

## ***Relative Exposure Index: an important factor in sea turtle nesting distribution***

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### ABSTRACT

1. The threatened status of many sea turtle populations and their vulnerability to coastal development and predicted climate change emphasize the importance of understanding the role of environmental factors in their distribution and ecological processes. The factors driving the distribution of sea turtle nesting sites at a broad spatial scale is poorly understood.

2. In light of the lack of understanding about physical factors that drive the distribution of turtle nesting, the relationship between nesting site distribution and the exposure of coastal areas to wind and wind-generated waves was analysed. To achieve this, a Relative Exposure Index (REI) was developed for an extensive area in north-eastern Australia and values of the index for nesting sites of five different sea turtle species and randomly selected non-nesting sites were compared.

3. Although there are differences between species, the results show that sea turtles nest in areas of higher REI values suggesting that wind exposure is related to the spatial distribution of sea turtle nesting sites, and it may also influence nest site selection in female turtles and/or the dispersal of hatchlings towards oceanic currents.

4. The combination of these results with further research on other driving environmental factors, like oceanic currents, has the potential to allow for the identification and prediction of future nesting sites, for which conservation and management may become essential.

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### INTRODUCTION

All sea turtle species have similar reproductive traits, such as the requirement to lay eggs on land and temperature-dependent sex determination. In addition, with the exception of the leatherback turtle, species breeding in eastern Australia show strong nest site fidelity (Miller, 1997). In general, successful reproduction will rely upon: (1) the ability of male and female turtles to time their migrations to meet at courtship areas; (2) beaches having sand characteristics (e.g. temperature) that will allow embryo development; and (3) the waters offshore of beaches having environmental and oceanographic features that allow the offshore movement of hatchlings (see reviews by Miller, 1997 and Hamann *et al.*, 2002). There is a clear link between the physical characteristics

of nesting beaches and coastal zone processes for maintaining successful future recruitment (Mortimer, 1990). However, while several studies have attempted to describe the specific qualities of nesting beaches, such as temperature, beach width, slope, grain size or vegetation cover (Stoneburner and Richardson, 1981; Mortimer, 1990; Chen *et al.*, 2007), few studies have examined climatic and/or oceanographic processes that may influence nesting beach selection and hatchling dispersal.

Some aspects of sea turtle behaviour at early stages are well documented. Hatchlings emerge from underground nests, crawl to the sea, and navigate through near shore waters towards the open ocean by swimming towards incoming waves irrespective of current direction (Lohmann *et al.*, 1990, 1995;

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Manning and Lohmann, 1997; Wang *et al.*, 1998). Once hatchlings are offshore they transfer this directional 'wave orientated' preference to a magnetic compass to continue their migration away from land even after contact with the coast is lost (Goff *et al.*, 1998). Hence wind speed and direction are factors underpinning initial hatchling dispersal.

Hatchlings facilitate their swim towards offshore waters by undertaking a period of hyperactive swimming, known as frenzy. The swimming frenzy allows hatchlings to disperse away from shallow and near-shore areas where predators are more abundant and active (Salmon and Wyneken, 1987; Wyneken and Salmon, 1992; Gyuris, 1994; Chung *et al.*, 2009), and swim towards less risky habitats (Whelan and Wyneken, 2007). Frenzy behaviour differs between species or between populations of the same species (Salmon and Wyneken, 1987; Wyneken and Salmon, 1992; Chung *et al.*, 2009). Inter-population variation could be attributed to different strategies used for dispersal, or distances separating nesting beaches from the hatchlings 'goal' oceanic currents (Dalton, 1979). These differences, in particular those associated with ecological or environmental factors, are particularly difficult to observe at local (beach) scales and thus are best studied over large spatial scales representative of the population.

The analysis of species – environment relationships are an important function of ecology (Guisan and Zimmermann, 2000). At broad scales, little is known about how environmental conditions influence sea turtle reproductive ecology (Pike and Stiner, 2007). Essentially this is because knowledge of the relationship between environmental factors and the distribution of sea turtle nesting sites is largely based on studies restricted by spatial and temporal scales. Nesting by sea turtles in areas exposed to wind and waves may influence sea turtles at both adult and early stages, such as improving females' beach finding ability or nest site selection, improving the ability of hatchlings to orient in a seaward direction and increase hatchling dispersal ability. Therefore, analysing the exposure of nesting sites at population scales would enhance our understanding of the influence environmental factors may have on sea turtle nesting distribution.

The threatened status of many sea turtle populations and their vulnerability to human disturbance and climate change emphasizes the importance of quantifying the relationships among environmental factors and sea turtle distribution. This is essential in coastal areas where sea turtle recruitment success or hatchling dispersal may be affected by human processes, such as coastal development, and the consequences of climate change such as temperature increases, more frequent cyclones and sea-level rise (see Hamann *et al.*, 2007 for examples). Although unpublished studies relate nesting distribution to wind velocity (Horrocks and Vermeer, 1995) or wave energy (Foley *et al.*, 1995) the relationship between sea turtle nesting site distribution and exposure to wind speed and direction has not been tested, probably because of the difficulty of quantifying exposure over an extensive area.

Using wind velocity, direction and fetch, Keddy (1982) developed a measure of wind exposure to quantify within-lake gradients of wave energy. The same algorithm was later refined by other investigators to quantify wind exposure, and used to predict the distribution and ecological characteristics of seagrass ecosystems (Fonseca and Bell, 1998; Kelly *et al.*, 2001; Robbins *et al.*, 2002). The refined model combined the calculation of fetch with local scale meteorological data to estimate a Relative Exposure Index (REI) that can be

compared through space or time. Puotinen's (2004, 2005) research in the Great Barrier Reef (GBR) provides a suitable method for estimating effective fetch over extensive complex reef–island systems. Effective fetch quantifies the effects of irregular shorelines on the wind and wave energy at a particular site. Improvements in geographical information systems (GIS) and digital data storage have made the articulation of these models across space possible for use in spatial and statistical analysis, as well as providing informative map products to visualize results (Kelly *et al.*, 2001).

Consequently, to investigate how the distribution of marine turtle nesting sites may relate to large-scale climatic variables associated with sea turtle nesting success and hatchling dispersal, turtle nesting distribution from Queensland Australia was used to explore (1) whether sea turtle species nest during periods of higher wind and wave exposure, (2) whether sea turtles nest at sites with significantly higher exposure than control (non-nesting) sites, and (3) to examine the between-species differences in nesting site exposure. Data are discussed in relation to population-specific knowledge and the implications of the results for future research and monitoring and the opportunities for future studies are detailed.

## METHODS

### Study region

The study region includes part of Torres Strait and the east coast of Queensland, Australia including the GBR (latitude 8° 54' to 28° 14' S (Figure 1). The spatial extent of the study region is limited by the availability of climatic data. Therefore, some important nesting areas, such as the Coral Sea Region and the outer northern GBR, were excluded from the study because available climatic data were considered deficient. Two regions are differentiated within the study area: (1) the northern region (north of Cooktown, Figure 1); and (2) the southern region (south of Cooktown, Figure 1). These regions were differentiated because of their varying wind patterns (the southern region has greater mean wind velocities) and some turtle species (e.g. *Chelonia mydas*) have different populations in each of the regions. Differences in wind patterns were tested for using Mann–Whitney's non-parametric analysis to compare randomly selected points throughout the study regions ( $N = 562$ ; north,  $n = 310$ ; south,  $n = 252$ ).

The study region was delineated by a raster surface using ArcGIS<sup>TM</sup> 9.2 ESRI<sup>®</sup> (ESRI, 2001). A resolution of 4 km grid cells was set as it was assumed that this allows an accurate assessment of the relationship between REI (see below) and the distribution of nesting sites at a large scale. The grid was converted to a point coverage (one point per grid cell), with each point linked to an identification number of a database.

### Sea turtle nesting sites

There are four species of sea turtle currently nesting within the study region: loggerhead turtle (*Caretta caretta*); green turtle (*Chelonia mydas*); flatback turtle (*Natator depressus*); hawksbill turtle (*Eretmochelys imbricata*). The leatherback turtle (*Dermochelys coriacea*) had rookeries in southern Queensland up until the early 1990s (Hamann *et al.*, 2006). All known nesting sites throughout the study area were located

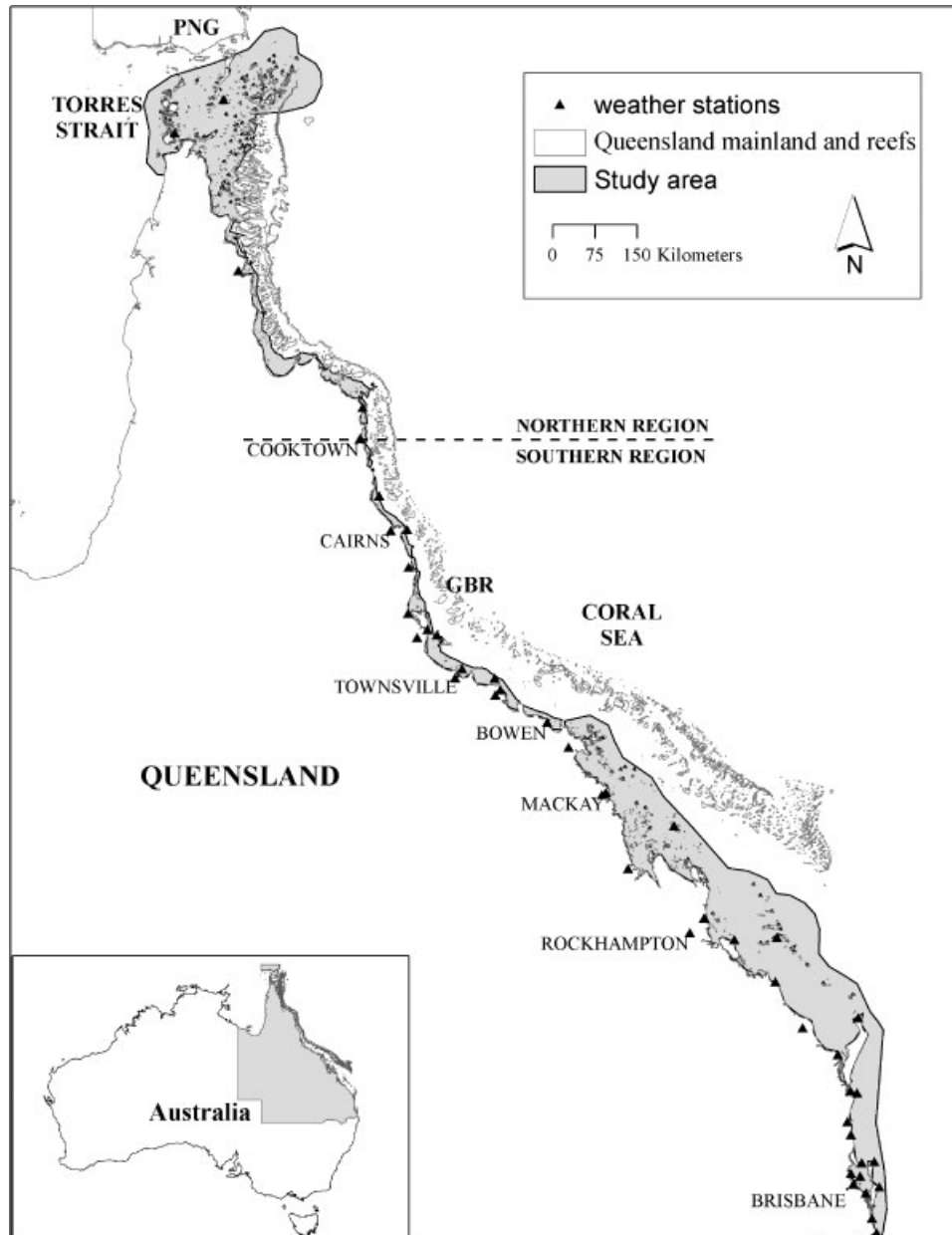


Figure 1. Study area with main Queensland cities and weather station sites (Australian Bureau of Meteorology). Dashed line shows the division between northern and southern regions.

from the literature and through personal communication with experts (loggerhead: Limpus *et al.*, 1984a; McLachlan *et al.*, 2006; green: Limpus *et al.*, 1984a, 2003; flatback: Limpus *et al.*, 1989; Limpus, 2009a; hawksbill: Limpus, 2009b; leatherback: Hamann *et al.*, 2006; also see Dobbs *et al.*, 2008 and Dryden *et al.*, 2008 for nesting distributions). There are no records of nesting leatherback turtles in Queensland since 1996, so the nesting sites used in the study account for their past breeding locations (Hamann *et al.*, 2006). Flatback and green sea turtles have populations in both eastern Queensland and in the Gulf of Carpentaria (including western Torres Strait) (Limpus, 2009a). However, the limited availability of climatic data on the western side of the Gulf of Carpentaria restricted this study to focusing just on the eastern populations.

Each of the 203 nesting sites used in the study were grouped by population and region (north,  $n = 81$ ; south,  $n = 122$ ; Figure 2). A 12 km buffer zone, made up at a scale of 4 km by 4 km grids, around each site was created in order to study the wind exposure in the area that hatchlings encounter during frenzy swimming. Twelve kilometres (i.e. three grid cells) are assumed to be within the area swum by hatchlings during their first 24 h at sea (Salmon and Wyneken, 1987; Witherington, 2002). It is acknowledged that research on the east coast of the USA has demonstrated that marine turtle hatchlings use wave cues for a relatively short period of the swimming frenzy before switching to a magnetic compass (Salmon and Lohmann, 1989; Lohmann and Lohmann, 1992). However, wind speed and direction calculated across the three grid cells

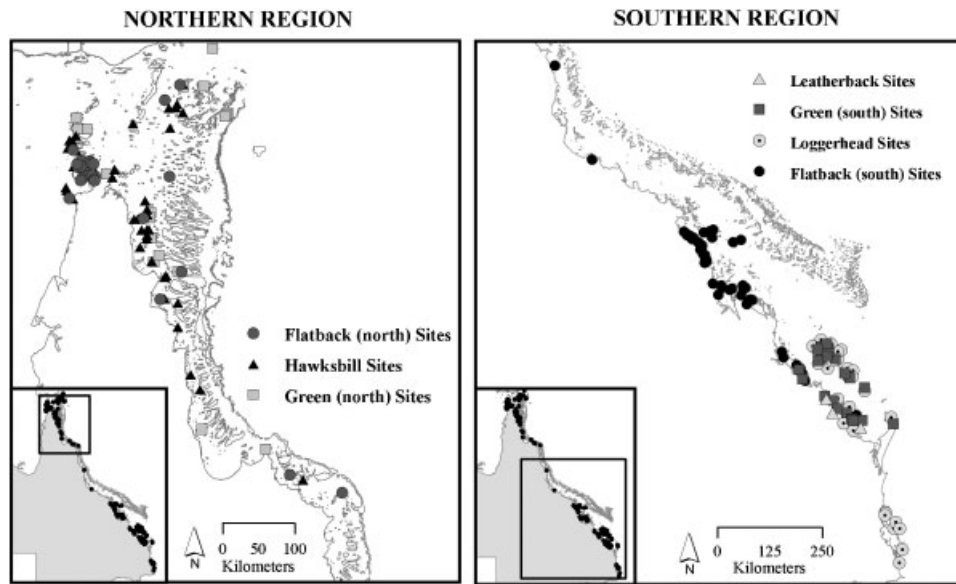


Figure 2. Distribution of sea turtle nesting sites within the study area. Site locations have been slightly modified for a better visual presentation when superposition occurred.

(12 km) represent near-shore coastal conditions relevant to hatchling dispersal. The distance covered during the frenzy has been tested only for loggerhead, green and leatherback turtles and could vary between species, populations or individuals, as well as depending on factors such as weather conditions.

### Control sites

To test whether turtles select primarily exposed nesting locations, control sites were created by randomly selecting points within the study area that intersected with islands (with sandy beaches) or mainland beaches ( $n = 197$ ) that receive no nesting, or rare nesting (less than five nests per year). These were also classified into the northern ( $n = 62$ ) and southern ( $n = 135$ ) regions, and 12 km buffer zones around the sites were defined following the same procedure as for the nesting sites.

### Relative Exposure Index (REI)

#### Climatic data

Climatic information for 45 weather stations was obtained from the Australian Bureau of Meteorology (BOM) (Figure 1). Note that the density of weather stations is greater in the southern region (mean Euclidean distance 54 km ( $n = 40$ )) than in the northern region and Torres Strait (mean Euclidean distance 151 km ( $n = 5$ )). The mean distance between rookeries and their closest weather station for each population is variable (loggerhead – 29 km; flatback (north) – 33 km; flatback (south) – 36 km; leatherback – 31 km; hawksbill – 64 km; green (north) – 97 km; and green (south) – 30 km). The climatic variables used for the calculations were as follows:

- (1) Mean wind velocity ( $V$ ), the average monthly wind speed ( $\text{m s}^{-1}$ ) based on two daily readings, at 9am and 3pm, from May 2005 to April 2007.
- (2) Directional percentage frequency ( $P_i$ ), the frequency (%) at which wind occurs from the  $i$ th compass

direction. Data are based on two daily readings, at 9am and 3pm, from May 2005 to April 2007 at each weather station. These are the standard times of data collection for the Australian BOM.

Multiple REIs were generated for various time periods relevant to turtle ecology including: (1) nesting season (November to March) and the non-nesting season (April to October), loggerhead: (Limpus, 1985; green: Limpus *et al.*, 1984a; Limpus and Limpus, 2001), flatback: (Limpus *et al.*, 1984b), hawksbill: (Dobbs *et al.*, 1999); leatherback: (Hamann *et al.*, 2006); (2) to assess variation throughout the nesting season, monthly average wind velocity ( $V$ ), directional percentage frequency ( $P_i$ ) and REI were calculated for each of the five months within the nesting season (November to March).

#### Effective fetch

Effective fetch is defined as the distance between a site and the nearest wave-blocking obstacle (i.e. shoreline or reef) along a given compass direction (US Army Coastal Engineering Research Center, 1977). Effective fetch was calculated for each of the 4 km by 4 km grids in ArcView GIS 3.3 (ESRI®) using the equation:

$$F_i = \sum_{n=1}^5 (y_n \times \cos x_i)$$

where  $y_n$  is the length of the radiating lines (direct fetch), and  $x_i$  the angle of departure from the  $i$ th compass heading ( $i = 16$ ) (i.e. 1 to 16 from headings N, NNE, NE, E, etc. in  $22.5^\circ$  increments). As a result, the effective fetch ( $F_i$ ) of each point was stored in the spatial database. If  $y_n$  was greater than 50 km, it was assumed that fetch was unlimited in the  $i$ th direction (Puotinen, 2004).

### Relative Exposure Index

REI was calculated for each 4 km by 4 km grid in ArcGIS 9.2 (ESRI) using the following equations (Keddy, 1982; Fonseca and Bell, 1998; Kelly *et al.*, 2001; Robbins *et al.*, 2002; Grech, unpublished data):

$$REI = \sum_{i=1}^{16} (V \times P_i \times F_i)$$

where  $i$  is the  $i$ th compass heading,  $V$  the mean wind velocity in  $\text{m s}^{-1}$ ,  $P_i$  the wind direction frequency (%) and  $F_i$  the effective fetch in kilometres. Zonal statistics (ArcGIS 9.2 Spatial Analyst tool (ESRI, 2001)) were used to calculate the mean REI within the buffer area of each nesting and control site within each time period.

### Data analysis

Mean relative exposure was significantly greater in the southern region (106.57) than the northern region (70.98; Mann – Whitney  $U = 25879$ ,  $N = 562$ ,  $P < 0.001$ ). Therefore, when comparing different exposure values, the northern and southern regions were treated separately.

To determine the overall exposure of nesting sites during different times of the year, REI values during the nesting and non-nesting periods were compared using Student's  $t$ -tests. The exposure at nesting sites during each month of the nesting season was compared using the non-parametric Kruskal–Wallis test. To test whether sea turtles nest at significantly more exposed areas than randomly selected sites within each region, REI values at nesting sites were compared with those at control sites, again using Student's  $t$ -tests. This analysis was conducted separately for the nesting season and the non-nesting season.

The nesting site exposure among different sea turtle species, nesting and non-nesting season, and in the two different regions, was tested using the non-parametric Kruskal–Wallis test due to non-normality of data. The Conover non-parametric *post hoc* analysis was used to evaluate specific differences in nesting exposure between the seven following subpopulations (Conover, 1980): loggerhead ( $n = 32$  sites); flatback-north ( $n = 24$ ); flatback-south ( $n = 62$ ); leatherback ( $n = 3$ ); hawksbill ( $n = 30$ ); green-south ( $n = 25$ ); and green-north ( $n = 17$ ). Conover procedures allowed comparison of all possible combinations of pairs, and thus grouping of populations that nest at sites of similar exposure and differentiation of those that nest at sites with significantly different REI. The Conover *post-hoc* analyses were conducted using the BrightStat package (Brightstat © 2006) and all other analyses were done using SPSS 14.0.

## RESULTS

The REI across the GBR and Torres Strait are shown for each seasonal time period (Figure 3). Temporal exposure patterns differed between the northern and southern breeding sites. The sites in the northern region had significantly lower mean REI during the nesting season (45.76) than during the non-nesting season (54.27; Student's  $t$ -test,  $t = -2.615$ ,  $n = 162$ ,  $P < 0.05$ ) (Figure 3(a), (b)). However, the sites in the southern region had significantly greater mean REI during the nesting season

(93.84) than the non-nesting period (77.56; Student's  $t$ -test,  $t = 4.617$ ,  $n = 244$ ,  $P < 0.001$ ) (Figure 3(c), (d)). The southern region showed an area of very low exposure from Cooktown to Bowen (22°00' S, 148°14' E), but a general medium-high exposure with some patches of high REI values south of Bowen (Figure 3(a)–(d)). Overall, there were similar patterns of REI for the nesting and non-nesting seasons, however, values were higher in the northern region during the nesting season (Figure 4(a)) and lower in the southern region during the non-nesting season (Figure 4(b)).

Within the nesting season both regions also show different temporal patterns. The northern area shows a statistically significant decrease in REI values from November to March (Kruskal–Wallis,  $\chi^2 = 27.786$ ,  $P < 0.001$ ) (Figure 5(a)), while the southern area slightly increases from November to March although the difference is not statistically significant (Kruskal–Wallis,  $\chi^2 = 8.026$ ,  $P > 0.05$ ) (Figure 5(b)).

$t$ -tests were used to assess whether sea turtle nesting sites are more exposed than the randomly selected sites (control) within each region. Table 1 shows that nesting sites and their surrounding areas are more exposed to wind and waves than the control sites both in nesting and non-nesting seasons for both northern and southern regions.

The different sea turtle species and populations nest in sites of significantly differing exposure (Kruskal–Wallis,  $\chi^2 = 121.301$ ,  $P < 0.001$ ). Using the Conover non-parametric *post hoc* analyses, three significantly different groups were defined: (1) loggerhead, leatherback and green-south; (2) flatback-south; and (3) flatback-north, hawksbill and green-north (Figure 6). Groups 1 and 2 nest within the southern region and group 3 nests in the northern region. Therefore, within the southern region flatback turtles nest at significantly less exposed sites than loggerheads, green and leatherback turtles. In the northern region, no significant difference among species was found, which could be a result of not being able to include the outer GBR locations such as Raine Island and Moulter Cay, which are important rookeries for green turtles and which would have, by proxy of location, high exposure.

## DISCUSSION

Sea turtles have been exposed to large-scale variation in climatic conditions in the past and have life history traits that enable them to survive climatic events that threaten seasonal reproduction (Hamann *et al.*, 2007). One coping strategy could be that new 'first time' breeding turtles in areas particularly affected by sea-level rise or temperature increase will shift their nesting distribution to new suitable areas. Understanding the processes influencing nesting site distribution and how they affect each population is essential to predict potential future nesting sites. Consequently, the use of methods that use current distribution to enable prediction of future nesting habitat distribution is fundamental for the management and conservation of coastal areas. Using an REI that incorporates wind speed, wind direction and fetch in an extensive coastal area of north-east Australia to test relationships between nesting sites of five species of sea turtle showed that exposure to wind and thus waves is related to the distribution of nesting sites, and may influence the dispersal of hatchlings through inshore waters.

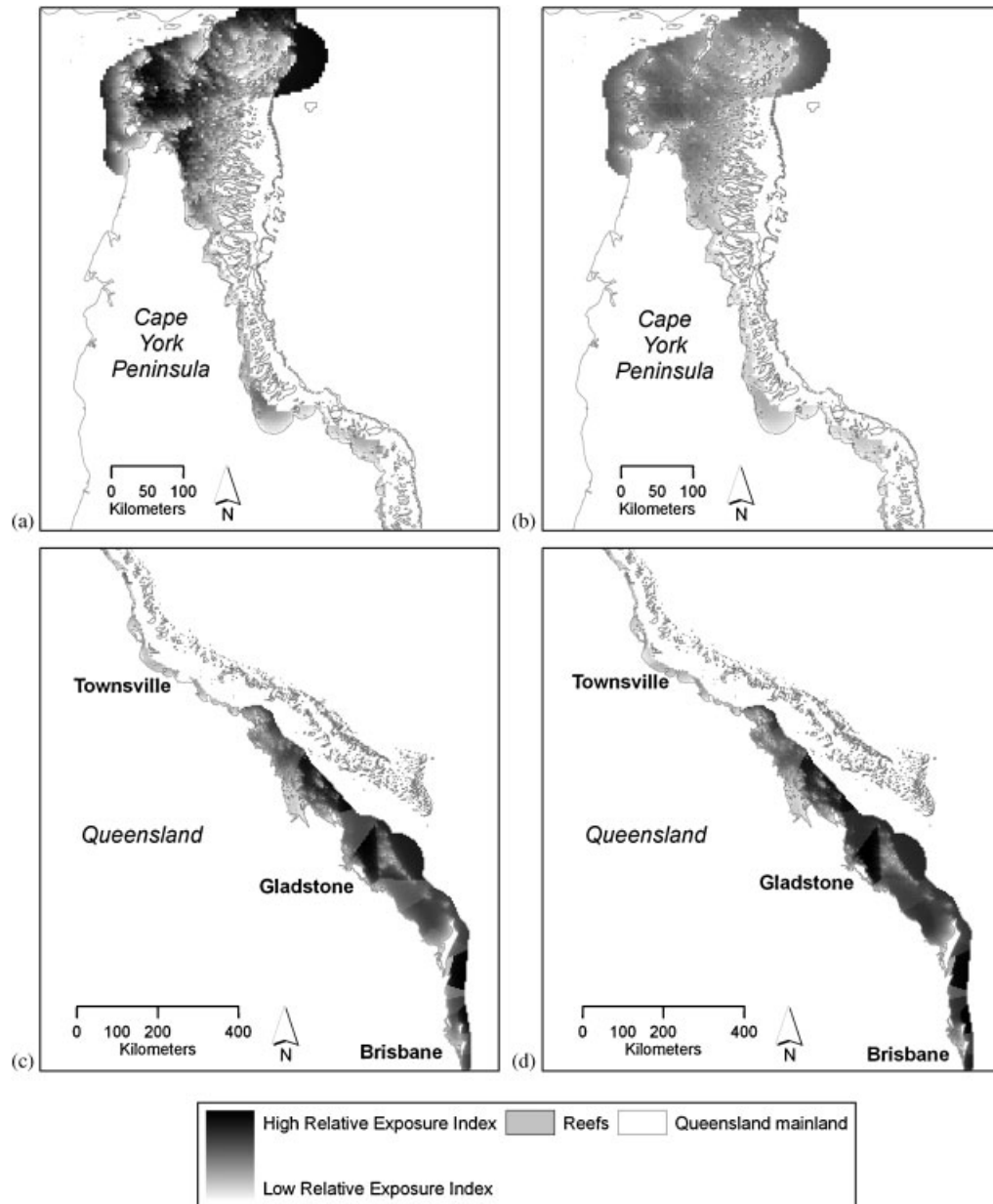


Figure 3. Relative Exposure Index in the northern region (a) non-nesting season (b) nesting season, and for the southern region (c) non-nesting season and (d) nesting season.

The majority of sea turtle nesting sites in eastern Queensland occur in the northern GBR and Torres Strait (north of Cooktown), and south of Bowen in the southern GBR region. With the exception of occasional nesting by flatback and green turtles, beaches and islands lying in the central region of the GBR (between Cooktown and Bowen) are not used by turtles for nesting (Limpus *et al.*, 2003; Limpus, 2009a). In relation to this geographic spread of turtle nesting, the REI model also shows a geographic pattern. First, the data indicate that exposure is higher in marine turtle nesting sites in comparison with control sites that have very little or no turtle nesting. Second, during the turtle-nesting season the area north of Cooktown has low to medium exposure, the area south of Bowen has medium to high exposure and the middle section of the GBR is the least

exposed of the three areas. Presumably low exposure in the Cooktown to Bowen region occurs because this area of the GBR is largely buffered from wind and long period waves (swell) approaching the complex from the open sea by the outer GBR (Young and Hardy, 1993), thus, supporting use of the REI as an important descriptor for the spatial distribution of nesting sites at a geographical scale.

The phenology of the nesting phase of the sea turtle reproductive cycle is largely determined by temperature (Weishampel *et al.*, 2004; Hawkes *et al.*, 2007) and other environmental factors (reviewed by Miller, 1997; Hamann *et al.*, 2002), and although there are slight species variations, the majority of nesting for each of the four species that breed in eastern Queensland occurs between November and March. The REI data indicate there are also significant seasonal

# RELATIVE EXPOSURE INDEX: AN IMPORTANT FACTOR

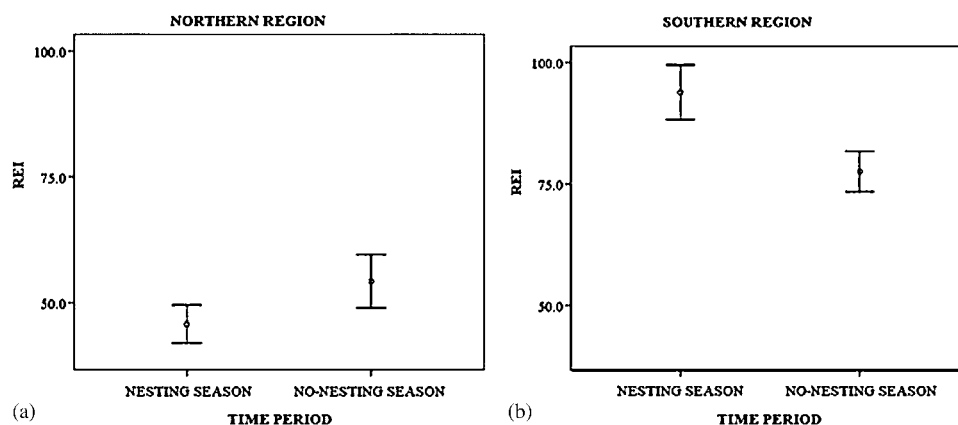


Figure 4. Comparison of the mean exposure (REI) between the sea turtle nesting and no-nesting seasons at the northern (a) and southern (b) regions. Error bars indicate 95% confidence intervals.

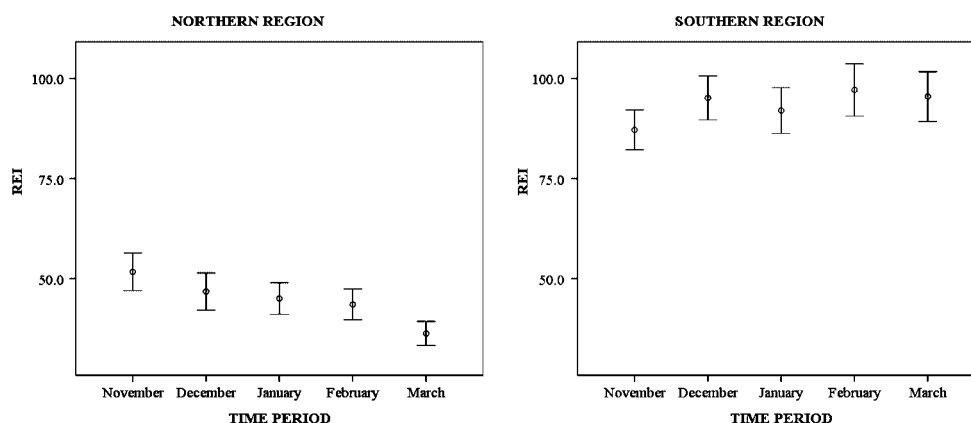


Figure 5. Comparison of the mean exposure (REI) for each month of the nesting season (November to March) at the northern (a) and southern (b) regions. Error bars indicate 95% confidence intervals.

Table 1. Comparison of the mean exposure (REI) between sea turtle nesting and randomly selected sites (control) for each region (north and south) and time period (nesting and non-nesting) using Student's *t*-tests

Time period	Region	Mean REI (nest sites/ control)	<i>t</i>	<i>n</i>	<i>P</i>
Nesting season	North	45.76/35.29	3.564	143	<b>&lt;0.001</b>
(November–March)	South	93.84/57.7	8.752	257	<b>&lt;0.001</b>
Non-nesting season	North	56.34/44.49	2.86	143	<b>0.005</b>
(April–October)	South	77.56/48.89	9.024	257	<b>&lt;0.001</b>

*P* values in bold (*P* < 0.05) indicate significant differences between nesting and control sites.

differences between geographic regions; the northern region is less exposed during the nesting season and exposure declines throughout the nesting season to be lowest coinciding with the end of hatchling emergence. In the southern region the opposite occurs; higher exposure during the nesting season with significant monthly increases in exposure peaking in February and March. Interestingly the region of the GBR between Cooktown and Bowen shows no differences in exposure between seasons. Hence, although there is

significant geographic variation, exposure varies seasonally and will influence different species or populations differently.

When the REI values at nesting areas are compared among populations, three significantly different groups can be defined (Figure 6). First, the three species nesting in the northern area; hawksbill, flatback and northern-green turtles can be grouped together because they nest at sites with similar exposure conditions. However, it was not possible to include two important green turtle nesting sites in the study because of a lack of climatic data (Raine Island and Moulter Cay). This omission is noteworthy because both locations are on reef systems detached from the outer GBR and as such, similar to other outer-shelf GBR areas, it is expected that they would also have high exposure to incoming wind and waves. Extending the REI model to these sites would undoubtedly increase the exposure index for green turtles in the northern GBR. Second, the species nesting south of Cooktown are divided into two groups: (1) loggerhead, southern-green and leatherback turtles that nest at more exposed sites; and (2) the southern-flatback population, which nest in locations significantly less exposed than other species nesting in the south. While the timing of the breeding season is strongly linked to temperature, successful reproductive effort will

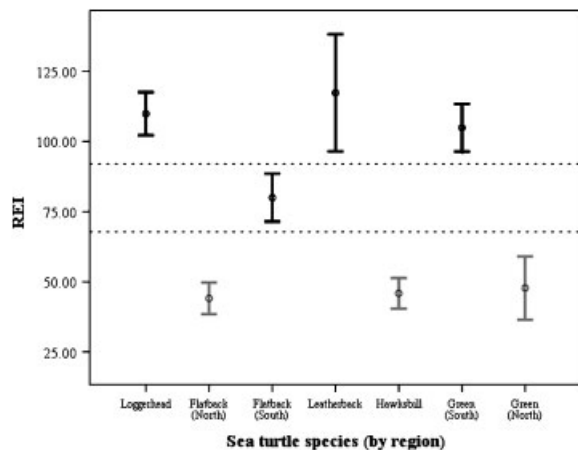


Figure 6. Relative Exposure Index comparison between the nesting sites of seven sea turtle populations classified by region (north and south). Northern populations are presented in grey, southern populations in black. Error bars indicate 95% confidence intervals. Dashed lines show three groups of statistically significant different REI (tested using Conover (1980) *post hoc* analysis).

require hatchlings to be able to emerge from beaches and swim through near-shore waters to reach goal environments or currents. Indeed the species classification resulting from comparing REI at nesting sites resembles that of species classified depending on their frenzy behaviour and duration.

The highest density of hawksbill nesting in the northern GBR and Torres Strait occurs during December–February (Dobbs *et al.*, 1999; Limpus, 2009b), with the peak of hatchlings emergence during March, which is estimated to be the month of lowest exposure to wind and waves in the area. As inferred from the results, hawksbill turtles prefer to nest on more protected coasts and their nesting season is reported to occur in months of higher rainfall (wet season) when wind velocity also drops (Horrocks and Vermeer, 1995). The characteristics of hawksbill hatchling frenzy and post-frenzy behaviour are known to differ from those reported for green, loggerhead and leatherback turtles (Chung *et al.*, 2009). Hawksbill hatchlings are less active on the first days of entering the water than other species. This behaviour could represent a different survival strategy since less active hatchlings may attract less attention of predators than active swimmers (Chung *et al.*, 2009), and may be an adaptation of hawksbill hatchlings to the low exposure described in their nesting areas.

The other species reported to nest at lower exposed sites throughout the study area is the flatback turtle (Figure 6). The flatback turtle is endemic to the continental shelf of northern Australia and is the only sea turtle species with such a restricted geographical distribution (Limpus, 2009a). It also appears to be unique among sea turtle species in not having a pelagic phase in its development and always remaining in neritic areas (Walker and Parmenter, 1990; Luschi *et al.*, 2003). Moreover, Walker and Parmenter (1990) state that flatback turtles, as species with non-pelagic offspring, produce fewer but larger hatchlings than other species, which protects them from small and medium predators and provides them with stronger swimming ability and larger energy reserves to oppose seaward currents and remain in their natal coastal area. The absence of oceanic dispersal and a strategy different from

other sea turtles could explain both the restricted geographical range of flatback turtles, and the distribution of their nesting sites in less exposed areas.

The distribution of sea turtle nesting sites has, to date, been studied at a very broad scale (worldwide location of sea turtle nesting habitats) or at a very narrow scale (distribution of nests within a beach). This study, however, analyses data at a scale large enough to allow for the analysis of the environmental factors associated with sea turtle nesting site distribution of various species, but with enough resolution to focus on particular regions or populations. Moreover, it is this scale that will be most relevant in the development of risk or vulnerability assessments to anthropogenic and climate change (Grech and Marsh, 2008; Grech *et al.*, 2008). Thus it will add to the toolbox of predictive models that can be used to aid management in light of climatic events and coastal development. Moreover, the REI model can be readily updated to observe changes in the exposure patterns through time, extended to other regions, or refined to focus on specific areas with higher resolution.

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