

## Reports

# The rate of predation by fishes on hatchlings of the green turtle (*Chelonia mydas*)

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**Abstract.** This study addresses the need for empirical data on the survival of sea turtle hatchlings after entry into the sea by (1) developing a method for measuring marine predation; (2) estimating predation rates while crossing the reef; and (3) investigating the effect of environmental variables on predation rates. Predation rates were quantified by following individual hatchlings, 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 separate trials. Predation rates varied among trials from 0 to 85% with a mean of 31% (SE = 2.5%). The simplest logistic regression model that explained variation in predation contained tide and moon phase as predictor variables. The results suggest that nocturnal emergence from the nest is a behavioral adaptation to minimize exposure to the heat of the day rather than a predator-escape mechanism. For the green turtle populations breeding in eastern Australia, most first year mortality is caused by predation while crossing the reef within the first hour of entering the sea.

## Introduction

Green sea turtles (*Chelonia mydas*, Linnaeus 1758) spend most of their lives at sea. The females leave the water briefly to dig deep nests in coastal and island sand dunes in which they lay a relatively large clutch of about 100 eggs (Carr 1967; Bustard 1972; Ehrhart 1982). In each nesting season 500–800 eggs are laid in several clutches. Individual turtles do not breed annually but return to the nesting beach at 4–6 year intervals (Limpus et al. 1984). Age to sexual maturity has been estimated to be between 30 and 50 years and may differ significantly between populations using different foraging areas (Limpus and Walter 1980; Balazs 1982; Bjorndal and Bolten 1988). The reproductive life span of marine turtles is not known, but has been estimated

for a population of loggerhead turtles (*Caretta caretta*) in the southern United States as 32 years (Frazer 1983).

The only parental care offered to the eggs is the female's choice of the nesting site and the construction and burial of the nest (Carr 1973; Bustard and Greenham 1969; Bustard 1972; Hendrickson 1980). The eggs hatch after incubating for 7–11 weeks and the hatchlings take several days to dig through the sand before they emerge, usually during the night (Carr 1973; Mrosovsky 1968; Bustard 1967; 1972; Miller and Limpus 1981; Miller 1985). On emergence, they 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 habitats as small juveniles (Carr 1973; Limpus et al. 1984).

Many aspects of sea turtle life history are a direct consequence of anatomical and physiological limitations imposed by terrestrial ancestors (Hendrickson 1980). The unusually large number of eggs produced distinguishes marine turtles from most other reptiles (Hendrickson 1980). High mortality during the early life stages (i.e., eggs and hatchlings) is usually considered one of the major factors leading to such high fecundity. The fertility of eggs may exceed 95% but emergence success of the hatchlings may be somewhat lower even in undisturbed nests (Miller 1985; Whitmore and Dutton 1985; Wyneken et al. 1988; Harry and Limpus 1989). Although the effect of predators recently introduced by man into sea turtle nesting habitats can be substantial, most workers have suggested that few of the natural predators of eggs and hatchlings on the beach normally inflict heavy losses (Limpus 1982; Stancyk 1982).

Thus, natural mortality of eggs and hatchlings prior to entry into the sea does not seem high enough to explain the observed high fecundity. However the survivorship of hatchlings once they enter the water is unquantified. Estimates of mortality after hatchlings enter the sea are mostly anecdotal or based on theoretical considerations (Hendrickson 1958; Hirth 1971; Bustard 1972; Witham 1974; Frith 1975; Balazs 1980; Richardson and Richardson 1982; Crouse et al. 1987). Witherington and Salmon (1992) recently attempted to measure predation on loggerhead turtle (*Caretta caretta*) hatchlings but their conclusions are limited by small sample sizes and non-standardized methods.

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This study addresses the need for empirical data on 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.

## Material and methods

### Study site

Heron Island reef, at the southern end of Australia's Great Barrier Reef, is an elongate lagoonal platform reef approximately 11 km long and 5 km wide at its eastern end (Fig. 1). A vegetated sand cay, Heron Island, is situated on the western end of the reef. Tidal range varies between 2 m (springs) to 1 m (neaps). On spring tides a large proportion of the reef crest and reef flat is 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  $\approx 5.5 \text{ km}^2$ , reef flat  $\approx 14.3 \text{ km}^2$  and lagoon  $\approx 8.4 \text{ km}^2$  (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.

Heron Island provides a nesting habitat for green turtles which dig their nests in the vegetated sand dunes. The emerged young cross 10–30 m of dune and beach area before entering the sea. As with

other green turtle rookeries, the total 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 this study, however, the numbers of nesting turtles at the Heron Island rookery were similar to a total of approximately 500–1000 females for the season, and 80–120 turtles nesting nightly at the peak of the nesting season. (Limpus 1989). As there were no cyclones or other major environmental perturbations during this period, it was assumed that the numbers of hatchlings were similar between nesting seasons. Thus, three years' data were analyzed as a single set.

### 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 which were kept in a cool, shaded area. Most animals were used in experiments within 12 h of capture and no animals were held in captivity for a period exceeding 24 h. After placement in the boxes the hatchlings would soon assume quiescence, but would regain activity in response to handling. Occasionally hatchlings failed to regain their post-emergence vigor and such animals were not used in the experiments.

### Observations of predator-prey interactions

Free-swimming hatchlings ( $n = 57$ ) were followed by snorkel divers during mid- to late afternoons at the maximum distance allowed by conditions of visibility (generally about 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 were tracked by compass.

### Measures of predation

Most predation trials were carried out on the northern reef flat and the adjacent reef slope because the prevailing south-easterly wind often made other sites unsuitable. Predation rates were quantified by following individual hatchlings for a period of ten minutes as they swam from the water's edge towards the reef crest and the deep water beyond. Hatchlings were tethered by a fine, monofilament, nylon line (Platyus 27 N 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. This prevented the hatchling disengaging itself, but allowed the tug of a predator to release the hatchling. The hatchlings' swimming ability was unimpaired by this tether except for some reduction in speed (see later). In most cases, the observer holding the free end of the line could feel the predation event.

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 Cylume 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 Cylume 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 just sufficient to allow the hatchlings to swim without having to crawl over much exposed coral. During high tide at night, most observers used surf ski paddle boards to follow the turtles 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 the general technique was used to investigate predation over the reef slope. Hatchlings were attached to a 20 m

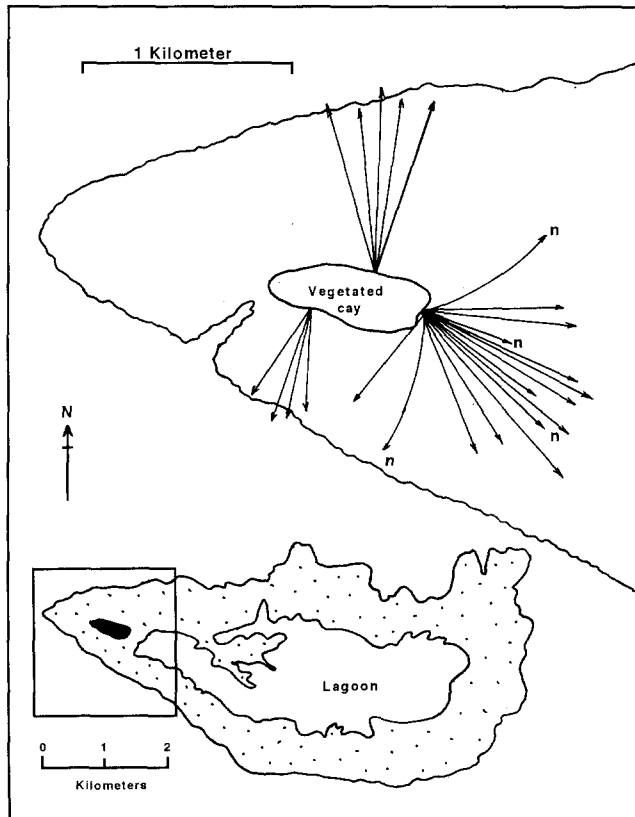


Fig. 1. Map of Heron Island reef showing boundaries of major habitats. The island is shown in solid colour, the reef flat surrounding the lagoon is stippled. The western end of the reef and Heron Island is enlarged. Arrows indicate the directions taken by free-swimming hatchlings after release from the beach. "n" denotes those hatchlings released at night

monofilament line without Cylume (20 m was chosen to approximate the width of the reef slope). Hatchlings were released with the observer standing on the reef crest at low tide or were released from a dinghy anchored at the crest. The turtles were allowed to swim 20 m in any direction.

These predation experiments were used to investigate the effects of three environmental variables on the rate of predation of hatchling green turtles. The variables investigated were tide, as an index of water depth (high and low tides were 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. No experiments took place at dawn and only a few at dusk. Predation experiments over the reef slope covered only a 6 day period (12–18 February 1990) and therefore moon phase was not 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 predictor 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 these predictor variables on predation rates. Because predation rates were expressed as the proportion of hatchlings preyed upon in each trial, resulting in a non-continuous variate, logistic regression was considered the appropriate method for analysis (Anon 1990; G. De'ath, personal communication). When comparing successively simpler models, the usual analysis of deviance using  $X^2$  was replaced by the  $F$ -ratio test, based on the mean deviance because the data were overdispersed. The general form of this test is as follows:

$$F = \frac{\frac{RSS_{\text{simple model}} - RSS_{\text{more complex model}}}{df_{\text{simple model}} - df_{\text{more complex model}}}}{RSS_{\text{more complex model}}/df_{\text{more complex model}}}$$

(where  $RSS$  = residual sum of squares and  $df$  = degrees of freedom).

If the successive 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 factor that was removed from the more complex model, had a significant effect on the dependent variable (i.e., predation rate).

### Validation of techniques

*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.

The length of the tether 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 would quite often get tangled on handling and because of the extra drag it presented to the hatchlings towing it, 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 was compared with free-swimming hatchlings to provide a basis for calculating overall predation rates during the hatchlings' swim across the reef flat. The

width of reef flat to be crossed was 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  $P < 0.01$ ). Salmon and Wyneken (1987) obtained a similar swimming speed for free swimming loggerhead turtle hatchlings.

*Observer bias.* Numerous observers assisted in the field project, usually on a replacement basis. Thus, the investigation of observer bias was limited to two periods where individual observers overlapped long enough to be compared. The proportion of hatchlings preyed upon within each trial was calculated for each observer. The average proportion for each observer was then compared by the Friedman two-way ANOVA (Siegel 1956) using 'trials' as a blocking factor. The analysis was conducted separately for each period between the two different sets of observers. No significant difference was detected between individual observers ( $df = 3$ ,  $P = 0.5945$  and  $df = 2$ ,  $P = 0.2668$  for the two periods).

## Results

A total of 84 predation trials were performed in 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, nine were attacked by seagulls at the water's edge. Fresh animals were substituted for these individuals.

### Observations on the behavior of hatchlings and their aquatic predators

Fish predation on the free-swimming hatchlings was high (93.6%). Of the 57 free swimming hatchlings that were followed by snorkel divers, ten were lost from sight, 44 were eaten by fish and three survived to reach the reef slope (Table 1). Most attacks were sudden rushes by demersal predators. Often hatchlings were attacked unsuccessfully by one or more predators before one 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 hatchlings ever took evasive action to avoid predation.

Compass tracking of the free-swimming hatchlings ( $n = 25$ ) indicated that they swim directly away from the island's beaches, towards the reef crest (Fig. 1). Because the circumference of the reef crest is much greater than that of the island (Fig. 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.

As summarized by Table 1, the most commonly observed predators were fish of the family Serranidae, followed by Lutjanidae and Labridae. Small sharks, lethrinids and eels were occasionally observed to prey on hatchlings. Long toms (Belonidae) often attempted to prey on hatchlings but were never successful. In the predation experiments with tethered hatchlings over the reef flat, *Choerodon cyanodus* (Labridae) was the most commonly observed predator. No data were obtained on the identity of nocturnal predators although some of the predators observed during the daytime are known to feed at night also (Hobson 1965; Smith et al. 1971).

**Table 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

Date/time	Outcome			Predators
	Eaten	Survived	Lost from sight	
9 Jan 1987 1650 h	5		1	3 <i>Epinephelus</i> (var. spp.) 1 Black tip reef shark 1 <i>Lutjanus carponotatus</i>
12 Jan 1987 1700 h	2			1 <i>Epinephelus</i> sp. 1 Black tip reef shark
10 Jan 1987 1700 h	31		4	24 <i>Epinephelus</i> (var. spp.) 1 <i>Cromileptes altivelis</i> 1 Scarid 1 <i>L. carponotatus</i> 2 Serranid 1 Muraenid eel 1 <i>Choerodon cyanodus</i>
3 Feb 1990 <sup>a</sup> 1600 h	5		3	1 <i>C. cyanodus</i> 1 <i>L. mahsena</i> 1 <i>C. cyanodus</i> 1 <i>L. carponotatus</i> 1 <i>Epinephelus</i> sp.
4 Feb 1990 <sup>a</sup> 1600 h	1	3	2	1 <i>L. carponotatus</i>
Total ( $\Sigma = 57$ )	44	3	10	

<sup>a</sup> 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). Some of these hatchlings survived to reach the reef crest and open water

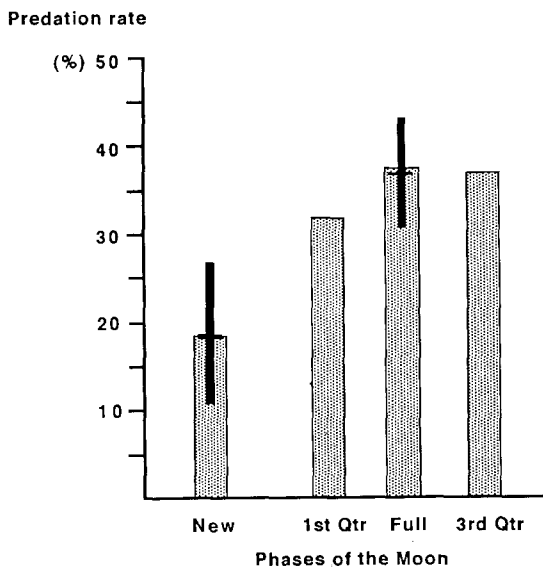
*Environmental variables influencing predation: reef flat*

Predation rates varied among trials from 0 to 85% with a mean of 31% (SE = 2.5%).

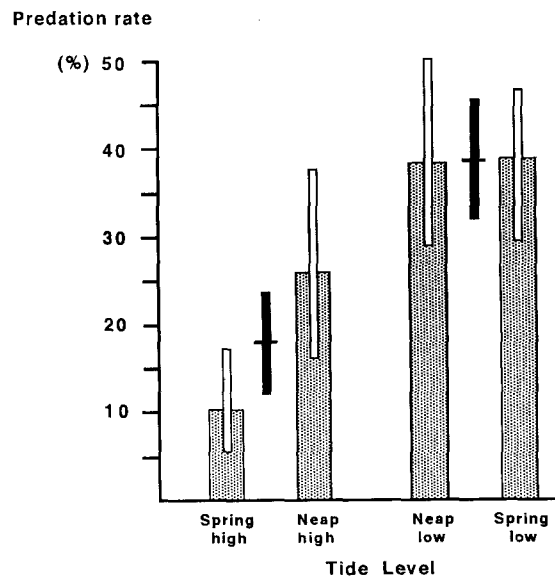
The simplest model that explained variation in predation contained tide and moon phase as predictor variables. Moon phase was entered into the model as the quarter about the new moon. Tides were entered into the model as high and low with no distinction made between spring

and neap periods (Figs. 2 and 3). The *F*-ratio test was significant when either tide ( $P < 0.0001$ ) or moon phase ( $P = 0.0015$ ) was removed from the regression model indicating that both factors are important as determinants of predation rates (Table 2).

The observed and calculated probabilities of survival under the various tidal and lunar conditions are summarized in Table 3. The model fits the data well. Survival rate was the lowest under conditions of moon phase 2, 3



**Fig. 2.** Predation rates of hatchling green turtles after 10 minutes swimming over the reef flat under the four different moon phases. The mean and 95% confidence intervals of predation rates obtained in trials during the new moon and during other moon phases (combined) are indicated



**Fig. 3.** Predation rates of hatchling green turtles after 10 minutes swimming over the reef flat during various tides showing the 95% confidence intervals for each tide level (clear bars). The mean and 95% confidence intervals of predation rates obtained in trials during the combined neap and spring low and high tides are also shown (dark bars)

**Table 2.** Summary of logistic regression analysis of predation trials over the reef flat showing deviance and degrees of freedom

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)	<0.0001
			(i.e., tide has a significant effect)	
Analysis 2: night time only predation trials in reef flat habitat				
Model 1				
Tide				
Presence of moon	181.9	36	N.A.	N.A.
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				
Model 1				
Tide				
Moon phase	123.1	4	N.A.	N.A.
Model 2				
Moon phase	207.9	43	28.9025 (1,42)	<0.0001
			(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)	

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 successive steps involved in the backward elimination steps are shown). Analysis 1: 'Model 1' is the initial model followed by the simplest model (5) that adequately describes the data. Analysis 2: Results obtained when trials were run during the night are re-analyzed with tide and presence/absence of the moon in the night sky being the predictor variables. Analysis 3: Results obtained when trials run during daytime only are re-analyzed with tide and moon phase being the predictor variables

**Table 3.** Survival rates (S) (observed and estimated) of hatchling turtles after 10 minutes swimming over a reef flat under various environmental conditions

	High tide	Low tide
New moon	Observed = $\frac{171}{180} = 0.95$	$\frac{187}{260} = 0.72$
	Estimated = <b>0.91</b> (0.85–0.95)	<b>0.75</b> (0.62–0.84)
Full moon, 1st and 3rd quarters	Observed = $\frac{336}{420} = 0.80$	$\frac{446}{820} = 0.57$
	Estimated = <b>0.82</b> (0.73–0.87)	<b>0.56</b> (0.44–0.58)

(95% confidence intervals for the estimated values are shown in parenthesis)

and 4/low tide and the highest during new moon/high tide.

The data were analyzed further to test whether predation is affected by the availability of light, 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, it was determined 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. The availability of moonlight was not significant in determining predation rates ( $P = 0.2111$ ). Also moon phase could not be entirely disregarded as a factor of significance for the daytime trials ( $P = 0.0719$ ) adding further support to the conclusion that the phase of the

the moon significantly effects predation. Results of these analyses are shown in Table 2.

*Environmental variables influencing predation:  
reef slope*

Logistic regression analysis of 13 predation trials over the reef slopes identified no predictor variables (see methods) that accounted for the observed variability in predation rates. The observed survival rate was comparatively high and ranged between 0 and 25% with a mean of 7% (SE = 2.4%). However, a considerable proportion of the hatchlings were preyed upon (approximately 40% of those surviving at the end of their 20 m swim) while they were being retrieved in order to disengage them from their 20 m lines. Mortality that occurred during retrieval was not considered in the regression analysis. This type of predation was not observed over the reef flat.

*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 was estimated. The number of hatchlings surviving for a given period can be estimated from 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 number alive 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 1 unit of time, in this case 10 minutes.

The probability of survival derived from the logistic regression analyses was used to estimate the value of "S" for the various environmental factors of interest. (See Table 3 for the values of "S" which apply under various combinations of environmental conditions)

If one considers the approximately 1 km wide section of the northern reef flat, for example, which takes 30 min for the average free-swimming hatchling to cross, 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.

## Discussion

While digging out from the nest, and to a lesser degree while crossing the beach, group facilitation is quite an important feature of the hatchlings' behavior (Carr and Hirth 1961; Bustard 1967; Carr 1973). Once hatchlings enter the water, however, all associations between individuals cease (Frick 1976; Carr 1982). No semblance of schooling was ever observed in this study, nor has this behavior been noted in the literature. The seaward orientation of the hatchlings entering the water at Heron Island is consistent with the observations of previous workers (Frick 1976; Salmon and Wyneken 1987).

Because the observations on the free swimming hatchlings were timed to coincide with water depth convenient for the observers and not with high or low water explicitly, and because the period of observation was not standardized, the results obtained through the observations of free swimming hatchlings are not considered as actual measures of predation. However, in the experiments involving the tethered hatchlings, the categorical predictor variables (day/night, moon phase and tide) were determined without error and the experimental conditions (habitat, tether length and period of observation) were standardized. Thus, with certain assumptions, these experiments may be considered to approximate the true rates of predation of hatchlings over the reef flat per unit of time.

The tether, when kept slack, imposed no impediment, other than some reduction in speed, to the swimming ability of the hatchlings. However, even the relative 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 the free-swimming hatchlings and their fish predators; 44 of the 47 hatchlings successfully followed over various periods (most often less than 20 minutes) were eaten by fish (i.e., 93.6%). Furthermore, few of the tethered hatchlings were taken by fish as they swam seaward over the reef slopes, although many of these hatchlings were taken by predators when their swimming became poorly coordinated thrashing while being retrieved by the observer, indicating that tethering per se is not likely to increase the probability of predation.

The lower predation rates on sea turtle hatchlings during high as opposed to low tides are consistent with known patterns of fish behavior. The majority of shallow water reef fish show a strong avoidance of swimming far above the protection of the substrate as they themselves might then be exposed to predation (Shulman 1985). This is especially so with 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 would likely be further from the bottom and thus less accessible and, in addition, less detectable, 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 known patterns of fish feeding behavior. 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 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 2). Further, it would appear that the moon phase cannot be dismissed as a factor affecting predation during daylight hours (Table 2). It is therefore likely that lunar periodicity, rather than degree of illumination alone, is a significant factor influencing predator behavior. In support of this hypothesis there are numerous accounts of associations between moon phase and behavior of fish and other reef animals (Johannes 1981).

Two advantages of nocturnal emergence of hatchlings from the nest 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. Mortality of loggerhead, *Caretta caretta*, hatchlings due to predation was less than 2% 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% of emerged flatback, *Natator depressa*, hatchlings were preyed upon while crossing the beach (Limpus et al. 1983). In addition there are a few anecdotal accounts of heavy bird predation on hatchlings that emerge during the day (e.g., Mrosovsky 1971; Fowler 1979; Stancyk 1982). In the absence of comparative studies of nocturnal versus diurnal predation it is not possible to conclude whether nocturnal emergence offers 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 1967, 1972; Limpus 1978; and this study). Reef fish 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 predictor variable. Crossing the reef flat at night as opposed to during daytime conferred no detectable protection from aquatic predators. Considering further that most terrestrial predation occurs while the eggs/hatchlings are still concealed under the sand, soon after oviposition and again after hatching (Carr 1973; Fowler 1979), it is most likely that nocturnal emergence from the nest is a behavioral response to minimize exposure to the heat of the day rather than a predator-escape mechanism.

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. Limpus (1978) and Mortimer (1982) noted that the intensity of predation in the water may be influenced by the type of offshore habitat that hatchlings must cross. Published descriptions of turtle rookeries seldom give details of the type of aquatic habitat immediately adjacent to the nesting beach, but throughout their

global distribution, nesting beaches are not necessarily bordered by coral reefs, e.g., Tortuguero (Meylan 1982) and Ascension Island (Mortimer 1982). Predation rates are likely to be different for different seaward zones. Predation on logger-head turtle hatchlings was relatively low on the east coast of Florida (Witherington and Salmon 1992).

Most green turtle nesting in eastern Australia occurs on coral cays which are surrounded by reefal habitats comparable to Heron Island reef (Limpus 1978). It is therefore reasonable to extrapolate from the results of this study and conclude that for the green turtle populations nesting along the Great Barrier reef cays, most first year mortality occurs as a result of predation within the first hour of entering the sea.

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