hatchlings and (iii) hatchling tracks. Because previous authors have suggested that the emergence behaviour of very small groups of hatchlings may deviate from that seen in larger groups (Bustard 1967; Carr 1973) an emergence event was defined as the synchronous emergence of a group of 20 or more hatchlings. In most cases distinct hatchling tracks made it possible to unambiguously identify an emergence event. However, when hatchling tracks gave no clear clues as to the origin of the hatchlings in the buckets, counts of over 120 hatchlings in neighbouring buckets were interpreted as two hatching events based on the finding that less than 5% of the 155 nests examined at Heron Island during the 1986/7 season produced more than 120 hatchlings (Limpus, unpublished).

4.2.2.3 Sand temperature measurements.

Sand temperatures were measured hourly while hatchlings were being collected and counted. Two methods were used. In February 1988, thermistor probes (Phillips Industries, 10 K 5% NTC disk type thermistors) were buried in the sand at six locations representing a variety of nesting habitats. At each location, the thermistors were positioned at depths of 70, 50, 30, and 3-5 cm. Resistance measurements were taken with a digital multimeter and converted to temperatures using the Steinhart and Hart (1968) temperature equations. Each thermistor was calibrated against a mercury in glass thermometer prior to installation. The thermistors were rechecked and found accurate after all temperature readings were completed. The accuracy of the multimeter was tested daily against three 'standard' resistors. In February 1990, sand temperatures were measured using a mercury in glass thermometer at the surface and at 10 cm depth. at haphazardly chosen locations within the nesting habitat behind the hatchling fence on the northern side of the Island.

The depth of 10 cm was chosen for two reasons: 1) diel temperature variation is still pronounced at this depth whereas the magnitude of this variation rapidly diminishes with increasing depth, so that at 30 cm daily fluctuations are generally less than 1°C; and 2) as green turtle hatchlings measure approximately 5 cm in length, the hatchlings positioned within the upmost 10 cm of sand at the top of a quiescent clutch can perceive daily temperature changes while still being adequately covered.

4.2.2.4 Tides.

Tide height was read directly from the standard tide gauge installed at the Heron Island harbour.

4.2.3 MODELS OF HATCHLING EMERGENCE.

Three possible models for predicting the timing of hatchling emergence were generated and tested against the observed pattern.

Uniform model - assumptions.

This model assumes that hatchlings emerge at uniform rate throughout the day.

Threshold model - assumptions.

The model assumes that above a set sand surface temperature hatchling emergence is inhibited. In this model 31°C was chosen as the threshold temperature, based on the work carried out at Heron Island by Bustard (1972). Thus the 'window' during which emergence would occur commenced when all surface temperature measurements were below 31°C and ended when all were at or above 31°C.

Thermal gradient model - assumptions.

This model assumes that hatchlings respond to thermal gradients in the top 10 cm of sand. Thermal gradients were calculated as the temperature difference between the surface and 10 cm depth ($\Delta T = T_{surface} - T_{10\ cm}$). Thus under the assumptions of this model, the window would be open when surface temperatures were all less than the temperature at 10 cm (*i.e.* negative thermal gradient) and would be closed when all measurements showed the thermal gradient to be ≥ 0.

The following assumptions and definitions common to the threshold - and thermal gradient models were also made: 1) hatchlings that approach the surface during the period of favourable thermal conditions (i.e. within the window) would emerge without delay; 2) hatchlings encountering inhibitory thermal conditions would cease emergence activity and wait below the surface until thermal conditions initiate or permit emergence. During daytime, a number of clutches would thus normally accumulate below the surface ready to emerge when conditions permit; 3) emergence of these 'waiting' clutches would follow the onset of favourable thermal conditions with a one hour lag period; 4) to account for thermal variability of the habitat, approximately one fifth of the 'waiting' clutches were designated to emerge an hour before and an additional one fifth an hour after the time that the accumulated clutches were expected to emerge; 5) a unit of emergence was defined as the number of emergence events expected each hour if emergences were distributed uniformly through the diel cycle. Both models assume that the hatchling's response is the same, regardless of the nature of the cue.

The observed pattern of emergence was compared with that predicted by the models using Chi-square goodness of fit tests which, in this situation, may be considered as measures of similarity (Zar 1974).

4.2.4 RESULTS.

Of the 11 days and nights during which the number and time of emergence events were recorded, four coincided with periods of continuous cloud cover and frequent rain while the remaining seven days were sunny. Data obtained during these different weather conditions were treated separately.

4.2.4.1 Sand temperatures.

Diel temperature variation from the surface to 70 cm below the surface was essentially similar to that reported by Maloney *et al.* (1990) on the adjacent Queensland coast. On the surface, temperature peaked between midday and 1400 hrs when the highest temperature of 54°C was recorded. Temperatures dropped during the afternoon and night to a minimum of 24.5°C between 0400 and 0600 hrs (Figure 4.2). At 10 cm depth, temperature fluctuated between 38°C at 1300 hrs and 27°C at 0500 hrs.

Temperature profiles of the Heron Island rookery within the top 10 cm of sand showed considerable spatial and temporal variation. Temperatures obtained at different sites within the nesting habitat at the same time, or at the same sites at the same time but on different dates, varied greatly. The greatest spatial variation was found during the early afternoon when surface temperatures around the island typically ranged between 34.5°C and 46°C. Spatial variability decreased as the afternoon progressed, and by midnight the maximum difference in surface temperatures between sites was generally found to be less than 3°C. With increasing depth, spatial and temporal variation in sand temperature decreased.

At 10 cm, during the study period, the greatest variation was found at approximately 1600 hrs when temperatures ranged between 31.5°C and 38°C. Spatial variation decreased during the night and after 2300 hrs it was generally less than 1°C (Figure 4.3). During the night, between 1900 and 0800 hrs, temperatures recorded at 10 cm exceeded surface temperatures. At sunrise the temperature changes observed during the afternoon and evening were reversed when, at approximately 0600 hrs, the surface temperatures suddenly started to increase (Figure 4.4). Although absolute temperatures at 10 cm and at the surface varied between sites at any one time, the change between positive and negative thermal gradients occurred at a similar time at different sites.

At 30 cm below the sand surface, daily temperature change was generally less than 1°C even on bright sunny days. Temperatures at this depth were highest during the night and varied among sites between 29°C and 32.4°C. The lowest temperatures were recorded around midday and ranged between 28.2°C and 31.6°C

During days of heavy overcast and intermittent rain the maximum temperature at the sand surface seldom exceeded 30°C and spatial and temporal variation throughout the day and between sites was reduced to less than 5°C.

Figure 4.2 Sand surface temperatures at different times of the day during early February 1990.

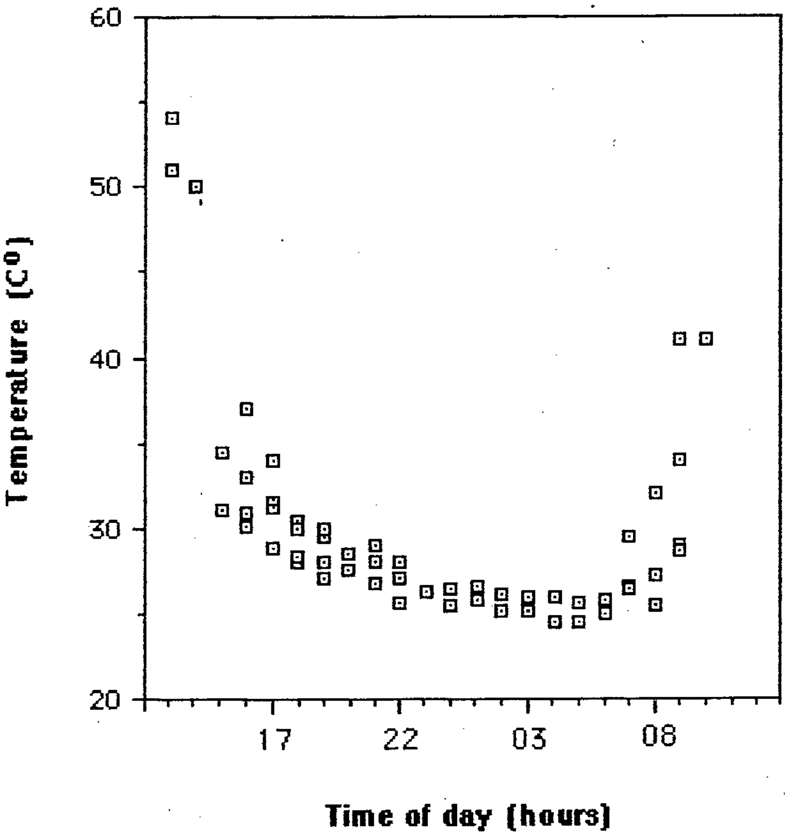


Figure 4.3 Sand temperatures at 10 cm depth at different times of the day during early February 1990.

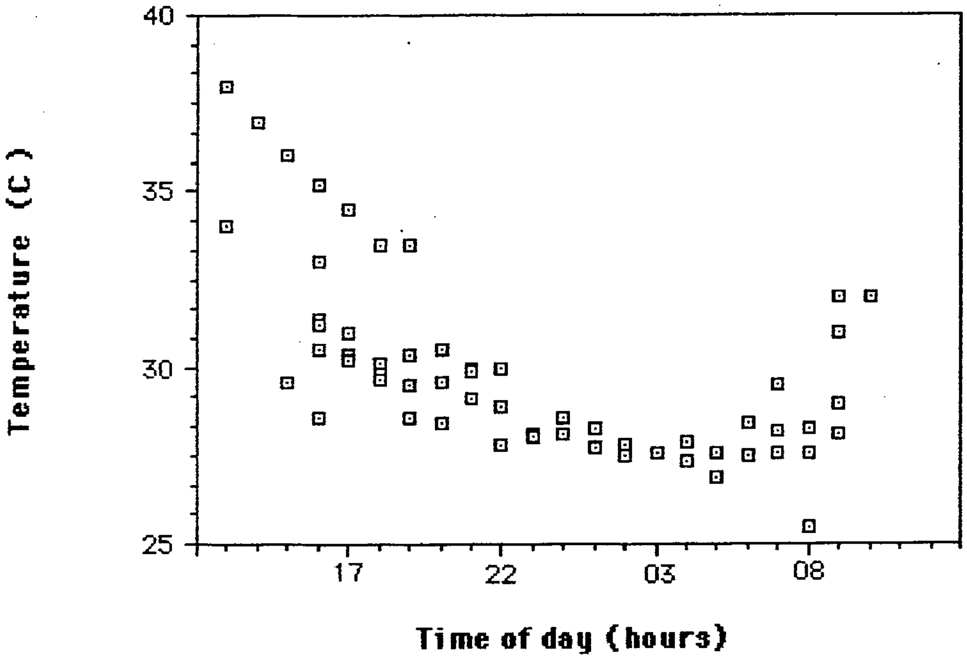
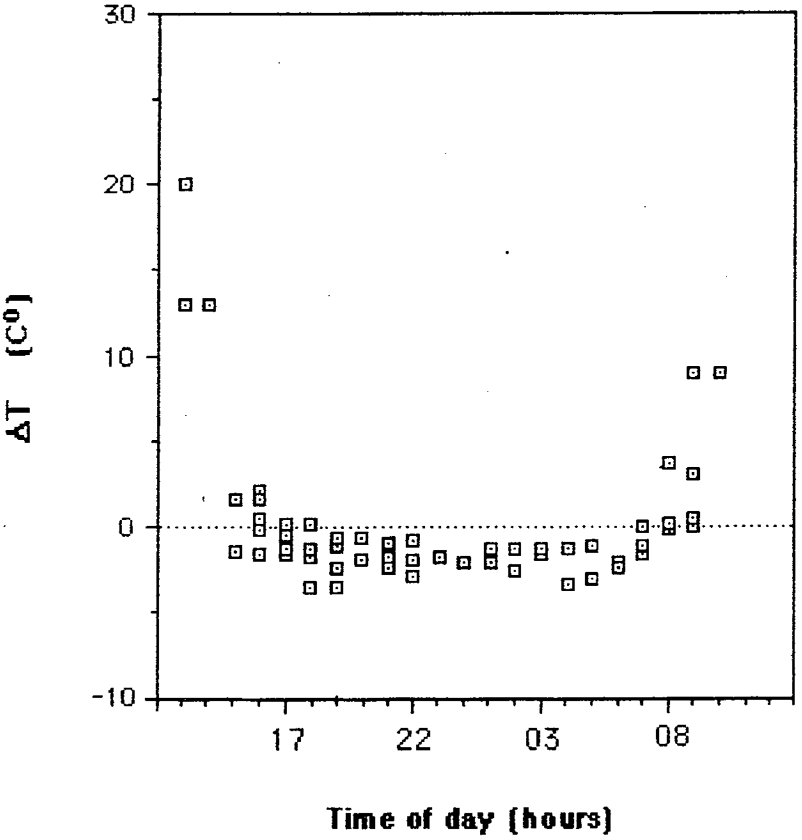


Figure 4.4 Changes in sand temperature gradients ($\Delta T = T_{surface} - T_{10\ cm}$) with time of day. Along dotted line the temperature difference between the surface and 10 cm depth is 0^0C.



4.2.4.2 Observed pattern of emergence.

The timing of 22 emergence events was recorded during two separate 24 hour periods of cloud and intermittent rain. The observed distribution was compared with that expected if hatchlings were emerging uniformly throughout the day, *i.e.* 0.916 emergences per hour. Data were clumped into four 6-hour periods (starting at midday) to allow for sufficient number of expected emergences per cell as required by the test. The frequency distribution of these emergences was not significantly different from uniform distribution ($X^2 = 1.64$; df = 3; $P \approx 0.6$).

The eastern aspect of the island is the first to lose direct sunlight and this might result in an earlier onset of emergence there. I examined this possibility using data obtained for the northern and eastern beaches on the nights of 7,12 and 23 Feb. 1988. Using statistical procedures for circular distributions (Zar 1974), I found no significant difference in the mean time of emergence between these two aspects of the island ($F = 1.08$; df = 1,29; $p > 0.5$) and casual observations over several years indicate that the onset of emergence is similar around the island.

The timing of 58 emergence events was recorded during seven days of bright sunny weather. The tidal regime varied between these nights. On the 07, Feb. 1988 and on the 9,10, and 11, Feb. 1990, high tide occurred between 1900 and 2300 hrs. The times of 38 emergence events were recorded during those four nights. On the 2, 3 and 4, Feb. 1990, low tide occurred between 1900 and 2200 hrs and 20 emergence events were timed. These markedly different tidal regimes did not result in a significant difference in the frequency distribution of emergence (Kolmogorov-Smirnov two-sample test statistic = 0.20, p = 0.68). Therefore the 7 days' data were treated as a single set.

4.2.4.3 Expected pattern of emergence: The uniform emergence model.

Emergence was not uniformly distributed throughout the diel cycle (Table 4.1). During the 7 days of sunny weather no emergences occurred during daylight between 0700 and 1700 hrs. Emergence events were most frequently observed between 2000 and 2100 hrs. This observed frequency distribution was found to be significantly different from that expected if hatchlings were emerging uniformly throughout the day, *i.e.* 2.42 emergences per hour ($X^2 = 59.986$; df = 6; $P < 0.001$).

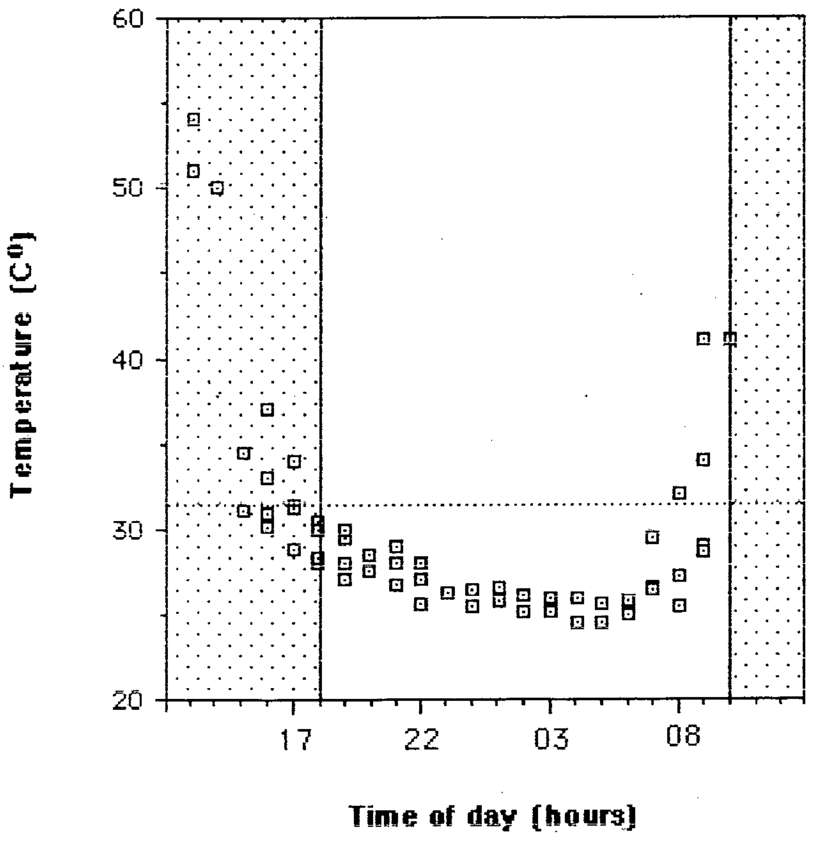
Table 4.1 Observed pattern of hatchling emergence events and that expected under assumptions of uniform emergence, the temperature gradient and temperature threshold ($31^{o}C$) models. Horizontal bars indicate groupings for the three separate X^2 goodness of fit tests. For each test the grouping for the 'observed distribution' corresponds to the grouping shown alongside the expected distribution. (*Actual number of emergences per hour, accumulated over seven days)

Time periods	Observed emergences*	*Number of emergence events expected under assumptions of*		
		Uniform distribution	Gradient model	Threshold model
1200-1300	0	2.42	0	0
1300-1400	0	2.42	0	0
1400-1500	0	2.42	0	0
1500-1600	0	2.42	0	0
1600-1700	0	2.42	0	0
1700-1800	2	2.42	0	0
1800-1900	0	2.42	0	6.20
1900-2000	7	2.42	7.26	14.52
2000-2100	16	2.42	19.36	6.20
2100-2200	5	2.42	7.26	2.42
2200-2300	4	2.42	2.42	2.42
2300-2400	3	2.42	2.42	2.42
2400-0100	4	2.42	2.42	2.42
0100-0200	5	2.42	2.42	2.42
0200-0300	2	2.42	2.42	2.42
0300-0400	2	2.42	2.42	2.42
0400-0500	3	2.42	2.42	2.42
0500-0600	2	2.42	2.42	2.42
0600-0700	3	2.42	2.42	2.42
0700-0800	0	2.42	2.42	2.42
0800-0900	0	2.42	0	2.42
0900-1000	0	2.42	0	2.42
1000-1100	0	2.42	0	0
1100-1200	0	2.42	0	0
Σ	58	58	58	58
Value of X^2 when compared with the observed distribution		59.986	4.239	12.736
Degrees of freedom		6	3	4
P =		<0.001	≈0.25	0.025

4.2.4.4 Expected pattern of emergence: The threshold model.

Surface temperatures below 31°C occurred between approximately 1800 and 1000 hrs and were defined as inhibitory under the model (*i.e.* above 31°C) for eight hours (Figure 4.5) resulting in the accumulation of eight units of emergence (i.e. 8 x 2.42 clutches). Hatchlings approaching the surface between 1800 and 1000 hrs, were expected to emerge without delay at a uniform rate of one unit of emergence per hour. The accumulated eight units of emergence were expected to emerge between 1900 and 2000 hrs (i.e. after a one hour lag period). To allow for thermal variability of the habitat, one and a half units, or approximately one fifth of the waiting clutches (see section 4.2.3), were arbitrarily designated to emerge one hour before and after this time (Table 4.1). A significant difference was found between the distribution of hatchling emergence expected under the threshold model and the observed pattern of emergence ($X^2 = 12.736$; df = 4; $P = 0.025$).

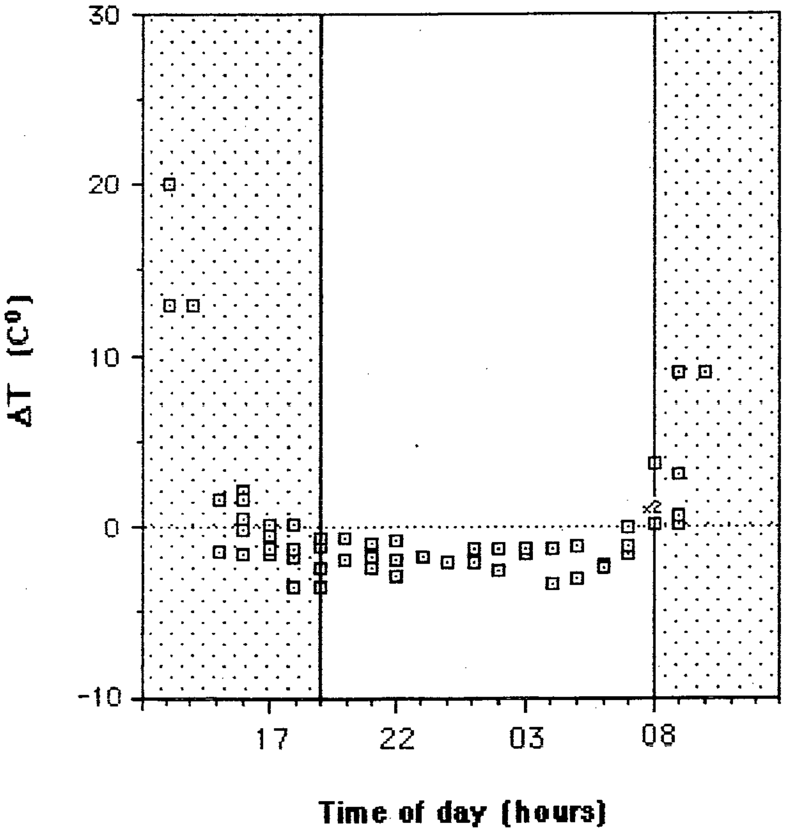
Figure 4.5 Window for emergence: Threshold model. Sand surface temperatures at different times of the day measured during early February, 1990. Dotted line drawn at 31°C. Shaded area indicates conditions defined as inhibitory to emergence under the threshold model.



4.2.4.5 Expected pattern of emergence : The gradient model.

Temperature gradients were generally positive for the 11 hour period between 0800 and 1900 hrs (Figure 4.6) resulting in the accumulation of 11 units of emergence (i.e. 11 x 2.42 clutches). By 1900 hrs all measurements indicated a negative gradient with temperatures at the surface being lower than those below. The accumulated 11 units of emergence would be expected to emerge between 2000 and 2100 hrs, that is, an hour after the reversal of the temperature gradient. Once again, to account for thermal variability of the habitat, two units of emergence (approximately one fifth of the waiting clutches) were assigned to occur one hour before and a further two units one hour after this time (Table 1). No significant difference was found between the observed distribution of emergence and that expected under the assumptions of the thermal gradient model ($X^2 = 4.239$; df = 3; $P \approx 0.25$).

Figure 4.6 Window for emergence: Gradient model. Changes in sand temperature gradients ($\Delta T = T_{surface} - T_{10\ cm}$) with time of day. Along dotted line the temperature difference between the surface and 10 cm depth is $0^{o}C$. Shaded area indicates conditions defined as inhibitory to emergence under the gradient model.



4.2.5 DISCUSSION.

Green turtle hatchlings predominantly emerge from their nests during the evening, shortly after sunset. Thermal cues are believed to be important in controlling emergence (Hendrickson 1958; Bustard 1967, 1972; Mrosovsky 1968; Witherington *et al.* 1990). Hatchlings that approach the surface when thermal conditions are not inhibitory (usually during the night) are presumed to emerge without delay. In the absence of a thermal control mechanism, hatchlings would emerge uniformly throughout the diel cycle, which in fact occurs during prolonged periods of overcast and rainy weather. This study found no correlation between the timing of emergence and periods of reduced risk of predation associated with high water.

I consider it unlikely that a given fixed temperature in the sand column would act as a threshold above which emergence is inhibited. Normal incubation temperatures range between 24^{o}C and 33^{o}C (Miller 1985) and it is doubtful that a threshold temperature inhibiting emergence would evolve within that range. Further, the only data available so far suggest that poikilotherms can detect only changes in body or environmental temperatures which then trigger appropriate physiological and behavioral responses (H. Cogger, pers. com.) The magnitude and direction of a spatial or temporal temperature gradient in the sand appears to be a more reliable indicator of nightfall than the absolute sand surface temperature alone.

There is considerable variability in temperature profiles at different sites at the same time, and at the same site and same times of day on different dates. Absolute temperatures at the surface and at 10 cm varied markedly between sites at any one time, and the northern beaches are generally significantly warmer than the southern beaches at Heron Island (Limpus *et al.* 1983 a). However these differences were not consistent with the observed simultaneous and relatively sudden onset of emergence of turtle hatchlings around Heron Island. At some locations which were heavily shaded by *Tournefortia argentia* and *Pisonia grandis*, sand temperatures at depths of 3-5 cm seldom exceed 31°C, yet turtle nests incubate successfully at these sites and emergence was still primarily nocturnal. Sand temperatures in the upper 10 cm generally did not rise above 31°C until after 0900 hrs but hatchling emergence ceased by around 0700 hrs. Similar observations have been made elsewhere by Mrosovsky (1968) and Witherington *et al.* (1990). I have also observed hatchlings emerging at nest sites where adjacent sand temperature at the surface and at depths of 10 cm were as high as 40°C and 39°C, respectively.

During periods of extended rainy and overcast weather the maximum sand surface temperature seldom exceeded 30°C. Despite these low temperatures, hatchling emergence was greatly reduced for the first day or so (pers. obs.). The emergence rate then returned to normal but emergence tended to be spread throughout the diel cycle. This lends support to the hypothesis that hatchlings are cued not to simply low surface temperatures *per se* but to a change of temperature within the sand column. Hatchlings that extend their time spent just below the sand surface may suffer adverse effects, such as reduced energy reserves (Kreamer and Bennett 1981) or increased vulnerability to terrestrial predators (Fowler 1979). In periods of prolonged inclement weather, hatchlings would thus be compelled to emerge irrespective of the appropriate environmental cue. My study shows that the temperature gradient model provides a more satisfactory explanation of the timing of sea turtle hatchling emergence than a threshold temperature model. The temperature gradient model accommodates observations which are inconsistent with the threshold model such as the spatial variation in thermal regimes. It also explains the low rate of early morning emergences.

The timing of the emergence of turtle hatchlings from the nest is seen as an adaptation to increase hatchling survival (Gibbons and Nelson 1978). The hatchlings of many species overwinter in the nest while awaiting environmental cues that indicate conditions favourable for survival. As terrestrial mortality of the eggs and hatchlings of sea turtles is higher prior to emergence than during beach crossing (Fowler 1979, Stancyk 1982) and as there appear to be no differences in aquatic predation rates between the day and night (Chapter 3), nocturnal emergence among sea turtle hatchlings presumably evolved to reduce mortality due to physiological stress of the day time heat.

4.3 THE NATURE OF THE THERMAL CUE.

4.3.1 INTRODUCTION.

The previous section (4.2 above) presented convincing circumstantial evidence in support of the theory that hatchling emergence from the nest in sea turtles is controlled by thermal gradients rather than a specific absolute temperature. In this section, I extended this work by experimentally manipulating the vertical and temporal thermal changes in the sand column with the aim of elucidating a cause and effect relationship between changes in sand temperatures and the timing of hatchling emergence.

4.3.2 MATERIALS AND METHODS.

At the commencement of the nesting season in November 1991, an experimental hatchery was established on the southern beach of Heron Island in an area cleared of vegetation and measuring 4 m x 6.5 m. The hatchery was divided into quadrates, two of which were designated as treatment (or test) plots and two as control plots. To minimize lateral heat loss in the sand from within the treatments, 25 mm thick sheets of polyurethane foam were inserted into the sand to a depth of 30 cm along the boundaries of the treatment plots. The tops of these sheets of insulating material were flush with the surface of the sand. The entire hatchery was securely fenced with BORAL cyclone® fencing to prevent nesting turtles from disturbing the area. Sets of thermistors were buried into the sand at six locations (Figure 4.7). At each location, thermistors were positioned at depths of 5, 10,15, and 20 cm, and at two of the six locations additional thermistors were positioned at 50 cm below the surface. Thermistors were calibrated as previously described in section 4.2.2.3.

Following the completion of the hatchery construction, 18 entire clutches of eggs were collected during oviposition and transported to the hatchery on four consecutive nights (26-29 November, 1991). One half of each clutch was placed into 50-60 cm deep nest holes dug into the treatment plots and buried. The other half of each clutch was similarly buried in the control plots. The positions of the artificial nests were marked with wooden sticks. The delay between the collection and burial of any of these clutches was always less than 90 minutes. The eggs were left to incubate undisturbed.

4.3.2.1 Manipulation of sand temperature.

I used two methods to reduce heat loss from the sand that typically occurs around sunset and which is believed to control the timing of emergence: 1) Treatment plot "A" was warmed by 10 infrared lamps suspended from an aluminium framework placed over the area. Infrared light was not expected to affect the orientation behavior of the emerging hatchlings (Witherington and Bjorndal 1991); and 2) Three large, 10 cm deep Styrofoam boxes were placed over the sand in an attempt to prevent heat loss from within treatment plot "B" (Figure 4.8). Following the emergence of the first clutch, 26 January 1992, infrared radiation was applied to area "A" and the Styrofoam boxes were placed over area "B" (Figure 4.8). These treatments were applied over six consecutive days from 27 January to 1 February, between 1600 and 2200 hours. Resistance readings from each thermistor were recorded and surface temperatures at the same six locations were taken hourly between 1600 and 2400 hours over the six days. Surface temperatures were measured by the mercury in glass thermometer against which the thermistors were calibrated. Resistance readings were converted to temperatures as before (see section 4.2.2.3).

Figure 4.7 Site plan of hatchery. Hatchery divided into four quadrats (A through D).Heavy lines indicate position of polyurethane insulation around treatment areas. Encircled numbers: sets of thermisters. Lower case lettering indicates positions of nests. Same letter indicates split halves of the one clutch. Shaded areas: shrubs and trees. (Approximate scale 50:1)

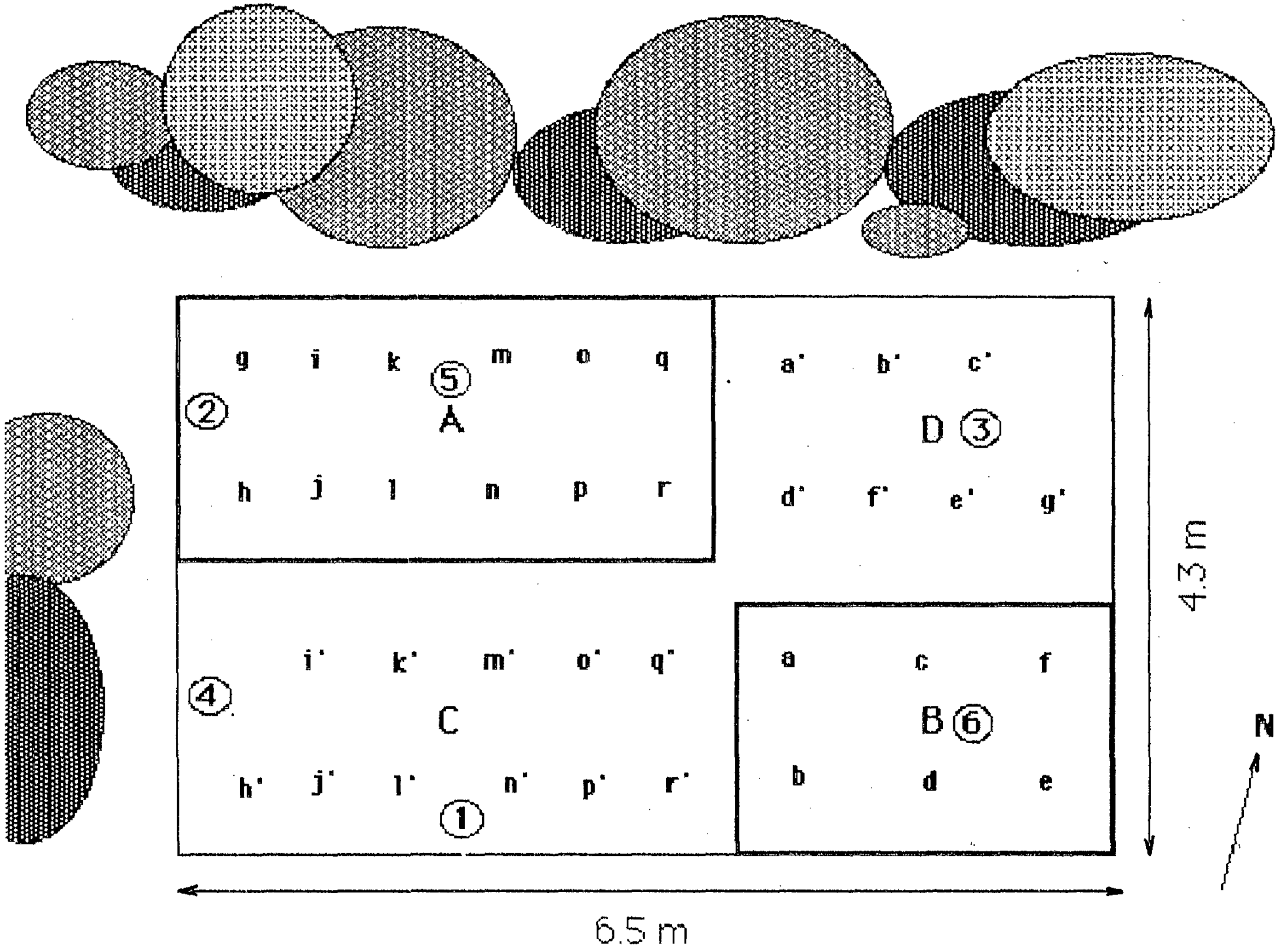


Figure 4.8 Hatchery during daytime and evening with infrared lamps operating and Styrofoam boxes in place.

4.3.2.2 Emergence behavior.

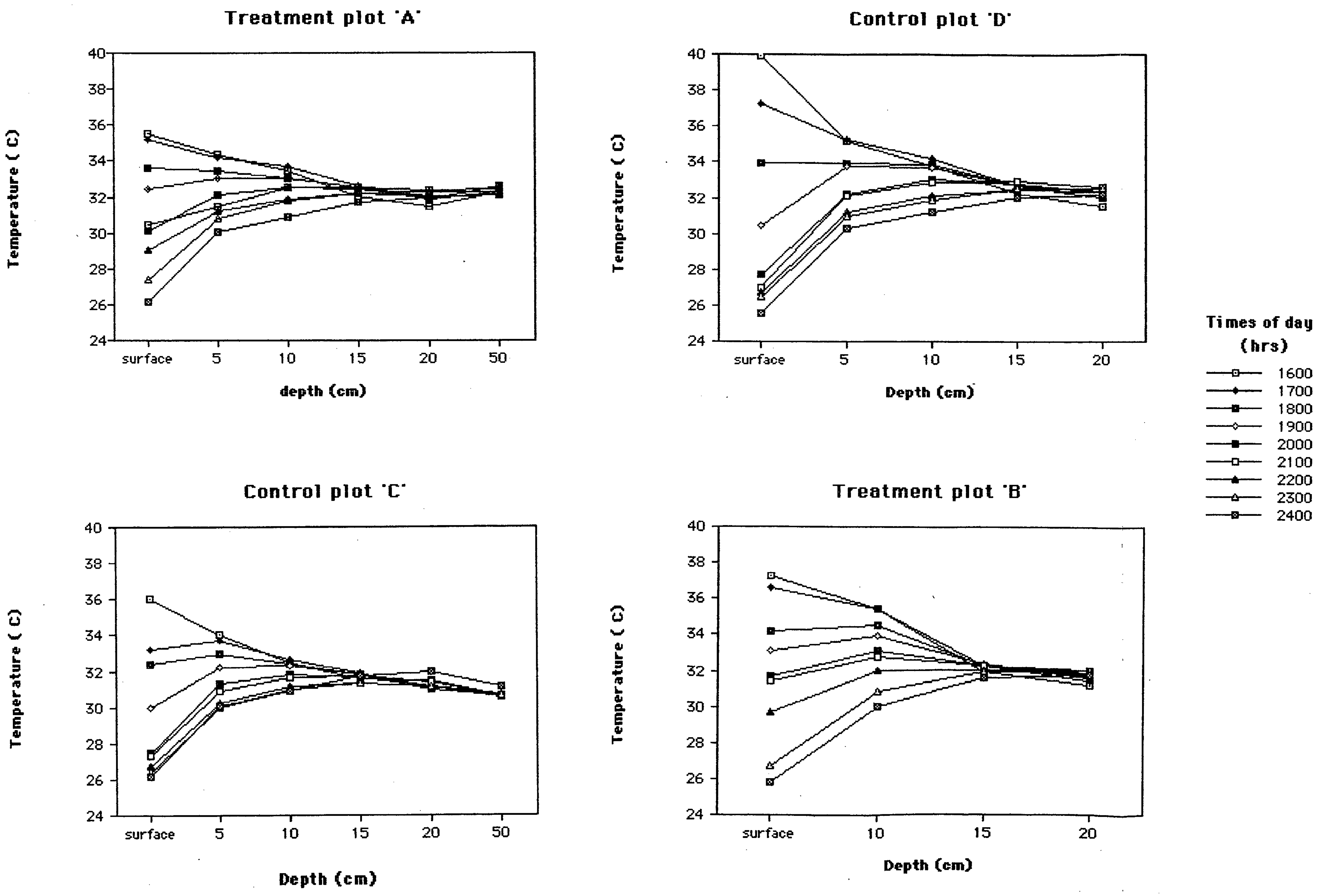
The time of emergence was recorded for each clutch. The times that hatchlings' heads first appeared on the beach surface were also noted whenever possible. Emerged hatchlings were allowed to proceed to the water unhindered.

4.3.3 RESULTS.

4.3.3.1 Sand temperatures.

One of the 26 thermistors (site 6, 5 cm depth) was damaged when recovered and temperature readings obtained from that thermistor were disregarded. Detailed information on the sand temperature profiles between 1600 and 2400 hours was obtained from three control and three treatment sites for the six days of the experiment. In accordance with earlier observations (section 2.4.1 above), the spatial variation in surface temperatures that was observed at 1600 hours diminished by midnight. Within both control plots and within treatment plot B sand surface temperature fell below 31°C between 1800 and 1900 hours. In treatment plot A this event occurred between 1900 and 2000 hours. Thermal variability also decreased with increasing depth. Temperatures at the surface fell below that at 10 cm depth between 1800 and 1900 hours at all sites within the hatchery (Figure 4.9).

Figure 4.9 Means of temperature readings taken hourly between 1600 and 2400 hours over six days in the four quadrates of the hatchery. Symbols indicate temperatures taken at different times of day.



To examine if the applied treatments altered the thermal gradients in the top ten centimeter of sand (ΔT), an analysis of variance model was used in which "site" (i.e. sites of the sets of thermistor probes) was considered a random factor, nested within "treatment" (Table 4.2). 'Time' and 'Day' were also considered as main effect factors. As expected, time had a highly significant effect on ΔT.

The main point of interest however was the interaction effect of treatment and time on ΔT. Under the null hypothesis (i.e. at any given time ΔT is the same in both the control and the treatment plots) the probability of obtaining these results is 0.046 (Table 4.2).

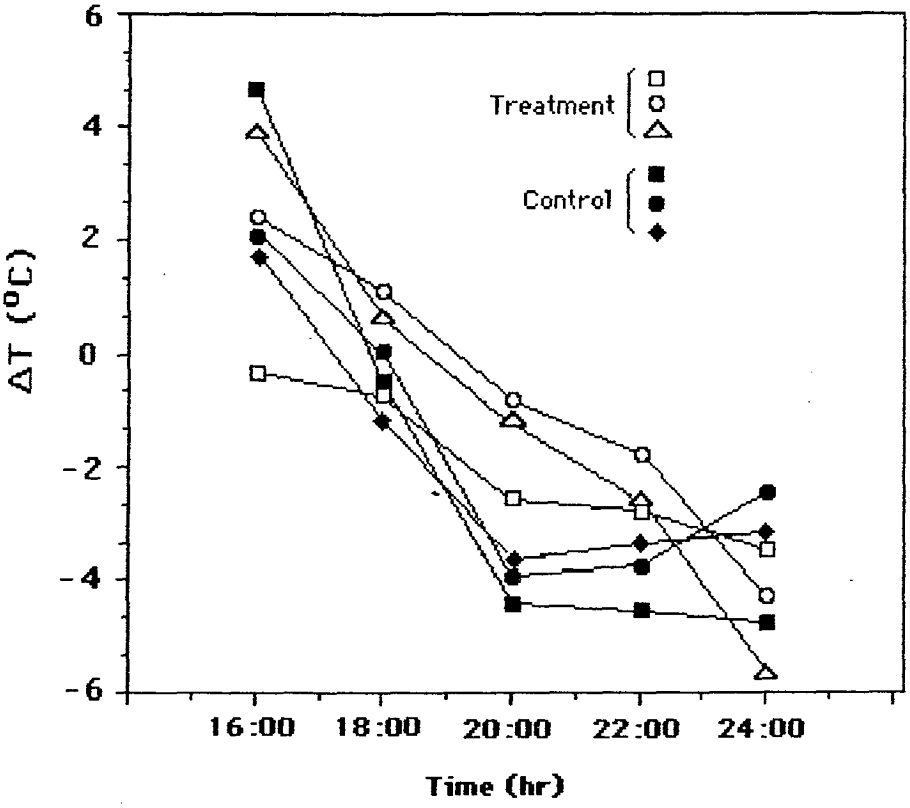
Table 4.2 ANOVA table for examining variation in ΔT.

Source	df	SS	MS	F	P
Treatment	1	71.622	71.622	10.98	0.029
Probe (Treatment) (error)	4	26.080	6.520		
Time	2	197.110	98.554	80.72	0.000
Time * treatment	2	1.302	5.651	4.63	0.046
Time * Probe (Treatment) (error)	8	9.767	1.220		
Day	5	16.766	3.353	5.89	0.002
Day * treatment	5	4.558	0.912	1.60	0.205
Day * Probe (Treatment) (error)	20	11.376	0.569		
Time * Day	2	14.383	7.190	19.95	<0.001
Time * Day * treatment	2	14.668	7.340	1.20	<0.001
Time * Day * Probe (Treatment) (error)	40	26.245	6.056		
TOTAL	107	403.88			

For the analysis, temperature readings used were those taken every second hour while treatment was applied (i.e. 1800, 2000, 2200 hours).

To explore the effect of the treatment in delaying the onset of a negative temperature difference in the top 10 cm of sand, the temperature differences between the surface and 10 cm below at each thermistor probe site were averaged over the 6 days at each time (Figure 4.10).

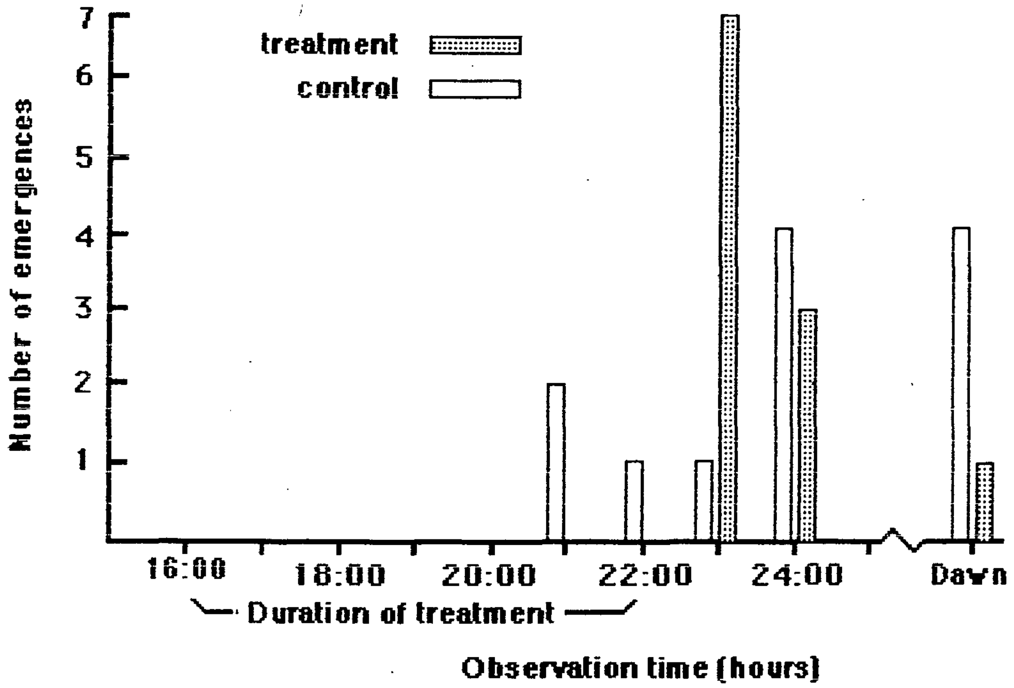
Figure 4.10 Two hourly measures of ΔT with time averaged over six days for each of the three sites within the test and three sites within the control plots. At both 2000 and 2200 hrs, the temperature gradient (ΔT) in the test plots was lower than in the control plots.



4.3.3.2 Hatchling emergence.

Emergence times for the hatchlings in 25 of the 36 artificial nests were recorded (Figure 4.11). Observations were terminated after six days due to cost constraints and the times of emergence of the remaining 11 artificial nests were not able to be recorded. There was reason to believe that Two of the emerging clutches were interfered with by tourists visiting the hatchery during the treatment period and these data points were excluded from the analysis. Temporal patterns of emergence are shown in figure 4.11. Emergence commenced shortly after 2000 hours and no hatchlings emerged after 0700 hours. In the treatment plots, no hatchlings emerged before 2200 hours, which was the time when the lights were turned off and the boxes were lifted and emergence peaked at 2300 hours. In the control plots, hatchlings commenced to emerge between 2000 and 2030 hours and emergence peaked at 2400 hours. Five emergence events occurred between midnight and 0700 hours. To compare the temporal distribution of emergences between the treatment and control plots a chi-square contingency table was constructed containing the number of emergences occurring before 2300 hours and those occurring after 2300 (excluding those that emerged around dawn the following morning). There was a significant difference in the distribution of emergences between the test and the control plots ($X^2 = 4.5$, df =1, $p \approx 0.03$). In both the test and control plots no emergence occurred until mean ΔT was below -3 ^oC and this temperature difference occurred significantly later in the test plots than in the control plots as a result of the applied treatment.

Figure 4.11 Distribution of hatchling emergence events within the test and the control plots. The histogram shows emergences occurring around the hourly observation times (eg. 2200 represents emergences between 2130 and 2230 hours).



The times that the hatchlings' heads first appeared at the surface were noted for 15 of the emerged clutches. The earliest time that heads appeared was 1600 hours. No difference in the timing of the appearance of hatchlings' heads was noted between the test and control plots (Table 4.3, Mann-Whitney U-test, $p = 0.5$). A considerable lag was observed between the appearance of heads and when the clutch emerged to cross the beach. A maximum of seven hours lag was observed in one of the clutches within treatment area "A". Clutches reaching the surface early in the evening tended to have a longer lag period to emergence. The minimum lag period noted was 1 hour (Table 4.3). For three clutches no lag was observed and as the hatchery was inspected hourly these clutches must have reached the surface and emerged within less than one hour.

Table 4.3 Time lag between the appearance of hatchlings' heads at the surface and emergence.

Treatment plots			Control plots		
heads appeared by (hours)	emerged by (hours)	lag (hours)	heads appeared by (hours)	emerged by (hours)	lag (hours)
1600	2300	7	1600	2000	4
1700	2300	6	1900	2300	4
1900	2300	4	1900	2100	2
1900	2300	4	2000	2200	2
2000	2300	3	2100	2300	2
2200	2300	1	2100	2400	3
2200	2400	2	2200	2400	2
			2200	2400	2

4.3.4 DISCUSSION.

The location of the hatchery was dictated by several constraints: 1) accessibility of electric power; 2) compliance with permit conditions; 3) requirement of nests to be above high water level; 4) requirement of a relatively level surface for the fencing and the insertion of the insulating foam material and 5) the desirability of a site which had uniform exposure to sunshine throughout the periods of incubation and experiment. The hatchery area chosen was not homogeneous with regards to several physical properties of the sand. Treatment area "B" consisted mainly of white, very loose sand in which it was exceedingly difficult to dig nest holes. The sand in area "A" was considerably better packed, containing more macroscopic plant particles. Here the digging of nest holes was easy. The two control areas, "C" and "D", were transition zones between these two. As a further source of heterogeneity, two large *Casuarina equisitifolia* trees, located a few meters due west of the hatchery, cast shadows over certain sections of the hatchery during the late afternoons.

Emergence of eleven clutches was delayed beyond the time available for field observations. Most of those clutches were located in treatment area "B" and control area "C", where the loose sand presumably prolonged the time required by the hatchlings to reach the surface.

In all quadrats in the hatchery, surface temperatures fell below the arbitrarily chosen threshold of 31°C between 1800 and 2000 hours. A negative thermal gradient was established between 1800 and 1900 hours at all sites within the hatchery. However, the pattern of emergences between the test and control plots showed a significant difference and the commencement of emergence in both coincided with ΔT reaching approximately -3 °C. In the control plots a ΔT of -3°C occurred around 2000 hrs and in the test plots it was reached after 2200 hrs when the lights were turned off and the boxes lifted. These data confirm and extend the conclusions reached in section 4.2; that is, emergence is controlled not by the temperature of the sand surface alone but by changes in temperature within the top 10 cm of the sand column. These results also support and extend the observations of Witherington *et al.* (1990) and Hays *et al.* (1992) who considered that a rapid decrease in temperature is the cue for hatchling emergence. Temperature differences between two points in the sand column will determine the rate of temperature change at any position between those two points, in accordance with the physical properties of the sand. It appears that at Heron Island, a spatial temperature gradient of -3 ^{o}C between the surface and 10 cm below would facilitate the rate of thermal change which would function as the cue for hatchling emergence.

The present experiment however is unable to clearly distinguish between the effect of thermal gradients and the confounding effect of the infra red (and/or near infra red) radiation on the emergence behavior of the hatchlings. Excepting on one particularly overcast night, the infra red light source did not affect the seaward orientation of hatchlings. This is in broad agreement with the findings of Witherington and Bjorndal (1991). While orientation behavior of hatchlings was affected by the infrared lamps only when background lighting from the moon and stars was negligible, it is conceivable that emergence behavior itself may have been influenced by these lights. No emergences occurred in treatment plot "A" before the lights were turned off, although several clutches reached the surface of the sand well before that time. The few clutches that emerged within one hour of reaching the sand surface all reached the surface after the lights were turned off.

These observations suggest that the infrared lights may have affected emergence behavior. It must be noted however that the infrared lamps were visible to all hatchlings (except to those under the Styrofoam boxes), yet emergence commenced significantly earlier in the control than in the test plots. (The intensity of infrared illumination of course would have been much less in the two control plots than in test plot 'A'.) It now appears possible that emergence behavior may be controlled by a combination of environmental cues: In addition to a required minimum difference in temperature between the surface and 10 cm below, light, if detected by the hatchlings upon reaching the surface of the sand, may also influence emergence behavior. Further experiments are needed to discriminate between these two factors.

4.4 PREY DEFENCE MECHANISMS IN THE SEA.

4.4.1 COUNTERSHADING.

4.4.1.1. Introduction.

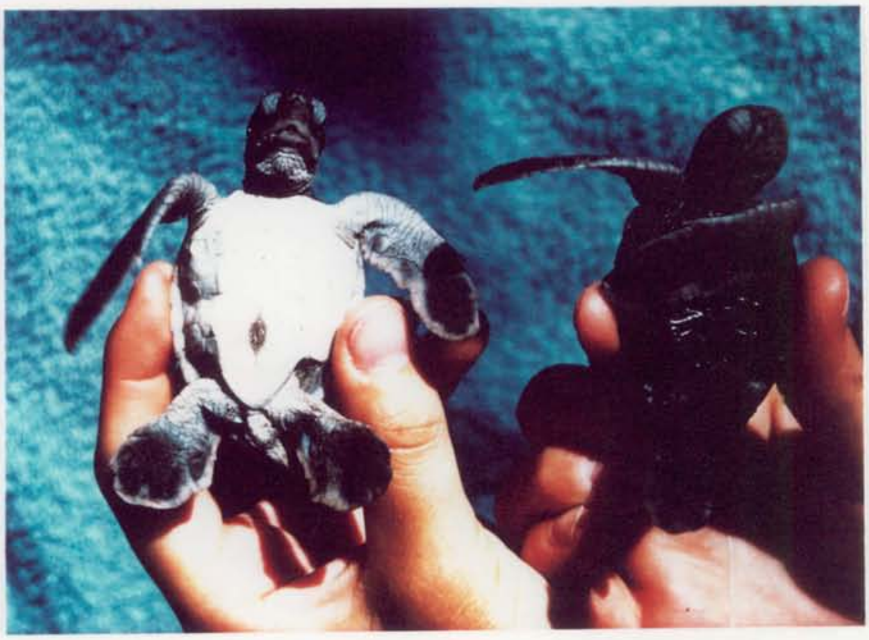
Disruptive color patterns, colour mimicry, countershading and other forms of camouflage have all been seen as adaptive evolutionary responses to predation (Gillis 1989, Jones *et al.* 1991, Cooper and Greenberg 1992). The countershaded coloration of many mid-water fishes has been interpreted in terms of benefits that would result from concealment from predators. Although widely accepted (Longley 1917, Hobson 1991), the effectiveness of countershading as a predator avoidance mechanism remains to be demonstrated.

Following emergence from their nests, sea turtle hatchlings enter the sea where they swim at or near the surface. They are believed to spend their first few years in oceanic current systems and convergence zones (Carr 1986). The hatchlings of green sea turtles (*Chelonia mydas*) display pronounced countershading. They are dark gray to black dorsally and cream-coloured ventrally. The dark dorsal surface is believed to be involved in thermoregulation (Bustard 1970) and presumably conceals the animals in the water from aerial predators. The cream-coloured ventral surface is thought to provide protection from fish predators below (Bustard 1970, 1972). Because it was possible to obtain a direct measure of predation on hatchling turtles, these animals provided an excellent model to test whether countershading is effective in reducing predation.

4.4.1.2 Materials and methods.

In February 1992, hatchling turtles were collected at Heron Island after emergence as they were crossing the beach on their way to the sea. The hatchlings were kept overnight in a Styrofoam container. The following morning a black quick drying spray paint was used to colour the plastron and the underside of flippers of several hatchlings. Control hatchlings were painted on the dorsal surface only (Figure 4.12). Extreme care was taken to keep paint out of the eyes and mouths of hatchlings. The hatchlings were tethered as described previously and two hatchlings, one painted ventrally and a control, painted dorsally, were followed while allowed to swim simultaneously across the reef flat (see Chapter 3). Hatchlings were followed until one was taken by a fish or reached deep water over the reef crest. All surviving hatchlings were retrieved and released. The water depth over the reef flat during the experiments varied between approximately 0.8 and 1.6 m. All these trials took place between 0700 - 1100 hrs.

Figure 4.12 A "test" hatchling with ventral surface painted black (right) and a "control" hatchling displaying the natural colour scheme (left).



4.4.1.3 Results and discussion.

Predation was significantly more intense on the ventrally painted hatchlings than upon those displaying the natural colour pattern. Fifteen pairs of painted test and control hatchlings were successfully followed over the reef flat. In two cases, the pair swam past the reef crest into deep water where they were released. In eleven of the remaining thirteen cases, observations terminated when the ventrally painted, test hatchling was taken by a predator. In only two cases was the dorsally painted, control hatchling taken first. These results are significant (McNemar's test for symmetry, Table 4.4, $X^2 = 6.231$, df = 1, $p = 0.0126$) and provide a strong argument in support of countershading as a predator avoidance mechanism in green turtle hatchlings and possibly in other mid-water marine animals.

Table 4.4 Data obtained in the 'painted hatchlings' experiments cast in a 2x2 contingency table which was used in Mcnemar's test for symmetry.

			PAINTED	
			not eaten	**eaten**
NOT PAINTED	**not eaten**	**observed**	2	11
		expected	2.00	6.50
	eaten	**observed**	2	0
		expected	6.50	0.00

Hatchlings of the flatback turtle (*Natator depressus*) and the leatherback turtle (*Demochelys coriacea*) display contershading similar to green turtle hatchlings, but hatchlings of the loggerhead, *Caretta caretta*, the hawksbill, *Eretmochelys imbricata* and the two species of ridley, *Lepidochelys olivacea* and *L. kempi* are the similar shade of medium brown on both the ventral and dorsal surfaces. There is no readily available explanation as to the absence of countershading in these species as they often share nesting areas with green and flatback turtles (Miller and Limpus 1991, pers. obs.). Hatchlings entering the sea at the same nesting beach are presumably all subject to similar predation pressures. However, no data are presently available to determine if the difference in ventral coloration between the different species of turtle hatchlings is significant in terms of the visual perception of fishes.

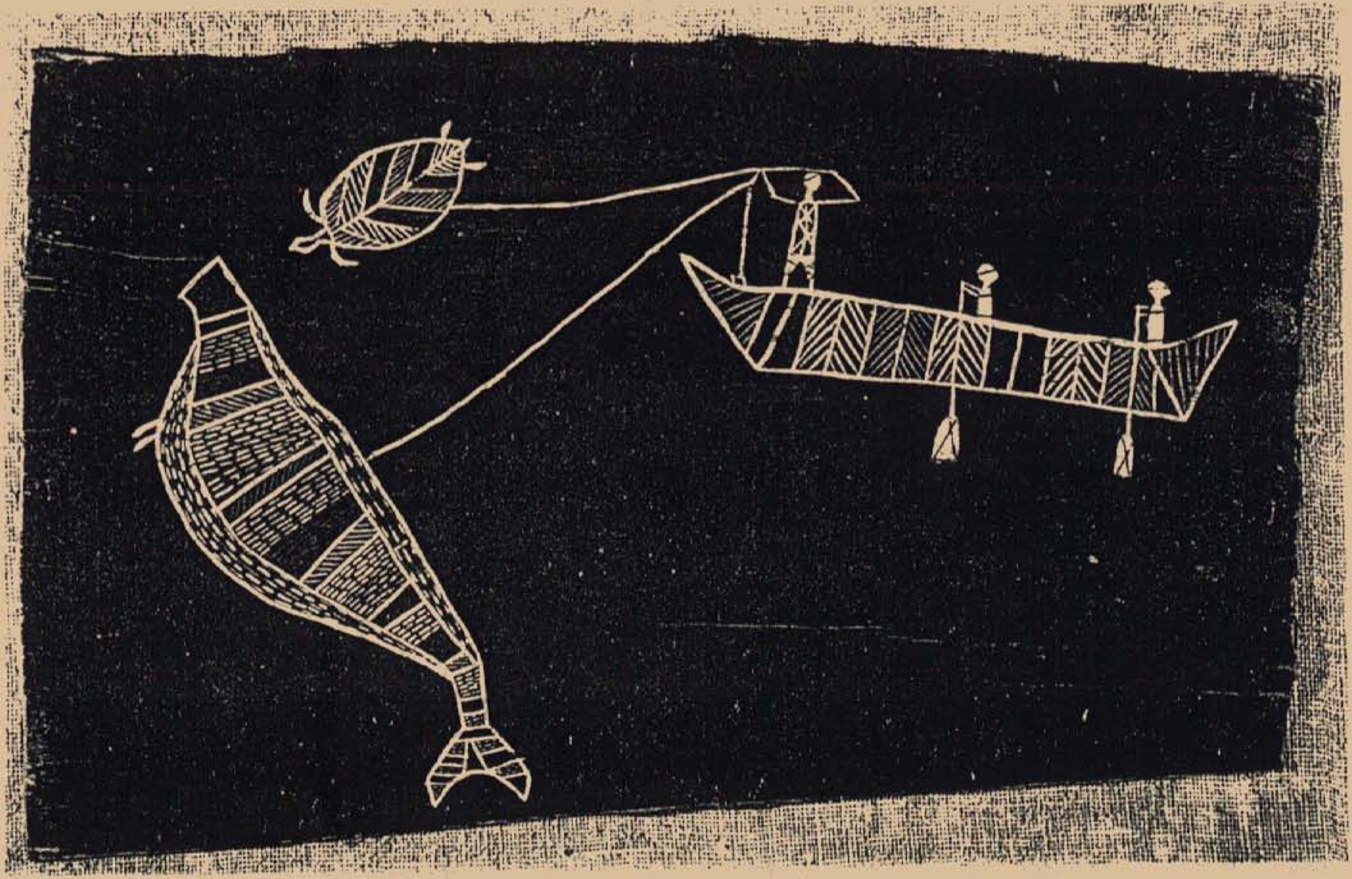
4.5 ADAPTATIONS TO REDUCE EARLY HATCHLING MORTALITY: RECAPITULATION.

In this chapter, I examined some behavioral and morphological attributes of sea turtle hatchlings which conventionally have been considered as adaptive in reducing predation on the newly emerged hatchlings (nocturnal emergence, the hatchling frenzy and countershading). The results of my inquiries can be summarized as follows:

Nocturnal emergence from the nest functions primarily as a mechanism to reduce physiological stress of the daytime heat and not as predator avoidance. This conclusion is based on several independent lines of arguments. Firstly, terrestrial predation appears to be highest on the eggs and hatchlings in the first few days after oviposition and again after hatching while the hatchlings are digging up from their nest chambers (Fowler 1979, Carr 1973). The eggs and hatchlings are vulnerable to nest predators while below the sand surface during both day and night and this type of mortality would not be influenced by restricting emergence to any given period of the diel cycle. Secondly, there are scant quantitative data on predation during beach crossing (Limpus 1973, Limpus *et al.* 1983b, CJ Limpus and V Baker pers. com.) but predation rate appears low relative to the losses sustained in the nest and while crossing the shallow water reefal habitats. Thirdly, there is no significant difference in the rates of aquatic predation between day and night (Witherington and Salmon 1992 and this study).

The frenzied swimming that the hatchlings maintain for approximately 24 hrs following emergence has been considered a significant adaptation to reduce the time that the hatchlings spend exposed to the many predators of coastal and reefal habitats. Considering the high predation rates in shallow water reefal habitats (Chapter 3) that assertion is probably correct.

The adaptive significance of countershading in reducing predation has been demonstrated experimentally.



CHAPTER 5

HATCHLING SURVIVORSHIP, POPULATION DYNAMICS AND MANAGEMENT

Fishing Scene.
Bark painting by Nangapiana (Groote Eylandt)
National Gallery of South Australia

The aborigines of Groote Eylandt , who are essentially people of the sea, have produced many paintings depicting fishing activities. In this painting the fisherman has speared both a turtle and a dugong. In reality it is unlikely to that both these animals would be speared at the same time. The successful landing of only one of these creatures, using traditional gear, requires considerable skill.

5 HATCHLING SURVIVORSHIP, POPULATION DYNAMICS AND MANAGEMENT.

In his review, Iverson (1991) concluded that the highly fecund sea turtles had significantly higher survivorship in the first year of life than did the less fecund freshwater turtles, but could not offer a simple explanation for his findings (section 2.3.4.1). The demonstration in Chapter 3 of high and variable mortality in the early life stages provides an explanation of the high fecundity which characterizes sea turtles.

There are several causes of mortality in the first year of life (stage 1 of the life table): mortality of eggs in the nest (genetic or developmental abnormalities, infection, adverse physical conditions in the nest, predation); mortality while crossing the beach (disorientation, heat exhaustion, predation); mortality in the shallow water habitats prior to reaching the oceanic developmental habitat (predation) and mortality sustained during the first year within the oceanic habitat (predation, starvation, and loss to unsuitable habitats/current systems). It now appears that hatchlings are subject to high rates of mortality while *en route*, prior to reaching their oceanic developmental habitat. The ways in which the dynamics of the population may be affected by this brief period of high mortality may be explored by using standard population models, such as the one used by Crouse *et al.* (1987), based on the Lefkovitch stage class matrix.

In this population projection technique, the elements of fecundity, mortality and growth rates of each stage class are incorporated in matrix A which is postmoltiplied with the by the population vector to predict future population states.

Thus $An_t = n_{t+1}$

or

$$\begin{bmatrix} a_{11} & a_{12} \cdots & a_{1s} \\ a_{21} & a_{22} \cdots & a_{2s} \\ \cdot & \cdot \;\cdots & \cdot \\ a_{s1} & a_{s2} \cdots & a_{ss} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ \cdot \\ n_s \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ \cdot \\ n_s \end{bmatrix}_{t+1}$$

In this model the stage classes may differ in their duration and each individual may remain in a stage for several time periods. The intinsic rate of population growth, r, is obtained from the dominant eigenvalue, λ which is equal to e^r . Thus if $\lambda = e^r = 1$ then $r = 0$ and the population is stable.

In exploring the effect of changes in survivorship in various life stages on the intrinsic rate of population increase Crouse *et al.* (1987) concluded that the population dynamics of the Little Cumberland Island loggerhead turtles was relatively insensitive to even large changes in first year survivorship. I used a similar stage-based population model, written by Ian Somers of CSIRO Div. of Fisheries, with parameter estimates approximating the loggerhead and green turtle populations of eastern Australia shown in Table 5.1 (I Somers and CJ Limpus pers. com.). The most significant differences in parameter estimates between Crouse's model and the one I used were age at first reproduction (45 years for the Australian as against 22 years for the Little Cumberland Island population) and longevity (76 years and 54 years, respectively).

The sensitivity of the model to changes in survivorship at various life stages was explored by increasing survivorship of each stage in turn by approximately 5% of its baseline value (5% being chosen because that increase raises survivorship of mature breeders to approximately 1.00). The model is most sensitive to changes in survivorship in stage 2 (pelagic phase) and stage 3 (juveniles) (Table 5.1, simulations 6 -11). This is because survivorship in these stages is set lower than for any succeeding stage and the turtles spend a relatively long time in these stages.

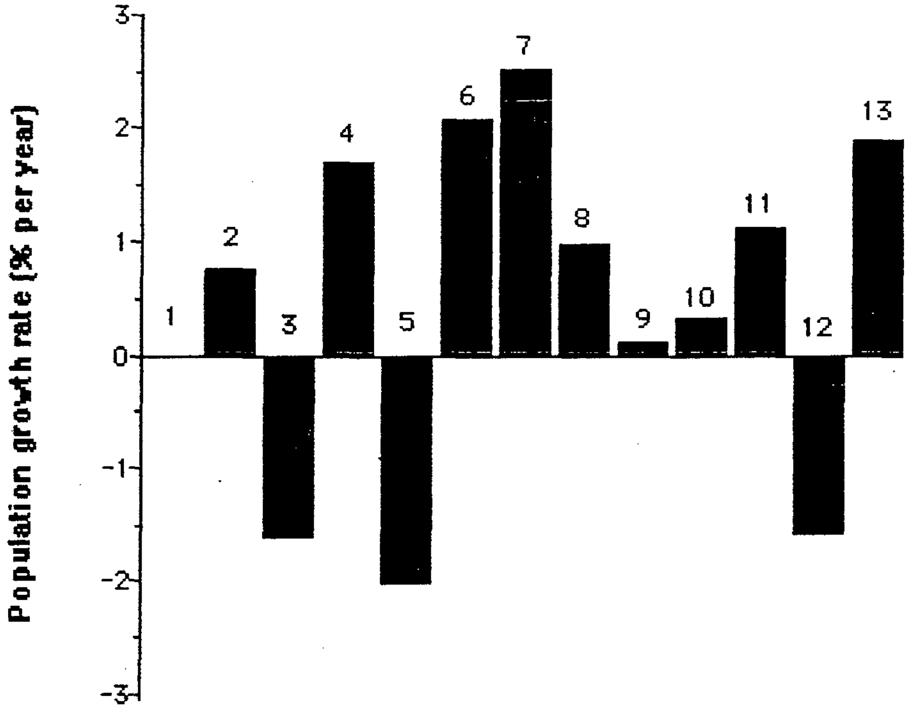
Table 5.1 Hypothetical sea turtle population model (after Crouse *et al.* 1987 and I. Somers pers.com.) Survivorship in the first year of life is a composite of survivorship in shallow water during reef crossing (variable, based on results obtained in Chapter 3) and survivorship during the first year of pelagic life which was arbitrarily set at a constant annual rate of 0.4. In this baseline model, to which the other models are compared, the shallow water survivorship during 30 minutes reef crossing, based on the average survivorship over the reef flat, is 0.4565.

Stage	Duration of stage (year)	Survivorship (annual)	Fecundity (no. eggs/year)	Initial pop'n distribution	Stable pop'n distribution
1) Eggs/hatchlings	1	0.1826	0	32.11	49.2
2) Pelagic	16	0.8038	0	56.65	46.92
3) Juveniles	19	0.93	0	9.42	2.9
4) Subadults	8	0.949	0	0.82	0.46
5) Novice breeders	1	0.94	127	0.1	0.05
6) 1st yr remigrants	3	0.94	4	0.1	0.12
7) Mature breeders	28	0.95	80	1.04	0.54

Population growth rate = 0.0024% per year (near equilibrium)

Figure 5.1 Changes in population growth rate resulting from changes in survivorship and fecundity in various life stages of a hypothetical sea turtle population described in table 5.1. For simulations 1-5 survivorship during a 30 minutes reef crossing is given in parentheses. For simulations 6-13 shallow water survivorship is as for baseline model.

Simulation 1: base line with average shallow water survivorship (0.456) **Simulation 2:** high tide (0.612). **Simulation 3:** low tide (0.227). **Simulation 4:** high tide new moon (0.857). **Simulation 5:** low tide other moon phases (0.185). **Simulation 6:** survivorship in the oceanic phase increased by approx. 5%. **Simulation 7:** survivorship of juveniles increased by approx. 5%. **Simulation 8:** survivorship of subadults increased by approx. 5%. **Simulation 9:** survivorship of novice breeders increased by approx.5%. **Simulation 10:** survivorship first year remigrants increased by approx. 5%. **Simulation 11:** survivorship of mature breeders adjusted to 1.0. **Simulation 12:** fecundity halved. **Simulation 13:** fecundity doubled.



Sea turtle conservation practices have undergone several changes as a result of our ever improving understanding of the biology of these animals (Mrosovsky 1983). For many years conservation efforts were focused on the protection of the eggs and the females on the beach. Headstart programs were initiated in the belief that larger, yearling turtles would suffer significantly less mortality than newly emerged hatchlings. Thus headstarting was envisaged as a powerful means to significantly increase the intrinsic growth rate of the population. These management programs have now been abandoned almost everywhere, partly because of the unknown effect of prolonged captivity on the animals when finally liberated and partly as a result of the demonstration by Crouse *et al.*. (1987) that reduction in the mortality of other stages, namely juveniles and subadults, has the relatively greatest potential to reverse the declining trend of loggerhead turtle populations in the southern USA. However it may prove difficult to achieve an increase in the survivorship of juveniles and/or subadults. It would also be difficult to quantify any increase achieved in survivorship in these stage classes as a result of various management startegies because of the absence of information on the size and structure of these sea turtle populations and the relative contribution of the various sources of mortality to the total (Poiner *et al.* 1990).

Sensitivity analyses showed that for the Australian population, changes in first year survivorship (stage 1) result in significant changes in the intrinsic rate of population growth (Figure 5.1). Hatchlings entering the water during high tide only (the period associated with lower predation, see Chapter 3) as opposed to entering during all tides, results in a 50%

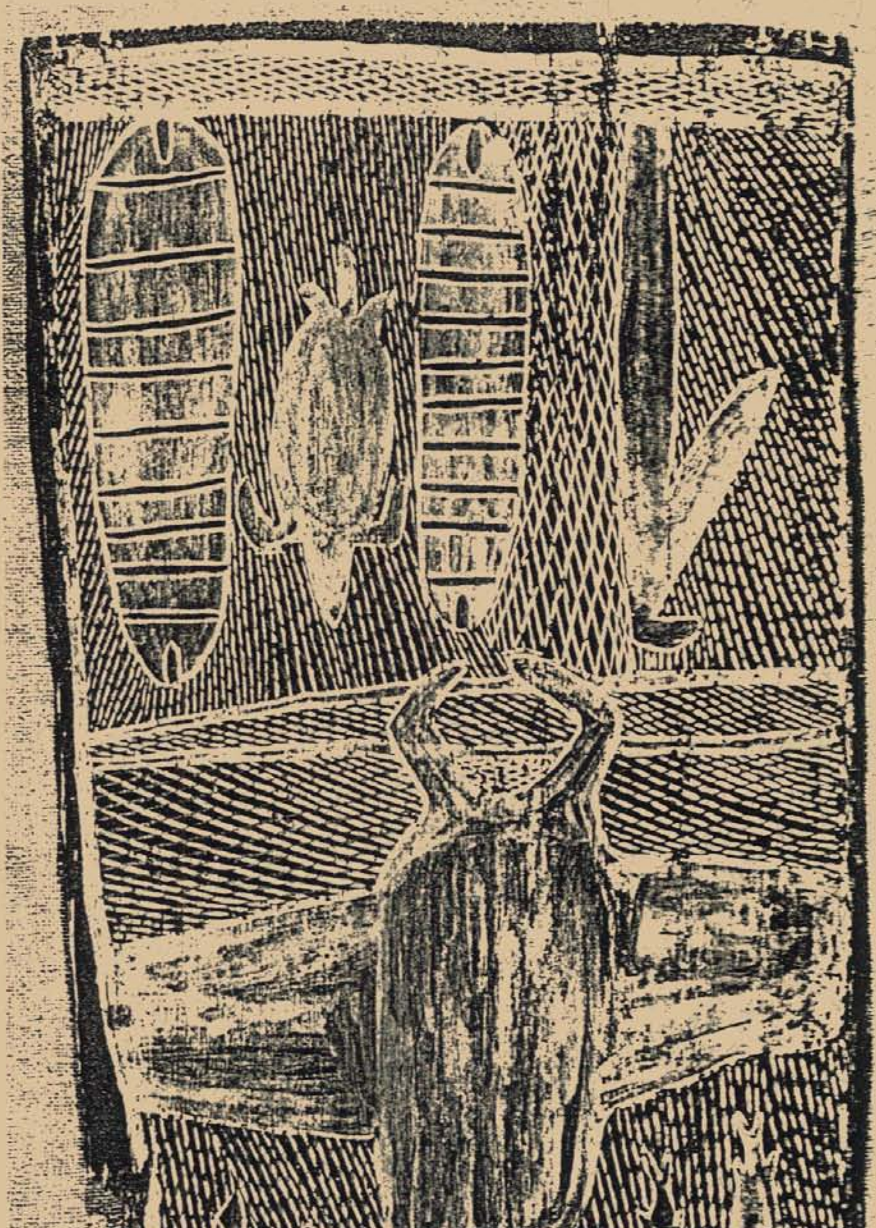
increase in the number of animals in stage I. This has a similar effect on the population growth rate as that of increasing survivorship of subadults by approximately 5% (Figure 5.1).

My findings of highly variable but generally low survivorship in the very early life stages provide an additional, potentially effective, and previously unrecognized management option. At rookeries where nearshore predation varies significantly with identified environmental conditions, in particular at rookeries where hatchery programs are underway, managers may wish to increase hatchling survivorship by timing the release of hatchlings to coincide with periods of lower local predation (e.g. during high tide at coral reefs in the Great Barrier Reef region). Alternatively hatchlings could be collected and released into deep water past the reef slope where, presumably, predation is reduced. In making an accurate assessment of the potential of these management tools, life tables (including duration of stages, age at maturity, annual fecundity and longevity as well as some good estimates of stage specific survivorship) for the population in question need to be better known. In addition, the following must also be considered:

1) What is the effect of extending the time spent by hatchlings on the beach before entering the water? (e.g. possibility of behaviour modifications affecting orientation and, later, rookery identification), and

2) what is the effect of depriving hatchlings from their natural entry into the water and their swimming across the shallow water habitats?

3) How can such effects be minimized?



CHAPTER 6

CONCLUDING REMARKS.

Totemic creatures, Cape Arnhem
Bark painting by Mungaraui (Yirrkalla)
National Gallery of South Australia

On the sea bottom of port Bradshaw, in the Gulf of Carpentaria, are special places belonging to the giant devil ray, the hawksbill turtle, the queen fish and the trepang. It is believed that passing over these special places belonging to of any of these sea creatures is dangerous. Here the artist depicted a number of these totemic creatures. In the top panel is the hawksbill turtle between two trepangs. There is a Malay anchor (or possibly fish hook) on the right. Below is a giant devil ray accompanied by four queen fish.

6 CONCLUDING REMARKS.

I suggested in Chapter 1 that the relatively large difference in mortality between adult and hatchling sea turtles would explain why the life histories of sea turtles are more in contradiction with those predicted from life history theory than those of most other Testudines. After reviewing the available data pertinent to testudine life histories, I concluded in Chapter 2 that a fundamental difference exists between turtles of marine and other habitats. The long distance, pelagic dispersal of hatchlings can explain the apparent dichotomy of a large body size coupled with the very high fecundity of marine turtles. One species of marine turtle, *N. depressus*, is the exception to this pattern as it lacks an oceanic dispersal phase in its life cycle and is more similar to freshwater and terrestrial Testudines in that the hatchlings and adults share the same habitat (Walker and Parmenter 1990). At the same time, the life histories of *N. depressus* and Testudines of freshwater and terrestrial habitats are relatively better explained by the accepted models of life history theory. Thus, pelagic dispersal has a profound impact on the life histories of the Cheloniidae, but the reasons for the evolution and the maintenance of a pelagic phase in the early life histories of all but one of the species of the marine turtles is poorly understood.

Like sea turtles, most tropical coastal marine fishes and many marine invertebrates have a two-phase life cycle that includes a planktonic larval stage and a demersal adult stage (Leis 1991, Robertson 1991). The causes of this pattern of life history have evoked considerable speculation and Leis (1991) provides an overview of the various explanations which can be summarized as follows:

1) avoidance of very high predation rates nearshore;
2) benefits that accrue from dispersal in patchy, uncertain environments;
3) benefits of reduced energetic requirement while drifting in open water currents;

One further point not considered by Leis in this context is that larvae may have special requirements which cannot to be met nearshore. Each of these explanations of the potential benefits of the pelagic stage is largely theoretical and lacks an empirical base. As pointed out by Leis (1991), the progression from observation of pattern to explanation without the benefit of experimentation is fraught with difficulties and to date, the reasons for the evolution and maintenance of the pelagic stage in the life cycle of fishes remain unexplained.

Sea turtle biologists consider that hatchlings spend as short a time as possible in nearshore waters because of the high predation pressure in that habitat (Walker and Parmenter 1990, Walker 1991, Wyneken and Salmon 1992). My finding that predation may be very high and also highly variable in shallow water reefal habitats (Chapter 3), lends substantial support to this view. But there is some evidence that predation rates on hatchling turtles in other nearshore habitats are not as high as found in this study. About 7% of 74 tethered loggerhead hatchlings, whose fate was monitored by Witherington and Salmon

(1992), were preyed upon in the water off the east coast of Florida. Frick (1976) at Bermuda similarly observed that approximately 8% of the 24 hatchlings of *C. mydas* followed were taken by fish. These results are not directly comparable with the present study as the observations of both Witherington and Salmon (1992) and Frick (1976) were over varied time periods and distances and as such they cannot be considered as actual measures of predation rate.

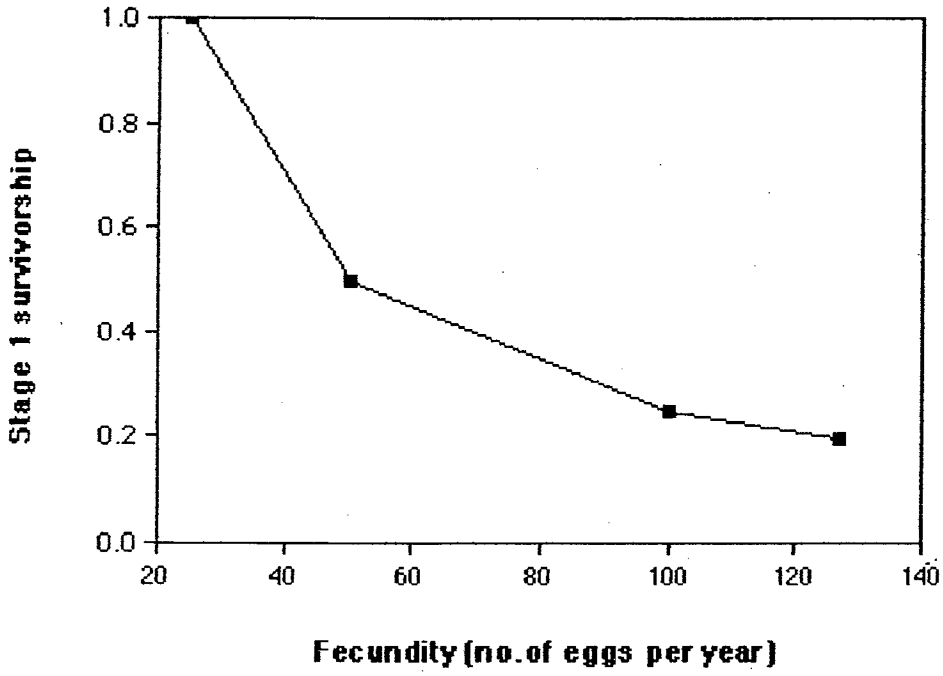
Considerable variation also exists between estimates of predation on the pelagic eggs of reef fishes. Colin and Clavijo (1988) found that egg predation was very low. Moyer (1987), on the other hand, observed that 90 of 213 gamete clouds of coral reef fishes studied in Japan were extensively preyed upon. Likewise, Samoilys and Squire (submitted manuscript) at the northern Great Barrier Reef observed that gametes released in 6 of 22 spawning rushes of coral trout were heavily preyed upon by caesionids (small to medium size epipelagic planktivorous reef fishes). In addition to variation in the predation of larvae and gametes nearshore, there is strong evidence to suggest that the pelagic stages of reef fishes are extensively preyed upon by adult oceanic and epipelagic fishes such as tuna and dolphinfishes (Leis 1991). In the absence of data on the relative mortalities in nearshore, reefal and pelagic habitats, it is not possible to conclude whether predation in reefal habitats is a major factor in the evolution of the pelagic stages of fishes (Leis 1991).

This study has provided data that now allow preliminary comparison of predation rates on hatchling turtles in shallow water reef flat and deeper, outer reef slope habitats. Comparison of these results is limited somewhat by the difference in observation times in the reef flat and reef slope trials. In the reef flat habitat, the duration of observation was set at ten minutes whereas in the reef slope habitat, observation was set for a distance of 20 m and the duration of observation varied between one and two minutes. During the ten minute trials the mean predation rate in the shallow water reef flat habitat was 31% (± 2.5%). In the reef slope habitat it was 7% (± 2.4 %) which, when adjusted for the difference in the duration of observation, results in a predation rate not unlike that found over the reef flat (i.e. approximately 46% per ten minutes). Although habitat was not controlled in the experiments of Witherington and Salmon (1992) and the total number of predation events was too small to be examined statistically, they noted that hatchlings were "lost to predators while swimming in relatively shallow water or within 10 m of a narrow reef system adjacent to the beach".

While flatback turtles may often share nesting beaches and feeding grounds with other species of sea turtles (*E. imbricata*, *C. caretta*, *C. mydas;* Miller and Limpus 1991, and pers. obs.), the hatchlings of *N. depressus* do not disperse into the oceanic environment. It is claimed that this modification of their life history is possible because their hatchlings are approximately twice as large as the hatchlings of the other species (Walker and Parmenter 1990). As for the other species of sea turtles, virtually nothing is known about the diet and behaviour of these hatchlings, but presumably predation on these larger hatchlings is reduced (Walker 1991).

The relationship between the size and the number of offspring has been discussed in section 2.3.2.2.3. The relationship between fecundity and survivorship in stage 1 of the life table (including eggs, and the hatchlings on the beach and in the shallow water habitat) can be described by an exponential function (Figure 6.1). Using the same population model as in Chapter 5, in order to keep the rate of population growth and all other parameters constant, halving fecundity (i.e. clutch size) must be coupled with a doubling of stage 1 survivorship.

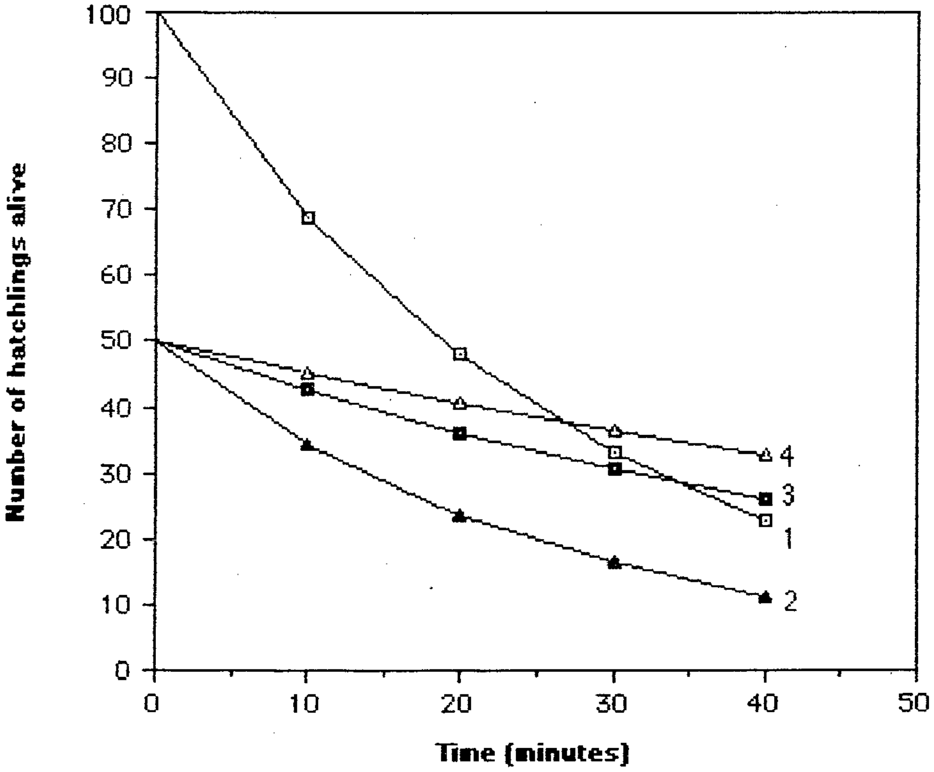
Figure 6.1 The relationship between fecundity and stage 1 survivorship based on the population model described in Chapter 5.



The consequences of increasing hatchling size at the expense of the number of hatchlings produced may be explored for *C. mydas* by a simple iterative process, the result of which is depicted in figure 6.2. Doubling hatchling size and reducing the number of eggs produced by half would accrue benefits if predation was significantly reduced on the larger hatchlings during reef crossing. If predation rates were inversely proportional to hatchling size one might expect there to be an advantage in producing fewer hatchlings of a larger size as reef crossing - at least in the east Australian green turtle rookeries - often requires 30 minutes or longer (see figure 6.2). However, all sea turtles with pelagic young produce a large number of relatively small hatchlings, suggesting that in reefal habitats, predation on larger hatchlings may not be substantially reduced. The mortality rate during reef crossing would be affected not only by the actual rate of predation but also by the speed at which the hatchlings are able to swim. Larger hatchlings would probably swim faster than smaller ones and thus also reduce the time they are exposed to predation by reef fishes. Experimental data are lacking to determine the relationship between hatchling size and predation rate. There may also be other, size independent, causes of mortality which would also influence the position of the hatchling size-number compromise.

Figure 6.2 A hypothetical comparison of the number of hatchlings surviving during 40 minutes of reef crossing when clutch size and predation rates vary. 1) 100 small hatchlings and 31%* predation per 10 minutes spent over reef flat; 2) 50 large hatchlings and 31% predation rate; 3) 50 large hatchlings and 15% predation; 4) 50 large hatchlings and 10% predation rate.

(* 31% predation per ten minutes is the mean predation rate obtained from the experiments with the tethered hatchlings (Chapter 3). The number of hatchlings alive at different times after entry into the water was estimated by the procedure given in section 3.2.3.3)



Under conditions of environmental unpredictability, life history theory predicts advantages from the partitioning of reproductive effort into numerous small as opposed to fewer but larger young. Shallow water reefal environments in which I demonstrated that hatchling mortality is highly variable may be considered as a typical r - selecting environment. Further, the oceanic habitat, characterized by pronounced variability in many of its physical and biological features over various spatial and temporal scales (Leis 1991), may also be considered as r - selecting; hence the r - selected features of the early life history of marine turtles with pelagic young.

One may only speculate that the geographical isolating mechanism that led to the speciation of *N. depressus*, presumably in the region of the Gulf of Carpentaria (see section 2.4.2), precluded oceanic dispersal of the hatchlings. Concomitantly, environmental conditions within the large Lake Carpentaria may have been relatively more stable or predictable than in the open ocean and larger offspring may have been selected for. Present day coastal habitats in northern Australia are likely to be similar to the environment within which this species evolved and the relatively large size of hatchlings of *N. depressus* has been maintained.

This "larger hatchling - reduced predation - no need for pelagic stage" scenario may however be oversimplistic. If predation rates on larger hatchlings are lower, why did other species of sea turtles not take up the same evolutionary option - to increase offspring size and abandon the pelagic stage. If, on the other hand, the size difference between hatchlings of *N. depressus* and other species of sea turtles does not make a significant difference to predation rates in the shallow water coastal and reefal habitats, one needs to search for reasons other than predator avoidance that make the pelagic stage biologically attractive. Predation may still be significant in the open ocean and Carr (1896) vividly describes the concentration of life, including many different kinds of pelagic fishes, along oceanic drift lines -"where life is arranged in lanes" - and where, presumably, the little turtles go. How predation rates in those habitats compare with predation rates nearshore is unknown.

One possible overriding advantage of a life cycle involving a pelagic stage is dispersal (Thresher *et al.* 1989). *N. depressus* is confined to the tropical coast of Australia, presumably because it lacks a pelagic phase in its life cycle. Dispersal may be particularly important in view of the transient nature of both rookeries and feeding grounds (Limpus 1987, Bowen *et al.* 1992). While open water crossing is possible only during the pelagic, larval stage for most reef and inshore fishes, sea turtles are well adapted for open water travel in their adult life. But while reproductive adults limit their long distance, purposeful travel between the feeding grounds and breeding areas, virtually nothing is known about the process of transition between the pelagic existence and settlement of juveniles into inshore feeding grounds. It is conceivable that colonization of new feeding grounds is greatly enhanced by pelagic dispersal.

A better understanding of the early life history of sea turtles still requires:
1) empirical data on the source, magnitude and variability of mortality in both the pelagic and a range of inshore environments;

2) a comparison of predation rates between hatchlings of *N. depressus* and other sea turtles known to nest sympatrically;

3) a better understanding of the evolutionary background of *N. depressus.*

Until then, all we have is conjecture, and the high rate of predation on hatchlings of *C. mydas* in coral reef habitats is not, by itself, proof that the pelagic phase is an evolutionary response to high predation in reefal or nearshore habitats.

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APPENDIX 1

Life history parameters of testudines compiled from Elgar and Heaphy (1989) (Ref 1) and Wilbur and Morin (1988) (Ref 2). Variables included in this table are: Habitat (fw = freshwater, ter = terrestrial, mar = marine); CL, straight linear length of carapace (mm); CS, clutch size; NC, number of clutches a female lays in a year in which she is reproductively active; Egg size, measured as egg volume (ml) by Wilbur and Morin and given as egg weight (g) by Elgar and Heaphy.

Taxon	Habitat	CL	CS	NC	Egg size	Ref.
Pelomedusidae						
Podocnemis unifilis	fw	381	20	2	23.04	1
"	fw	515	21	?	22.8	2
P. vogli	fw	304	12	2	15.42	1
P. expansa	fw	660	91	?	32.6	1
"	fw	890	83	1	?	2
Peltocephalus tracaxa	fw	457	15	?	?	1
Pelusios subniger	fw	290	13	?	9.78	1
"	fw	245	7	?	17.7	2
Pelomedusa subrufa	fw	170	15	1	?	1
"	fw	196	31	1	5.9	2
Chelidae						
Chelys fimbriata	fw	381	20	1	?	1
"	fw	275	16	?	?	2
Platemys platycephala	fw	180	6	?	?	1
Phrynops geoffroanus	fw	350	15	1	19.17	1
P. gibbus	fw	200	3	?	25.25	1
P. dahli	fw	205	4	?	?	1
Chelodina longicollis	fw	178	12	?	?	1
"	fw	318	15	1	6	2
C. siebenrocki	fw	320	14	?	?	1
"	fw	181	10.5	?	15.2	2
C. novaeguneae	fw	230	10	?	?	1
"	fw	219	10.5	?	?	2
C. expansa	fw	280	13	?	16.16	1
"	fw	199	15.4	?	?	2
Emydura macquarii	fw	310	21	?	10.6	1
"	fw	156	15.3	?	8.9	2
E. australis	fw	254	?	?	?	1
E. krefftii	fw	250	14	3	6.9	1
Pseudemydura umbrina	fw	130	4	1	8.6	1
Rheodytes leukops	fw	249	13	4	7.5	1
Emydidae						
Emys orbicularis	fw	140	10	?	6	1
"	fw	103	10	?	7.5	2
Pseudemys floridana	fw	290	18	?	11.64	1
"	fw	250	19	2	12.6	2
P. scripta	fw	210	7	2	10.8	1
"	fw	196	16.5	?	9.4	2

APPENDIX 1 (continued)

Taxon	Habitat	CL	CS	NC	Egg size	Ref.
P. concinna	fw	300	18	?	17.52	1
"	fw	328	18	?	13.4	2
P. decassata	fw	192	7	?	14.7	2
P. rubiventris	fw	230	11	?	5.9	2
P. terrapen	fw	?	3.5	?	15.8	2
Chrysemys picta	fw	125	4	4	4.69	1
"	fw	130	6.8	4	4.6	2
Graptemys barbouri	fw	270	11	2	13.93	1
"	fw	209	8.5	3	17.9	2
G. pulchra	fw	228	11	4	10.83	1
"	fw	250	6.9	4	13.7	2
G. pseudogeographica	fw	205	9	3	10.22	1
"	fw	198	9.5	?	8.7	2
G. geographica	fw	178	13	3	11.92	1
"	fw	202	13	2	7.4	2
G. oculifera	fw	180	3	?	11.86	1
"	fw	176	3	1.5	9.1	2
Terrapene ornata	ter	146	5	2	10.77	1
"	ter	110	4.7	1	8.9	2
T. carolina	ter	114	5	4	10.57	1
"	ter	132	5.5	1.5	6.6	2
T. coahuila	fw	120	2	2	?	1
"	fw	101	2.3	3	17.9	2
T. nelsoni	ter	145	3	?	?	1
"	ter	128	2.7	1	17.9	2
Deirochelys reticularia	fw	150	8	3	9.05	1
"	fw	186	6	3	8.8	2
Malaclemys terrapin	fw	180	10	?	7.7	1
"	fw	194	8.5	?	11.2	2
Emydoidea blandingi	fw	190	9	2	13.59	1
"	fw	159	8	?	12.2	2
Clemmys marmorata	fw	152	3	1	8.26	1
"	fw	148	7	?	9.1	2
C. guttata	ter	102	2	?	6.25	1
"	fw	132	3.6	?	4.8	2
C. insculpta	ter	165	6	1	9.8	1
"	fw	154	8.2	1	14.2	2
C. muhlenbergii	fw	76	3	1	4.66	1
"	fw	88	4.5	?	3.9	2
Mauremys capica	fw	190	4	?	?	1
"	fw	238	7	?	14.5	2
M. mutica	fw	180	?	?	10.28	1
M. leprosa	fw	130	7	?	?	1
Rhinoclemmys funerea	fw	290	3	4	?	1
"	fw	200	3.2	2.5	43.6	2
R. punctularia	fw	260	3	?	?	1
"	fw	194	1.5	?	49.4	2
R. pulcherrima	ter	191	3	?	?	1

APPENDIX 1 (continued)

Taxon	Habitat	CL	CS	NC	Egg size	Ref.
R. rubida	ter	166	1	?	?	1
R. annulata	ter	180	1	?	?	1
R. areolata	ter	140	1	?	36.05	1
Melanochelys trijuga	ter	152	5	2	10.40	1
Chinemys kwangtungensis	fw	200	2	?	?	1
Cyclemys dentata	ter	220	3	?	?	1
C. mouhoti	ter	170	?	?	?	1
Cuora flavomarginata	fw	180	?	?	?	1
C. amboinensis	fw	190	3	/	?	1
C. trifasciata	fw	200	3	?	?	1
Kachuga smithi	fw	210	6	?	?	1
"	fw	182	7	?	12.2	2
K. dhongoka	fw	380	32	?	?	1
"	fw	406	35	?	?	2
Ocadia sinensis	fw	220	3	?	?	1
Malayemys subtrijuga	fw	270	?	?	?	1
Siebenrockiella crassicollis	fw	300	?	?	?	1
Batagur baska	fw	540	20	3	?	1
"	fw	463	27	3	?	2
Testudinidae						
Gopherus agassizi	ter	279	5	1	?	1
"	ter	236	5	?	34.7	2
G. berlandieri	ter	165	1	?	?	1
G. polyhemus	ter	241	7	1	44.5	1
"	ter	233	5.5	?	37.8	2
Kinixys erosa	ter	260	5	?	?	1
"	ter	204	5	?	27.1	2
K. belliana	ter	164	2.7	?	26.9	2
K. homeana	ter	159	4	?	22.4	2
Testudo graecea	ter	210	2	1	?	1
"	ter	192	2	?	11.5	2
T. hermanni	ter	155	3	2	12.74	1
T. kleinmanni	ter	114	2	?	?	1
"	ter	137	?	?	7.8	2
T.horsfeldii	ter	197	?	?	16.8	2
Geochelone elephantopus	ter	1110	10	2	106.88	1
"	ter	717	9.5	1	90.5	2
G. chilensis	ter	280	2	1	?	1
"	ter	222	3	2	26.4	2
G. elegans	ter	210	3	2	27.4	1
"	ter	217	5.5	2.5	26.4	2
G. radiata	ter	355	4	3	37	1
"	ter	342	4.3	?	27.6	2
G. gigentea	ter	762	14	3	87.1	1
"	ter	750	3.8	2.5	?	2
G. pardalis	ter	296	12	6	28.4	2
G. sulcata	ter	517	17	?	38.7	2
G. denticulata	ter	330	3	?	36.7	2

APPENDIX 1 (continued)

Taxon	Habitat	CL	CS	NC	Egg size	Ref.
Malocochersus tornieri	ter	152	1	2	?	1
"	ter	177	1	?	20.2	2
Psammobates tentorius	ter	127	2	?	?	1
"	ter	121	2.5	?	7.6	2
P. geometricus	ter	125	13.5	?	?	2
P. oculifera	ter	133	?	?	19.9	2
Homopus aerolatus	ter	115	3	?	?	1
"	ter	95	3	?	7.7	2
H. boulengeri	ter	101	1	1	?	1
"	ter	92	1	?	9.9	2
Chersina angulata	ter	155	1	1	28	1
Staurotypidae						
Claudius angustatus	fw	114	6	2	?	1
Staurotypus salvini	fw	220	6	2	10.03	1
S. tripocatus	fw	305	4	?	?	1
Dermochelyidae						
Dermochelys coriacea	mar	1524	100	5	71.89	1
Chelydridae						
Chelydra sepentina	fw	258	29	3	11.1	1
"	fw	242	37	1	10.1	2
Macroclemys temmincki	fw	400	30	1	25.83	1
"	fw	270	24.3	1	26.8	2
Kinosternidae						
Kinosternon subrubrum	fw	89	3	3	4.71	1
"	fw	90	5	?	3.8	2
K. leucostomum	fw	127	1	?	7.1	1
"	fw	106	5.5	?	4.2	2
K. flavescens	fw	114	4	1	4.42	1
"	fw	100	5	?	4.4	2
K. bauri	fw	114	2	3	5.05	1
"	fw	75	2	2	4	2
K. hirtipes	fw	150	5	?	?	1
"	fw	115	5.5	?	4.2	2
K. integrum	fw	160	?	?	?	1
K. sonoriense	fw	155	?	?	?	1
K. angustipons	fw	115	2	2	?	1
"	fw	113	2.5	2	10.1	2
K. dunni	fw	160	3	3	?	1
"	fw	150	2	?	14.6	2
K. scorpioides	fw	140	10	?	6.08	1
"	fw	150	2.3	?	6.7	2
Sternotherus carinatus	fw	127	4	2	6.17	1
"	fw	105	3.6	2	4.5	2
S. odoratus	fw	80	4	3	3.52	1
"	fw	102	3	1	3.4	2
S. minor	fw	100	3	4	4.92	1
"	fw	112	7	2	?	2
Dermatemyidae						
Dermatemys mawi	fw	570	20	1	?	1

APPENDIX 1 (continued)

Taxon	Habitat	CL	CS	NC	Egg size	Ref.
Cheloniidae						
Caretta caretta	mar	965	120	5	34.4	1
"	mar	927	126	3	37.4	2
Chelonia mydas	mar	1020	140	6	51.65	1
"	mar	1000	110	3	56.8	2
Natator depressus	mar	914	50	4	65.32	1
"	mar	927	50	4	73.6	2
Eretmochelys imbricata	mar	764	112	3	26.4	1
"	mar	831	161	3	28.7	2
Lepidochelys kempi	mar	660	110	2	32.39	1
"	mar	646	110	3	30.8	2
L. olivacea	mar	655	106	3	35.94	1
"	mar	686	116	2	32.3	2
Trionychidae						
Trionix sinensis	fw	304	20	3	?	1
"	fw	210	22.5	3	4.2	2
T. muticus	fw	254	18	3	9.43	1
"	fw	121	17.1	2	6.4	2
T. spinifer	fw	330	18	1	11.9	1
"	fw	281	18.1	?	11.9	2
T. ferox	fw	387	16	?	14.02	1
"	fw	266	19.5	?	8.2	2
T. gangeticus	fw	650	30	?	25.3	1
"	fw	425	?	?	17.2	2
T. triunguis	fw	700	28	?	20.3	2
Lissemys punctata	fw	229	10	2	?	1
"	fw	370	3.2	?	15.8	2
Cycloderma frenatum	fw	508	20	?	?	1
"	fw	560	18	?	20.6	2
Cyclanorbis senegalensis	fw	255	6	?	24.4	2
Carettochelidae						
Carettochelys insculpta	fw	385	14	?	33.7	1

APPENDIX 2

Results of predation trials over the reef flat.

Trial no.	Date (day.mo.yr)	time start	day/night	tide (high/low)	moon phase*	no. of hatchlings preyed upon**
1	23.3.87	21.30	n	l	4	15
2	24.3.87	10.00	d	l	4	13
3	24.3.87	?	n	l	4	7
4	25.3.87	09.30	d	l	4	6
5	27.3.87	13.00	d	l	1	10
6	28.3.87	21.00	n	h	1	0
7	31.3.87	08.30	d	h	1	2
8	31.3.87	15.00	d	l	1	5
9	01.4.87	09.35	d	h	1	0
10	01.4.87	15.30	d	l	1	10
11	03.4.87	12.00	d	l	2	2
12	03.4.87	19.05	n	l	2	15
13	05.4.87	09.45	d	h	2	5
14	05.4.87	21.00	n	h	2	11
15	04.1.88	08.15	d	h	3	2
16	04.1.88	15.00	d	l	3	8
17	04.1.88	21.00	n	h	3	8
18	05.1.88	02.00	n	l	3	13
19	05.1.88	08.45	d	h	3	1
20	05.1.88	15.45	d	l	3	11
21	06.1.88	15.50	d	l	3	7
22	07.1.88	15.50	d	l	3	6
23	08.1.88	16.45	d	l	3	17
24	09.1.88	17.10	d	l	4	8
25	10.1.88	12.30	d	h	4	7
26	11.1.88	11.45	d	h	4	6
27	12.1.88	13.00	d	h	4	4
28	12.1.88	20.05	n	l	4	15
29	13.1.88	09.00	d	l	4	15
30	13.1.88	14.00	d	h	4	7
31	13.1.88	21.00	n	l	4	15
32	14.1.88	10.00	d	l	4	9
33	14.1.88	22.00	n	l	4	3
34	15.1.88	11.30	d	l	4	6
35	16.1.88	?	d	l	1	7
36	17.1.88	07.05	d	h	1	1
37	18.1.88	02.00	n	l	1	0
38	18.1.88	07.30	d	h	1	2
39	18.1.88	14.00	d	l	1	3
40	18.1.88	20.30	n	h	1	2
41	19.1.88	02.30	n	l	1	1
42	19.1.88	08.45	d	h	1	0
43	19.1.88	15.05	d	l	1	4
44	20.1.88	15.15	d	l	1	3
45	24.1.88	11.30	d	h	2	0
46	24.1.88	19.45	n	l	2	7
47	25.1.88	19.45	n	l	2	2
48	27.1.88	10.00	d	l	2	14
49	02.2.88	02.30	n	l	3	16
50	02.2.88	20.30	n	h	3	6

APPENDIX 2 (continued)

Trial no.	Date (day.mo.yr)	time start	day/night	tide (high/low)	moon phase*	no. of hatchlings preyed upon**
51	04.2.88	14.40	d	l	3	9
52	05.2.88	09.40	d	h	3	0
53	10.2.88	19.30	n	l	4	5
54	11.2.88	03.15	n	h	4	4
55	11.2.88	20.45	n	l	4	2
56	13.2.88	22.00	n	l	4	4
57	17.2.88	00.30	n	l	1	7
58	20.2.88	21.30	n	h	1	2
59	23.2.88	11.50	d	h	2	1
60	24.2.88	13.00	d	h	2	1
61	24.2.88	19.15	n	l	2	6
62	02.3.88	02.30	n	l	3	13
63	03.3.88	02.30	n	l	3	6
64	10.3.88	23.00	n	h	4	0
65	11.3.88	09.15	d	l	4	6
66	11.3.88	19.30	n	l	4	1
67	11.3.88	20.00	n	l	4	8
68	12.3.88	10.00	d	l	4	9
69	17.3.88	?	d	h	1	0
70	18.3.88	15.00	d	l	1	7
71	18.3.88	24.00	n	l	1	4
72	20.3.88	16.30	d	l	1	12
73	25.3.88	07.30	d	l	2	10
74	31.3.88	23.00	n	l	3	9
75	02.2.90	18.00	n	l	2	11
76	03.2.90	19.30	n	l	2	7
77	04.2.90	10.00	d	l	2	6
78	05.2.90	18.30	n	h	2	4
79	07.2.90	08.15	d	h	3	5
80	07.2.90	18.00	n	l	3	4
81	08.2.90	20.10	n	h	3	5
82	09.2.90	18.30	n	l	3	8
83	09.2.90	21.30	n	h	3	5
84	10.2.90	21.30	n	h	3	2

* New moon = 1, First quarter = 2, Full moon = 3, Last quarter = 4.

** number taken by fish in trials of 20 hatchlings each

APPENDIX 3

Results of predation trials over the reef slope.

Trial no.	Date (day.mo.yr)	time start	day/night	tide (high/low)	location (north/south)	no. of hatchlings preyed upon**
1	12.2.90	17.00	d	l	s	5
2	13.2.90	00.30	n	h	s	0
3	13.2.90	16.30	d	l	n	1
4	13.2.90	17.00	d	l	s	2
5	13.2.90	23.30	n	h	n	4
6	14.2.90	17.00	d	l	n	6
7	14.2.90	18.00	n	l	s	0
8	14.2.90	23.00	n	h	s	1
9	14.2.90	24.00	n	h	n	0
10	16.2.90	12.30	d	h	n	1
11	16.2.90	20.30	n	l	s	3
12	18.2.90	16.15	d	h	n	0
13	18.2.90	19.45	n	l	n	0

* number taken by fish in trials of 20 hatchlings each

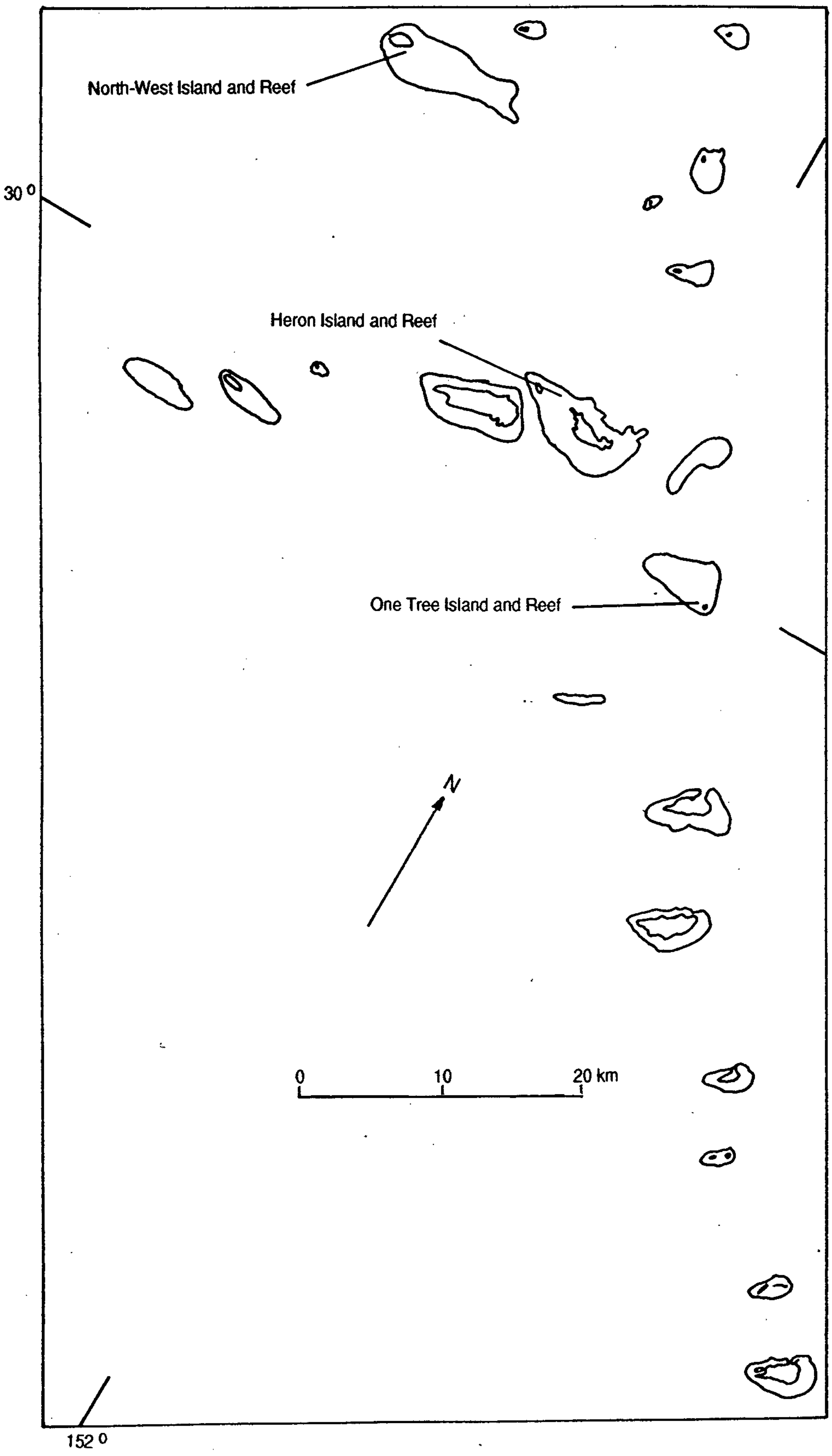
APENDIX 4

Fish predators of sea turtle hatchlings, additional to those given by Stancyk (1982)

Predator	**Locality (source)**
Tylosurus sp. (*Belonidae*), *Sphyraena barracuda* , and possibly *Seriola rivoliana* .	Bermuda (Frick 1976)
Seriola dumerili	Atlantic USA (Fletemeyer 1978)
Unidentified sharks	Raine Is., Australia (Carter 1985)
Lutjanus carponotatus, and other Lutjanids (var. spp.), *Cromileptes altivelis, Choerodon cyanodus*, *Epinephaelus megachir*, and other Serranids (var. spp), Muraenid, *Carcharhinus melanopterus* ,	Heron Is., Australia (Gyuris pers. obs.)
Caranx emburyi	Heron Is., Australia (Gyuris pers obs.)
Lethrinus miniatus	Heron Is., Australia (J. Paine, Marine Park Ranger, pers.comm.)

APPENDIX 5

Locality map of the Capricornia section of the Great Barrier Reef Marine Park, enclosing the Capricorn-Bunker group of reefs. The reefs mentioned in the text are identified.



APPENDIX 6

A ten minute audiovisual presentation - appended - documenting aspects of the experimental work, and prey-predator behaviour.

This short video is the result of many hours of filming and working with the cameraman under water, who later remarked that this has been the toughest assignment in his professional life. Viewers are reminded that this video is aimed primarily at demonstrating acts of fish predation on turtle hatchlings. It willl be noted that in some sequences the hatchlings' swimming was restricted by a tether. This was an unfortunate but necessary compromize to permit the cameraman to obtain sequences which show the hatchlings under water for long enough. When allowed to swim at their normal speed (as in the experiments), the tethered hatchlings still swam much too fast for the cameraman to keep them in focus. I would like to stress in the strongest possible terms that hatchling behaviour was not similarly interfered with during the actual trials reported on in this dissertation.

Filming was done on Heron Island during January 1992.

Camera work :	David Hannan, CORAL SEA IMAGERY
Editing and production:	CORAL SEA IMAGERY
Scientific advice and direction:	Emma Gyuris
Script :	Emma Gyuris