esa ECOSPHERE

Using habitat suitability models in an industrial setting: the case for internesting flatback turtles

Paul A. Whittock,[1,2,]† Kellie L. Pendoley,[1] and Mark Hamann[2]

[1]*Pendoley Environmental Pty Ltd, 12a Pitt Way, Booragoon, Western Australia 6154 Australia*
[2]*College of Science and Engineering, James Cook University, Townsville, Queensland 4811 Australia*

Citation: Whittock, P. A., K. L. Pendoley, and M. Hamann. 2016. Using habitat suitability models in an industrial setting: the case for internesting flatback turtles. Ecosphere 7(11):e01551. 10.1002/ecs2.1551

Abstract. To predict and manage ecological impacts of anthropogenic activities effectively, an understanding of at-risk species spatial ecology is first required. This is particularly difficult in the marine environment due to limited offshore access and wide-ranging movements of some species. Flatback turtles are a protected species potentially at risk from hazards associated with the resource sector in Australia, yet their at-sea spatial ecology is not well understood. We use habitat suitability modeling to identify environmental variables that influence flatback turtle internesting movement; identify areas of suitable internesting habitat; and determine overlap of identified internesting habitat with resource sector hazards. Internesting movements of 47 female flatback turtles, from five rookeries in the North West Shelf region of Western Australia, were recorded using platform terminal transmitters between 2006 and 2010. Environmental variables including sea surface temperature (SST), bathymetry, magnetic anomalies, distance from coastline, slope, and ruggedness index were combined with the tracking data from each rookery in an ecological niche model. We used the positions of resource sector vessels to represent areas of potential impact from resource sector hazards and identified overlap with suitable internesting habitat areas as a representative of the likelihood of impact. The primary environmental variables that influenced flatback internesting movement were bathymetry, distance from coastline, and SST. Suitable areas of internesting habitat were located in close proximity to many known flatback turtle rookeries across the region. Areas of suitable internesting habitat overlapped resource sector hazards in close proximity to four of the five rookeries and at other known flatback turtle rookeries. The cumulative overlap across the overall study area indicates a high potential for interaction with resource sector hazards, demonstrating the need for regional protection measures in these areas. This study provides a capability for regulators and developers to determine the potential offshore presence of internesting flatback turtles within the region, allowing for protection measures to be targeted appropriately as industrial development continues.

Key words: ecological niche modeling; flatback turtles; industry; internesting; spatial analysis.

Received 25 June 2016; accepted 5 July 2016. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** paul.whittock@penv.com.au

Introduction

Human population growth has increased demand for natural resources (UNEP 2012), resulting in expanding resource extraction across the globe and an increased pressure on natural environments (Bellamy et al. 2013). The predicted consequences of such resource extraction on threatened species, habitats and ecological function, as well as the effectiveness of proposed protection measures, are often uncertain (UNEP 2012). At a species level, the uncertainty largely stems from a poor understanding of the spatial ecology including their ecosystem role and habitat preferences (Franklin 1995, Bellamy et al. 2013). Moreover, understanding these gaps is challenging (Guisan and Thuiller 2005, Colwell and Rangel 2009) because (1) behavior and habitat use are underpinned by influencing environmental variables (Sobeŕon 2007), and (2) environmental variables may act independently of each other or in combination.

Statistical and mathematical modeling techniques have been increasingly used to improve our understanding of species' spatial ecology (Guisan and Thuiller 2005). One technique is the generation of habitat suitability models to predict species distribution based on species preferences for different habitats across a combination of environmental variables (Guisan and Zimmermann 2000). Species distribution data, required for the model, can be simple presence or presence–absence data based on random or non-random field sampling (Guisan and Thuiller 2005). For most species, information on absence is difficult to obtain due to logistical and budget constraints associated with field sampling across their range, with multiple samples required before a species can be classified as absent (Hirzel et al. 2002, Zaniewski et al. 2002, Ottaviani et al. 2004). Therefore, models that rely on presence data are more commonly used when determining habitat suitability for wide-ranging species (Phillips et al. 2006).

An ecological niche-based model (ENM) relies on presence data only (Hirzel et al. 2002, Phillips et al. 2006) and provides valuable information on habitat choice by quantifying the relationship between the presence data and environmental variables to generate habitat suitability predictions at unsampled locations throughout the study area (Guisan and Thuiller 2005). The model's output also includes a habitat suitability map detailing the predicted distribution of a species over an area based on the model's input, that is, environmental variables and presence data (Guisan and Zimmermann 2000). Consequently, an ENM can be a powerful tool in aiding the development of policy to mitigate impacts to species habitats and offer considerable scope for use along the coastal zone.

Ecological niche-based models have primarily been used for terrestrial species habitat modeling (Sattler et al. 2007, Basille et al. 2008, Falcucci et al. 2009), though more recently, they have also been applied to marine species (Pittman et al. 2007, Degraer et al. 2008, McKinney et al. 2012). Suitable habitat areas have also been overlapped with locations of anthropogenic hazards to determine the potential significance of the hazard, such as olive ridley turtle habitat overlap with fisheries (Pikesley et al. 2013) and whale shark habitat overlap with oil platforms and fisheries (McKinney et al. 2012). In general, the model outputs (i.e., habitat preferences and species distribution) have been used to identify areas where measures could be directed for further environmental protection of the species or aid in the prioritization of future research (Hirzel et al. 2004, Sattler et al. 2007, Gomes et al. 2009).

The North West Shelf (NWS) in Western Australia provides breeding and foraging habitat to globally significant marine turtle populations and has seen rapid industrial development related to the extraction, processing, and transport of natural resources. Absence of data relating to marine turtle spatial ecology, environmental drivers of change, and possible species level response to an impact (e.g., Grech et al. 2014, Whittock et al. 2014) presents a key knowledge gap for Government agencies and Industry proponents when minimizing impact. One species identified as having a high likelihood of a potential interaction with regional industry activities is the flatback turtle (*Natator depressus*; Whittock et al. 2014).

Although flatback turtles are protected under Australia's Environment Protection and Biodiversity Conservation (EPBC) Act (1999), there is little understanding of the flatback turtle's spatial ecology in the marine environment (Limpus 2007), particularly in the NWS region (Pendoley et al. 2014*a*). The need to develop a greater understanding of their spatial ecology in this region is particularly high as the resource sector presents multiple anthropogenic hazards to flatback turtles situated offshore during their nesting cycle and migration (Commonwealth of Australia 2003, Pendoley et al. 2014*a*, Whittock et al. 2014). Documented offshore hazards to marine turtles include the following: marine vessels (e.g., collision and disturbance; Dobbs 2001, Hazel et al. 2007, Meager and Limpus 2012, Chevron Australia 2013); oil spills (e.g., ingestion; Lutcavage et al. 1995); underwater blasting/seismic surveys/pile driving (e.g., noise and vibration; Keevin and Hempen 1997, McCauley et al. 2000); and dredging (e.g., entrainment and habitat burial; Dickerson et al. 1991). Mitigating or preventing these threats from impacting turtles during the breeding season is important; if female turtles are repeatedly disturbed, it can lead to reduced reproductive output (Hamann et al. 2002); and mortality of reproductively active female turtles could affect the survival of the entire species as they are considered to contribute disproportionately to sustaining the overall population compared to non-reproductively active turtles (Heppell et al. 1999, Gerber and Heppell 2004).

Protection of breeding turtles from disturbance requires knowledge of their habitat use and preferences. Like other marine turtle species, we expect that internesting flatback turtles will have specific habitat preferences, and small-scale variations in these will underpin variability in distribution over multiple seasons (e.g., Hays et al. 2000, Fossette et al. 2012). Quantifying habitat preferences and distribution of internesting flatback turtles on the NWS is therefore critical to providing a solid empirical foundation for development, implementation, and evaluation of protection measures in response to anthropogenic hazards.

The main aim of this study was therefore to improve understanding of flatback turtle spatial ecology within the NWS region in light of significant resource sector development. Specific objectives were to (1) identify the environmental variables that influence the spatial distribution and range of internesting flatback turtles on the NWS using ecological niche-based presence-only models; (2) produce a habitat suitability map that describes and represents the potential geographic distribution of internesting flatback turtles on the NWS; and (3) integrate resource sector activities to contextualize potential threat from industry hazards within the region.

Methodology

Study area

The NWS study area size is 48,526 km^2, extending offshore from North West Cape in the west to 50 km east of Port Hedland (latitude: −18.7° to −22.5°, longitude: 114.0–120.0°) and borders 1500 km of coastline within the Pilbara region of Western Australia (Fig. 1). The study area extent matched that of the NWS Joint Management Study used by The Commonwealth Scientific and Industrial Research Organisation (CSIRO) for regional planning and multiple-use management of the NWS marine ecosystems (CSIRO 2007). The NWS study area's offshore boundary extends to the 60-m bathymetric contour. The 60-m contour was selected to ensure all potential internesting flatback habitat within the region was included in the habitat analysis as this is deeper than internesting flatback turtles have been recorded diving to within Western Australia (Bare Sand Island = 44 m; Sperling 2007) and deeper than flatback turtles have previously been found to occur in other parts of Australia (40–45 m; Walker 1991, Poiner and Harris 1996, Robins and Mayer 1998).

The range of flatback turtle breeding within the NWS study area extends eastwards from Cape Range across the area to Port Hedland, with many offshore islands supporting suitable nesting habitat (Pendoley et al. 2016). The most significant rookeries within the area are found at Barrow Island, Mundabullangana, and collectively, the Mackerel Islands (includes Ashburton and Thevenard Islands) offshore from Onslow (Limpus 2007, Pendoley et al. 2014*b*, 2016). Smaller flatback turtle rookeries are found in Port Hedland; in the Lowendal Islands (including Varanus Island); at the Muiron Islands (Limpus 2007); and across the Dampier Archipelago (including Legendre and Delambre Islands; Prince et al. 2013).

The NWS study area is characterized by many natural features considered to be of high ecological value, including coastal and shallow water habitats such as mangrove forests, seagrass beds, coral reefs, and shelf habitats built around complex sponge communities (Condie and Andrewartha 2008). The area experiences an average of three to four cyclones a year that can cause massive destruction to coastal areas and seabed habitats, and contribute significantly to the region's natural interannual variability. The area is also affected by large-scale variations in ocean temperatures and salinity. These are influenced by the Indonesian throughflow (fluctuating flows in the Indonesian Archipelago between the Pacific and Indian Ocean) and by other regional currents (Condie and Andrewartha 2008).

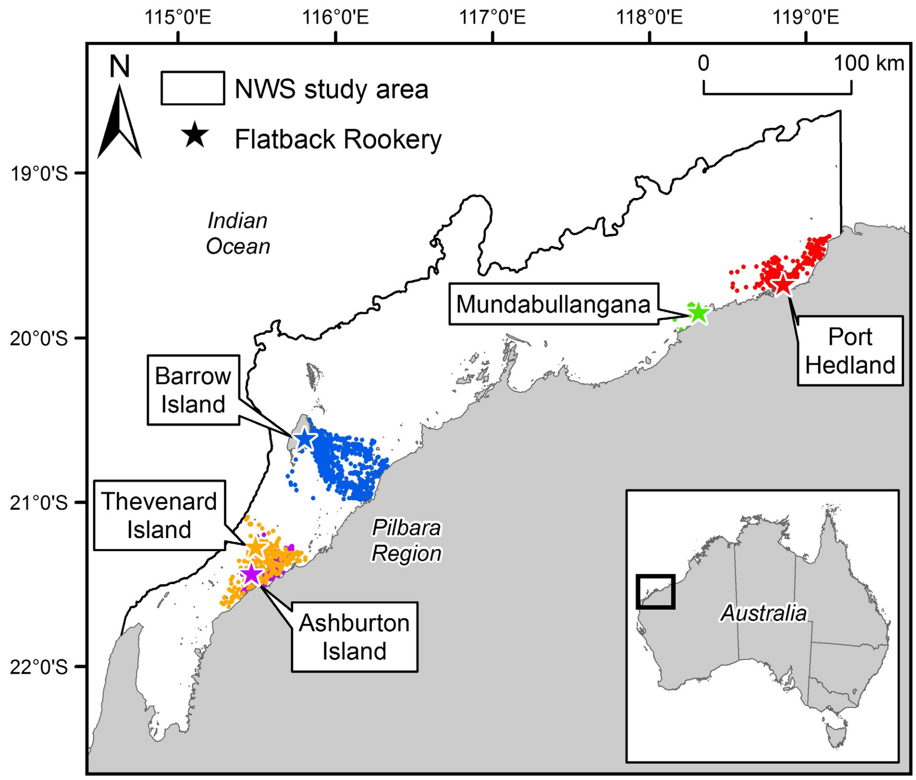

Fig. 1. Filtered internesting positions ($n = 5402$) from all rookeries ($n = 5$). Colored positions represent filtered internesting positions from each rookery.

Turtle tracking data set

The flatback turtle reproductive season in Western Australia extends from October through to February, with variations in peak nesting periods among rookeries (Pendoley et al. 2014*b*). Platform terminal transmitters (PTTs) were attached to 47 nesting female turtles during this period following clutch deposition at five rookeries located within the NWS study area, between 2006 and 2010: Barrow Island ($n = 26$), Thevenard Island ($n = 6$), Ashburton Island ($n = 4$), Mundabullangana ($n = 2$), and at Cemetery beach in Port Hedland ($n = 9$; Fig. 1). A summary of individuals tracked, their sizes, and tracking duration by deployment location is provided in Whittock et al. (2014). It was unknown whether the selected turtles were nesting for the first time in the season at the time of attachment; therefore, data used in this study may not represent the overall season's internesting distribution for each tracked turtle.

Four models of PTT were used: One model provided Argos only locations (Kiwisat 101, Sirtrack Ltd, $n = 2$) and three models provided Fastloc GPS locations (MK-10 AF, Wildlife Computers, $n = 4$; Fastloc GPS-Argos transmitters, Sirtrack Ltd, $n = 29$; Satellite Relayed Data Loggers, St Andrews Mammal Research Unit, $n = 12$). See Whittock et al. (2014) for PTT attachment technique and data recovery details, Argos and GPS location accuracy details and data filtering techniques. All tracking units were set up with a duty cycle of "on continuously," with a saltwater switch to restrict transmission attempts when the tracking unit was submerged.

To avoid pseudoreplication, we used filtered location data to calculate a median location for every six-hour period, from all location data received during this period (Schofield et al. 2010). Where locations were missing within the six-hour period, we interpolated these linearly to derive a location (Bailey et al. 2008).

The absolute end of internesting was indicated by the commencement of postnesting migration, which was deemed to have begun once movement away from the nesting beach was

Table 1. Summary of environmental variables considered for use in each ENM.

Environmental variable	Abbreviation	Unit	Source	Source resolution (km^2)
Bathymetry	Bath	m	GEBCO†	0.25
Distance from coastline	Dist	km	ArcGIS derived	1
Magnetic anomaly	MagA	nano Tesla (nT)	Geoscience Australia	0.08
Ruggedness Index	Rugg	m	ArcGIS derived‡	1
SST	SST	°C	GHRSST§	1
Slope	Slope	°	ArcGIS derived	1

Note: ENM, ecological niche-based model; GEBCO, General Bathymetric Chart of the Oceans; GHRSST, Group for High-Resolution Sea Surface Temperature project; SST, sea surface temperature.
† Bathymetry data obtained from the GEBCO (http://www.gebco.net/data_and_products/gridded_bathymetry_data/).
‡ Calculated by summarizing the change in elevation between adjacent neighboring cells (Riley et al. 1999).
§ GHRSST (http://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST.html).

directional and protracted (Zbinden et al. 2008). All data received following the commencement of postnesting migration were excluded from the analysis.

Objective 1: Environmental variables that influence distribution and range

Environmental variables considered for use in the model were derived from remotely sensed images and GIS analysis (Table 1, Fig. 2). An environmental variable was deemed suitable if it characterized the habitat suitability associated with the distribution of other internesting marine turtle species or if it had the potential to influence the distribution of internesting flatback turtles (as determined by published literature). This conservative selection approach was adopted due to the absence of primary literature relating specifically to the habitat suitability of internesting flatback turtles and follows the variable selection methods of other studies (e.g., McKinney et al. 2012).Environmental variables included the following: bathymetric depth data, obtained via the General Bathymetric Chart of the Oceans (GEBCO); a ruggedness index, based on the change in bathymetric depth between adjacent neighboring cells (Riley et al. 1999); and slope, calculated in ArcGIS using the bathymetric depth variable layer (Table 1, Fig. 2).

Monthly averaged sea surface temperature (SST) data were obtained from the Group for High-Resolution Sea Surface Temperature project (GHRSST; Table 1). The temporal extent of the tracking data set across each season was used to define the same temporal extent for the remotely sourced monthly SST data. The seasonal composites were averaged to provide one overall long-term SST environmental variable layer (range = 26.2–29.9°C), representative of the overall period for which satellite tracking occurred (Pikesley et al. 2013).

The minimum distance from the nearest coastline was calculated for each cell within the study area and used as an environmental variable layer (Fig. 2). The layer represented the distances travelled by internesting marine turtles away from the coastline before they returned to their nesting habitat on the coastline to lay subsequent clutches.

Magnetic anomaly data for the study area were obtained via Geoscience Australia and included as an environmental variable layer (Table 1, Fig. 2). This layer was included in the ENM as the prominent positive magnetic anomalies up to 1400 nT within the NWS study area (Veevers et al. 1985) may have influenced the location of nesting sites within the region and associated nearshore areas. Several marine turtle species are known to have the biological equivalent of a magnetic compass (Lohmann 1991, Lohmann and Lohmann 1993) and may use geographic variations in the Earth's magnetic field to determine their position and return to their nesting site (Wiltschko and Wiltschko 1995, Johnsen and Lohmann 2005).

Flatback turtles are considered to be capital breeders (Hamann et al. 2002) and thus are unlikely to be influenced by prey availability during their internesting period. Therefore, no environmental variables were included as a proxy for food availability, that is, chlorophyll, benthic habitat.

All spatial data (turtle tracking data set and environmental variables) were prepared and

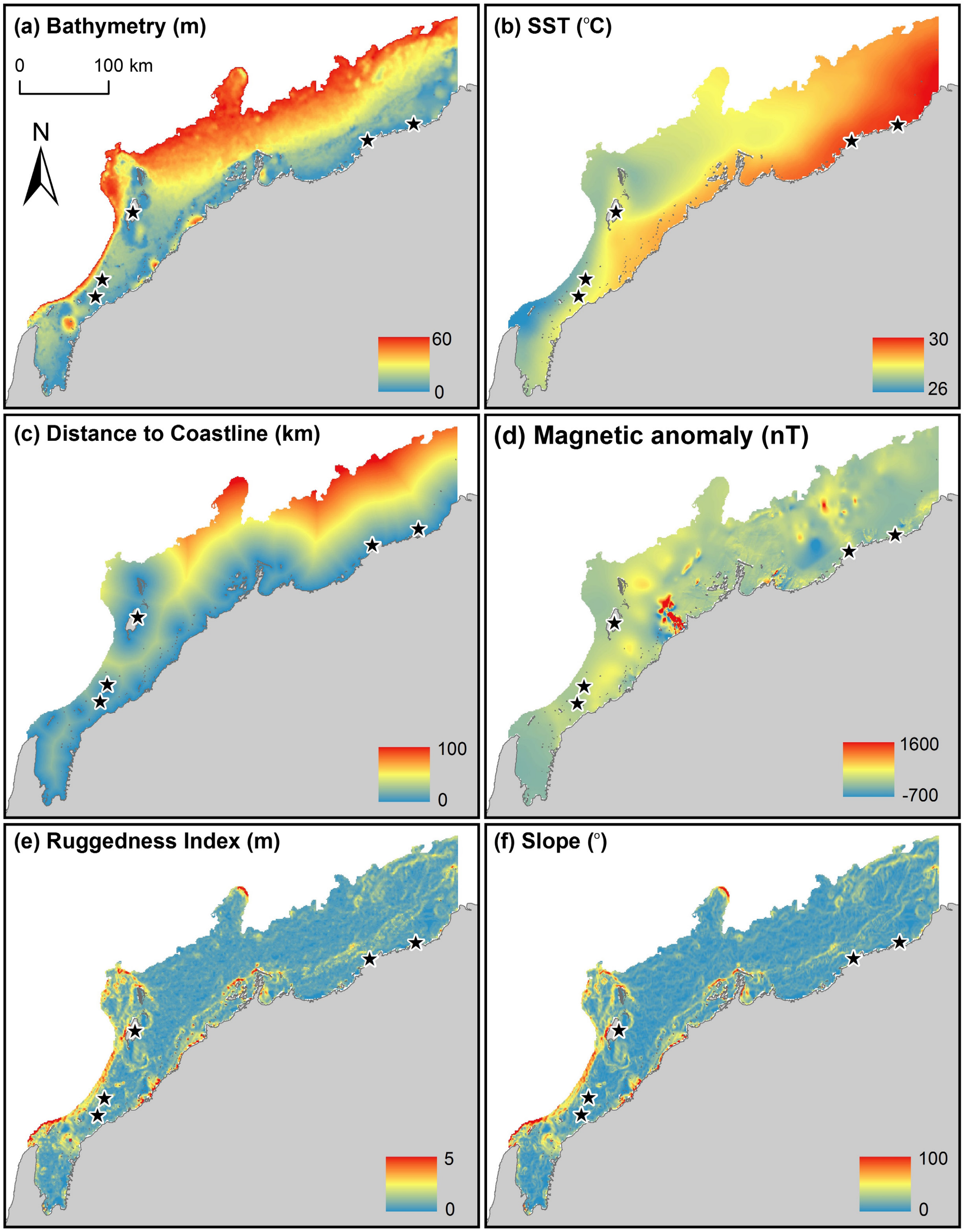

Fig. 2. Maps of environmental variable layers ($n = 6$) considered for use within ecological niche-based model. Black stars indicate location of each rookery.

analyzed using a combination of ArcGIS 10.1 (Environmental Systems Research Institute; Redlands, California, USA), IDRISI (Clark Labs at University of Clark), Quantum GIS (open source; www.qgis.org), and the Raster package for R (R Development Core Team 2013; Hijmans and Van Etten 2014). The working cell size was determined using the most common resolution of available spatial data (1 km^2; Table 1). All spatial data were resampled to the same 1 km × 1 km cell size (using bilinear interpolation), spatial extent, number of 1 km^2 cells, and geographic datum. The resulting data surfaces provided consistent environmental variable layers for the NWS study area.

To test for correlation within the environmental variable layers, a random sample of locations ($n = 1000$) was generated and coincident environmental variable data extracted for each location. A Spearman's rank correlation test was calculated for each paired variable, with any highly correlated variables ($P > 0.7$) removed from the data set. This ensured that only independent environmental variables were used in the final models and reduced the likelihood of the model over-fitting (Hirzel et al. 2002, Galparsoro et al. 2009).

Objective 2: North West shelf habitat suitability modeling

Habitat suitability modeling followed Pikesley et al. (2013) and was conducted using an ensemble ecological niche modeling approach (Araujo and New 2007, Rangel and Loyola 2012). Modeling was conducted using the biomod2 package in R (Thuiller et al. 2013). Three types of ENM were generated for each rookery: generalized additive model (GAM), multivariate adaptive regression splines (MARS), and MaxEnt modeling algorithms (Phillips et al. 2004).

The model's response variable was binary, either "presence" described by the turtle tracking data set or, due to the lack of accurate absence data, randomly generated "pseudoabsences"; these background absence data characterize the "available" environmental variables within the NWS study area. A 1:1 ratio of pseudoabsences to presence locations is commonly agreed as best in model building (Zuur et al. 2009), and therefore, the number of pseudoabsences used in the models matched the number of presence locations included in the tracking data set. All models were run using 10-fold cross-validation with a 75:25% random spilt of the location data for calibration and model performance testing, respectively.

The performance of each model was evaluated using five metrics: (1) area under curve (AUC; a measure of the ratio of true positives out of the positives vs. the ratio of false positives out of the negatives); (2) Cohen's kappa (Heidke skill score; KAPPA); (3) true skill statistic (TSS; a measure of accuracy relative to that of random chance); (4) success ratio (SR; the fraction of the true positives that were correct); and (5) accuracy (the fraction of the predictions (true and false) that were correct [Thuiller et al. 2009, 2013]). All evaluation metrics were scaled to the range 0–1 to enable the evaluation of model uncertainties within and between models.

If all models performed with similar accuracy, the ENMs were combined to form an ensemble projection using an unweighted average across models. This ensemble ENM described the relative suitability of habitat for internesting flatback turtles within the NWS study area, scaled between 0 and 1, where 0.5 represents areas of typical habitat suitability, 0 represents lowest suitability, and 1 indicates greatest suitability.

Tracking effort in this study was not spatially uniform across the NWS study area, and the proportion of tracking effort compared to the estimated number of females nesting at each rookery was not consistent (Spearman's rank correlation, $\rho = 0.783$). This inconsistency in tracking effort is a recognized limitation involved with conducting habitat modeling using satellite telemetry data across a large geographic area (Aarts et al. 2008). Pooling the telemetry data from all individuals across the NWS study area would therefore bias the results toward data-rich regions of geographic space that have been sampled more intensely, that is, Barrow Island (Aarts et al. 2008). To overcome this bias, the modeling technique was repeated to produce individual ensemble ENMs for each rookery using only presence locations for that specific rookery and the environmental variable layers for the entire study area. The individual ensemble ENMs were combined, and the maximum habitat suitability score for each cell across all five combined ensemble ENMs retained to determine the habitat suitability for the NWS study area in an overall single ensemble ENM.

The relative importance of each environmental variable, for each rookery, to the model was calculated using a randomization process (Thuiller et al. 2009). This process calculated the correlation between a prediction using all environmental variables and a prediction where the independent variable being assessed was randomly re-ordered. If the correlation was high, the variable in question was considered unimportant for the model and conversely, if low, important. A mean correlation coefficient for each environmental variable was then calculated over multiple runs. This was repeated for each environmental variable. The calculation of the relative importance of each environmental variable was made by subtracting these mean correlation coefficients from 1.

Objective 3: Resource sector activities hazard analysis

The spatial risk to suitable internesting flatback habitat (defined as areas with a habitat suitability score >0.5 probability) from resource sector activities in the NWS study area was estimated following methods outlined in Sutur (1993). The method involved the following: (1) identifying the hazards; (2) quantifying the exposure of internesting habitat to the hazards; and (3) estimating the risk to internesting habitat areas.

Hazard identification

In general, documented hazards to individual marine turtles and their habitat from resource sector activities involve the use of vessels. We therefore used the location of vessels directly involved in resource sector activities to represent the location of resource sector hazards within the NWS study area.

Vessel position data during the period of flatback turtle satellite tracking (2006–2010) were not available. As an alternative, vessel position data for the July 2012–January 2014 period, available from the Australian Maritime Safety Authority (AMSA), were used. The position data were collected from a variety of sources, including the terrestrial and satellite shipborne automatic identification system (AIS). Position data provided details of the type of vessel, vessel speed at the time the position was recorded, and actual time the position was recorded. Vessel types considered to be involved in resource sector activities included the following: cargo ships (60.5% of positions); tug vessels (26.9%); tankers (10.1%); dredge vessels (1.7%); and fishing vessels (0.8%). The provided data had been filtered to only include hourly positions for each vessel, with the first position recorded each hour retained.

Quantifying hazard exposure

Quantitative information and empirical data on the relative impact of the hazards associated with each resource sector vessel type to internesting flatback turtles on the NWS are not available. In the absence of this information, we used available published literature in combination with the results of a regional hazard assessment for marine turtles (Wallace et al. 2011) to quantify the relative impact factor of each hazard presented by vessel activities within the NWS study area. The use of a relative impact factor ensured a higher weighting to those vessel types involved in resource sector activities that presented a greater hazard to internesting flatback turtles and their habitats compared to other vessels.

The regional hazard assessment established scores for hazards on a 1 (low) to 3 (high) scale for flatback turtles within the South East Indian Ocean Regional Management Unit (RMU), which included the NWS study area (Wallace et al. 2010). Assessed hazards relevant to this study included fisheries and coastal development (including construction and dredging) activities. The relative impact factor for each hazard was based on the regional hazard assessment and published literature (Table 2).

The monthly vessel position data sets were combined and converted to a hazard layer with the same spatial extent and cell size (1 km^2) as the environmental variable layers. Cells which averaged <1 vessel position per month were removed from the layer to ensure that only cells with regular vessel use were included. The value of each cell in the hazard layer was derived by the sum of the impact factor of positions situated within the cell.

The hazard layer cells were reclassified as low cumulative impact (<33rd percentile of all hazard layer values), medium cumulative impact (≥33rd to ≤67th percentile), and high cumulative impact (>67th percentile).

The spatial risk of internesting flatback turtles and their available suitable habitats to cumulative resource sector hazards was evaluated by comparing the overlap of the cumulative impact

Table 2. Impact factor classification for different vessel types related to the resource sector (based on Wallace et al. 2011).

Vessel type	Regional hazard classification	Impact factor	Justification	Justification references
Fishing vessel	Medium	2	Entanglement in fishing gear or incidental capture remains a hazard to marine turtles in Australian waters despite implementation of turtle excluder devices (TEDs)	Meager and Limpus (2012) and Woodhams et al. (2012)
Dredge vessel	High	3	Dredging can cause direct habitat destruction via excavation of the seabed, or burial of habitat from dredge spoil disposal, and presents a hazard of entrainment and disturbance to internesting turtles	Dickerson et al. (2004)
Transport vessels, that is, tankers, cargo ships, and tug vessels, traveling <4 km/h	Low	1	Turtles were less vulnerable to collision with vessels traveling <4 km/h	Hazel et al. (2007)
Transport vessels, that is, tankers, cargo ships, and tug vessels, traveling >4 km/h	Medium	2	Turtles failed to completely avoid vessels traveling >4 km/h, leaving them vulnerable to collision	Hazel et al. (2007)

hazard layer with areas of typical suitable habitats identified within the ensemble ENM.

Results

Turtle tracking data set

Internesting flatback turtles ($n = 47$) recorded a total of 5402 filtered internesting positions over 1289 d of tracking time (2005/2006: 33 d, 2006/2007: 45 d, 2007/2008: 49 d, 2008/2009: 176 d, 2009/2010: 715 d, 2010/2011: 271 d; Fig. 1). All tracked flatback turtles remained within the boundaries of the NWS study area (see Whittock et al. 2014 for the specific movement patterns exhibited by individual turtles from each rookery except Ashburton Island).

Objective 1: Environmental variables that influence distribution and range

The environmental variables of slope and ruggedness index were highly correlated ($P = 0.93$, $P < 0.0001$; Fig. 2e, f). Slope was therefore excluded from any ENM analysis. All other variables were independent ($P < 0.7$) and included in the ENM.

Internesting flatback turtles from each rookery remained in water <44 m deep (Table 3), with the mean depth for all turtles at each rookery <10 m. The internesting locations from all five rookeries reached a maximum distance from the nearest coastline of 27.8 km, with the mean maximum distance away from the nearest coastline <6.1 km for each rookery. The mean magnetic anomaly values of internesting locations from each rookery were higher than background values, except at Port Hedland (Table 3). Internesting locations from rookeries located on the mainland (Mundabullangana and Port Hedland) recorded lower mean ruggedness index values than those rookeries located on offshore islands (Ashburton, Barrow, and Thevenard). Mean SST was coolest for the two most southerly situated rookeries in the study area (Ashburton Island: 27.9° ± 27.8°C; and Thevenard Island: 27.7° ± 27.8°C) and highest for the most northerly located rookery (Port Hedland; 29.6° ± 29.6°C). The values of environmental variable layers at the random background positions were significantly different when compared to the values of variable layers of each individual rookery ($P < 0.05$; Table 3).

Bathymetry was the most important contributory environmental variable at both Ashburton Island and Mundabullangana (Fig. 3; Appendix S1). SST was the most important contributory environmental variable at Mundabullangana and Port Hedland, with the variable also important at Ashburton and Thevenard Islands (Fig. 3; Appendix S1). Distance from the nearest

Table 3. Summary statistics of each environmental variable layer throughout the NWS study area (background), at all flatback turtle positions at each rookery for all years, and at areas identified as high habitat suitability for each rookery (defined as >0.9 probability).

	At flatback positions				At areas of high habitat suitability			
Rookery	Mean	SD	Range	*n*	Mean	SD	Range	*n*
Bathymetry (m)								
Background	27.9	17.4	0.0 to 61.0	1000	NA	NA	NA	NA
Ashburton Island	5.4	2.4	0.0 to 16.0	619	5.5	2.0	0.0 to 9.2	593
Barrow Island	8.6	3.2	0.0 to 25.6	3562	8.8	3.1	0.0 to 21.1	974
Mundabullangana	2.2	1.8	0.0 to 5.8	34	2.4	2.2	0.0 to 6.6	126
Port Hedland	4.0	3.7	0.0 to 16.2	645	6.1	3.3	0.0 to 14.0	404
Thevenard Island	9.9	4.6	0.0 to 44.0	542	7.1	4.6	0.0 to 16.0	313
Distance from Coastline (km)								
Background	29.3	24.1	0.0 to 97.2	1000	NA	NA	NA	NA
Ashburton Island	4.9	3.4	0.0 to 11.7	619	5.1	3.2	0.2 to 11.6	593
Barrow Island	6.1	5.8	0.0 to 27.8	3562	8.7	6.2	0.0 to 25.5	974
Mundabullangana	2.7	2.5	0.1 to 9.4	34	3.2	2.5	0.4 to 11.8	126
Port Hedland	4.5	4.4	0.2 to 21.6	645	4.9	2.9	0.0 to 14.4	404
Thevenard Island	4.4	3.7	0.0 to 23.1	542	2.8	1.7	0.0 to 6.8	313
Magnetic anomaly (nT)								
Background	23.3	166.3	−689.8 to 1587.8	1000	NA	NA	NA	NA
Ashburton Island	128.6	93.3	1.4 to 291.4	619	114.9	83.0	7.0 to 291.4	593
Barrow Island	42.1	100.1	−563.2 to 457.7	3562	42.0	163.0	−528.8 to 451.7	974
Mundabullangana	94.5	118.1	−183.5 to 277.7	34	−14.8	187.8	−242.5 to 654.7	126
Port Hedland	−3.5	125.6	−632.0 to 654.4	645	4.5	185.6	−689.8 to 654.4	404
Thevenard Island	171.3	69.6	−12.8 to 294.6	542	186.3	55.5	36.4 to 291.4	313
Ruggedness Index (m)								
Background	0.2	0.2	0.0 to 2.2	1000	NA	NA	NA	NA
Ashburton Island	0.1	0.1	0.0 to 0.7	619	0.1	0.1	0.0 to 0.7	593
Barrow Island	0.2	0.1	0.0 to 0.9	3562	0.2	0.1	0.0 to 0.7	974
Mundabullangana	0.1	0.1	0.0 to 0.3	34	0.2	0.1	0.0 to 0.6	126
Port Hedland	0.1	0.1	0.0 to 0.4	645	0.1	0.1	0.0 to 0.4	404
Thevenard Island	0.2	0.1	0.0 to 0.7	542	0.2	0.1	0.0 to 0.6	313
SST (°C)								
Background	28.1	0.8	26.2 to 29.9	1000	NA	NA	NA	NA
Ashburton Island	27.9	27.8	27.4 to 28.1	619	27.9	0.1	27.5 to 28.1	593
Barrow Island	28.0	28.2	27.6 to 28.7	3562	28.0	0.2	27.8 to 28.7	974
Mundabullangana	29.4	29.3	29.3 to 29.5	34	29.4	0.1	29.3 to 29.4	126
Port Hedland	29.6	29.6	29.3 to 29.8	645	29.6	0.1	29.5 to 29.8	404
Thevenard Island	27.7	27.8	26.9 to 28.3	542	27.7	0.2	27.0 to 28.2	313

Notes: NWS, North West Shelf.
Background values are represented by 1000 random positions within the NWS study area.

coastline was the most important contributory environmental variable at Barrow and Thevenard Islands. Distance from the nearest coastline was also considered important as a contributory variable at Ashburton Island, Mundabullangana, and Port Hedland. Ruggedness index was not considered to be an important environmental variable at any rookery (Fig. 3; Appendix S1).

Objective 2: North West shelf habitat suitability modeling

All models (GAM, MARS, and MaxEnt) performed better than random. The mean scores from all five evaluation metrics ranged from 0.90 to 0.98 (Appendix S2), indicating that the models had a substantial agreement with the testing data set. Evaluation scores demonstrated

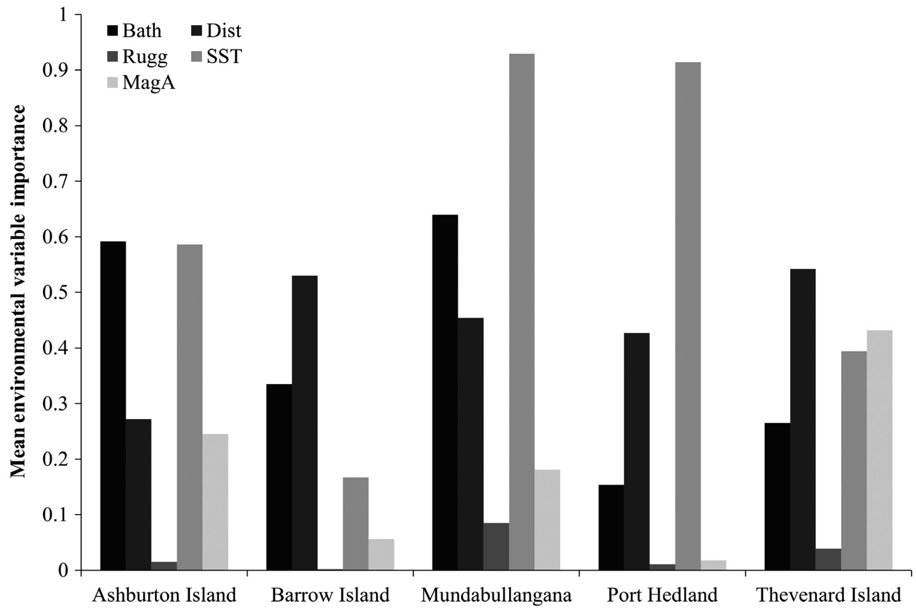

Fig. 3. Mean environmental variable importance calculated from the ensemble ecological niche-based model for each flatback turtle rookery.

that no one model outperformed the others (Appendix S2).

Typical suitable habitat (defined as areas >0.5 probability) was identified in close proximity to all five rookeries (Fig. 4). Typical suitable habitat was also identified across the Dampier Archipelago, including Delambre and Legendre Islands, and surrounding other islands within the Lowendal island group, including Varanus Island. Overall, 5847 km^2 (12.0% of total study area) was identified as typical habitat suitability (>0.5 probability) and 1049 km^2 (2.1% of total study area) as high habitat suitability (>0.9 probability; Fig. 4).

Summary statistic values for each environmental variable that overlapped with areas of high habitat suitability are described in Table 3 for each rookery. Areas of high habitat suitability for Barrow Island turtles were deeper (8.8 ± 3.1 m) and further away (8.7 ± 6.2 km) from the nearest coastline compared to all other rookeries (bathymetry: range = 0–21.1 m; distance from coastline: range = 0.0–25.5 km). Bathymetry values in areas of high habitat suitability were deeper compared to bathymetry values in all areas where flatback data were recorded for each rookery, except at Thevenard Island (Table 3). Areas of high habitat suitability were also situated further from the nearest coastline compared to the areas where all flatback data were recorded for each rookery, except at Thevenard Island (Table 3). There was no suitable habitat within areas where bathymetry >25 m, >27 km from the nearest coastline, and SST <27.1°C (see areas of absence in Fig. 4).

The overall mean value of important contributory environmental variable layers that overlapped with areas of high habitat suitability across the overall NWS study area were as follows: bathymetry: 7.4 ± 3.1 m, range = 0.0 –16.5; distance from coastline: 4.3 ± 3.4 km, range = 0.0–19.3; and SST: 28.2° ± 0.6°C, range = 27.6–29.8.

Objective 3: Resource sector activities hazard analysis

Areas of high cumulative impact associated with offshore resource sector activities were identified in close proximity to major resource developments and ports across the study area, including Onslow (Chevron Australia Wheatstone LNG [Liquefied Natural Gas] development), Barrow Island (Chevron Australia Gorgon LNG development), Dampier Port (Dampier Port Authority), Cape Lambert (Rio Tinto port expansion), and Port Hedland (Port Hedland Port Authority; Fig. 5a). Other areas of high cumulative impact exist within designated shipping channels that

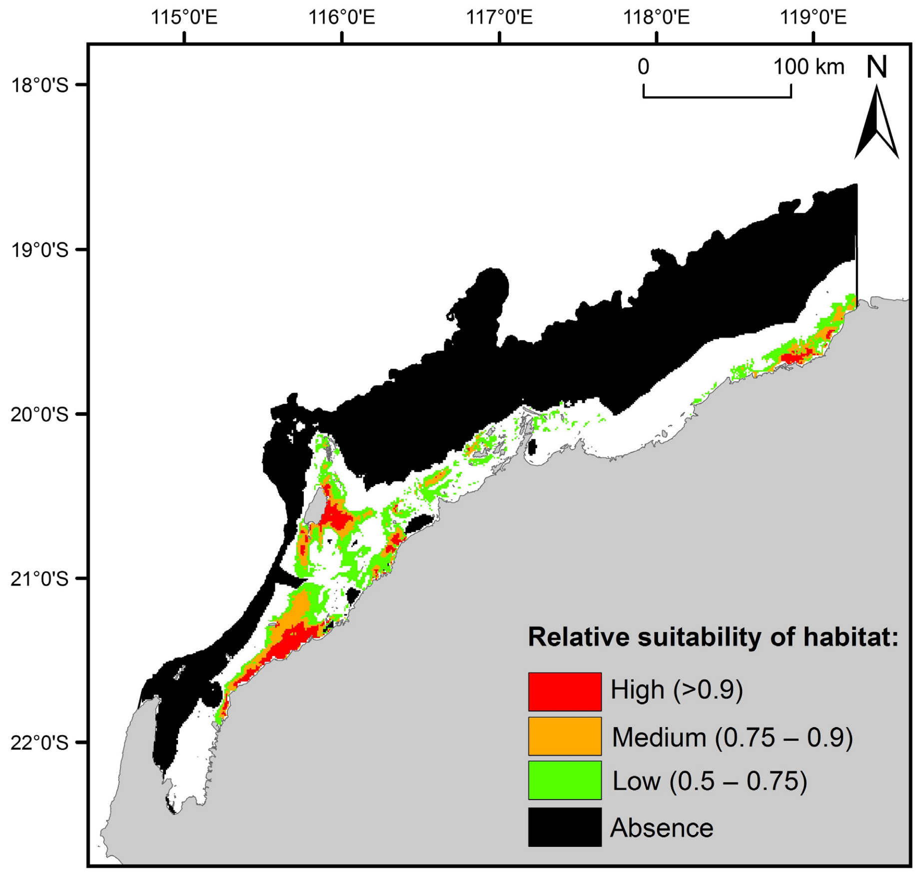

Fig. 4. Combined overall ensemble ecological niche-based model based on turtle tracking data set and environmental variables within the North West Shelf study area. Areas of absence are where environmental variable values are outside the range of environmental variable values that overlap areas of suitable habitat.

either extend beyond the NWS study area or provide connections between ports and resource developments within the NWS study area (notably between Dampier Port and Barrow Island).

Areas of high habitat suitability (Fig. 4) were found to overlap resource sector areas: 18% (546 km^2) overlapped resource sector areas with a high cumulative impact; 27% (808 km^2) overlapped areas with a medium and high cumulative impact; and 35% (1061 km^2) overlapped areas with a low, medium, and high cumulative impact. Areas of overlap existed in close proximity to all individual rookeries, with the exception of Mundabullangana (Fig. 5b). Overlap between areas of high cumulative impact from resource sector activities and high habitat suitability was also present in the Dampier Archipelago area and at Cape Lambert (Fig. 5b).

Discussion

This is the first study to use ENMs to spatially quantify the areas of habitat suitability for internesting marine turtles of any species, and to identify environmental variables that potentially influence their distribution across multiple rookeries within the same RMU.

We identified areas of suitable internesting habitat for five flatback turtle rookeries in the NWS region of Western Australia, representing all significant rookeries for this management unit of turtles. Suitable nesting habitat was in areas with a SST ranging between 27.0° and 29.9°C, within water depths ranging from 0 to 16.5 m and remaining in close proximity to areas of coastline (typically between 5 and 10 km). SST, bathymetry, and distance from coastline were the most

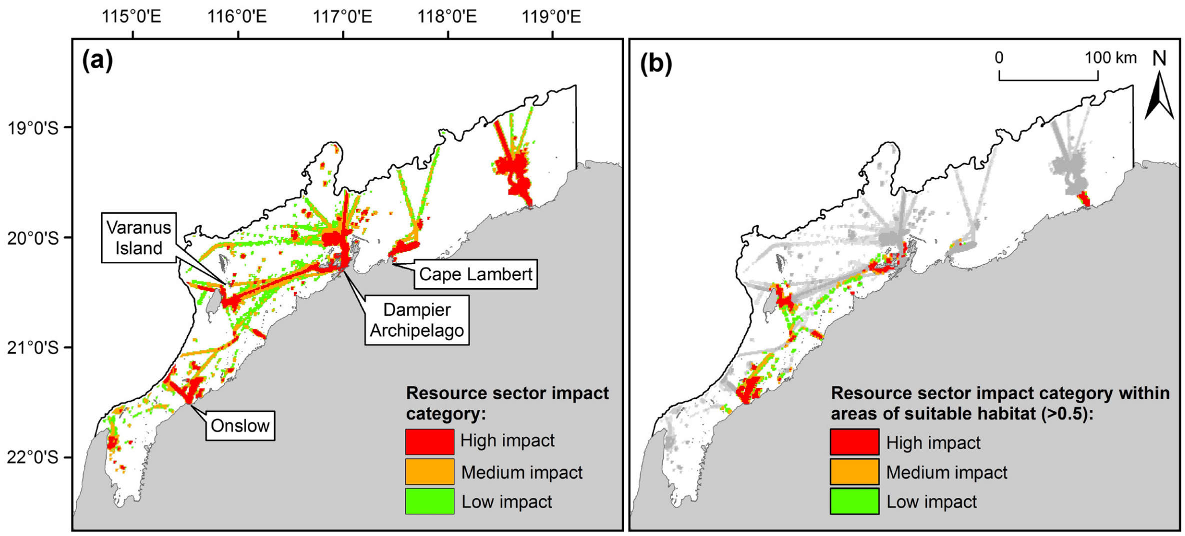

Fig. 5. (a) Resource sector cumulative impact categories across the North West Shelf study area. (b) Resource sector impact categories that overlap areas of typical habitat suitability (>0.5).

important contributory environmental variables to the models at four of the five rookeries. The ruggedness index variable layer was not considered an important contributory variables for any of the five rookeries and the magnetic anomaly variable layer only considered important at one rookery (Thevenard Island). Our models also allowed identification of areas where suitable internesting habitat may be absent within the study area (Fig. 4): no areas of high suitable habitat occurred in water deeper than 25 m, >27 km from the nearest coastline, and in water temperatures <27.0° and >29.8°C. This information is particularly useful for informing State/Federal regulators and developers charged with managing impacts to internesting flatback turtles. For example, it could inform spatial- or temporal-based closures to areas within the footprint of development or be used to guide the referral/screening process as their presence within a development footprint will trigger the referral of the project to the Australian Government's Department of Environment for approval and possibly an Environmental Impact Assessment (EIA).

Internesting flatback turtles have a high fidelity to their preferred nesting site, and as capital breeders, the distance they travel between their nesting area and internesting site has consequences for energy balance (Pendoley et al. 2014*b*, Whittock et al. 2014). Therefore, availability of an offshore internesting area is dictated by the location of the terrestrial nesting area. This spatial limitation supports the methods used in this study to prepare ENM for each individual rookery and combine into an overall ENM across the study area, as the suitable areas of internesting habitat should be unique for each rookery based on habitat availability in proximity to the nesting site.

The contribution of SST to suitable internesting habitat areas indicates that internesting flatback turtles are seeking and using areas with water temperatures that are higher than in surrounding areas. This thermoregulation behavior could be related to egg development (see Schofield et al. 2009, Fossette et al. 2012 for other species of marine turtle), with warmer water and body temperatures ultimately speeding up egg development rates prior to oviposition (Sato et al. 1998). As such, exposure of females to warmer temperatures across a nesting season may optimize the overall length of time required to lay the full complement of clutches (Hays et al. 2002), resulting in efficient energy expenditure across a nesting season.

Areas of high internesting habitat suitability were situated in deeper areas compared to the internesting positions at all rookeries, except at Thevenard Island. Deeper areas may be suitable for internesting for the following reasons: Deep areas may provide more stable hydrodynamic conditions for resting allowing flatback turtles to conserve energy reserves; deep areas may allow flatback turtles to remain immobile on the seabed for longer periods minimizing the energy cost of commuting to the surface (Hays et al. 2000, Minamikawa et al. 2000, Houghton et al. 2002); or deep areas may be optimum for flatback turtles to maximize their oxygen store while still attaining near-neutral buoyancy on the seabed (Hays et al. 2000). It is recommended that dive behavior of flatback turtles on the NWS is investigated to determine the actual activity of these turtles when internesting in these suitable deeper areas.

The identification of suitable internesting habitat across the entire study area provides an indication of the regional presence of internesting flatback turtles. Known flatback turtle rookeries situated within the NWS study area which were not featured in this study include Varanus Island within the Lowendal's, and Delambre and Legendre Islands within the Dampier Archipelago. The overall ENM included the presence of suitable internesting habitat in proximity to these three islands (Fig. 4) providing support for the model's output, as it would be more likely for areas of suitable habitat to exist in close proximity to these rookeries (as identified for other flatback turtle rookeries [Whittock et al. 2014]).

Our use of vessel positions to identify anthropogenic hazards associated with the natural resource sector within the NWS study allowed us to identify areas of high cumulative risk and areas in proximity to known operational, and currently under construction, major resource developments (Fig. 5a). One identified hazard not represented by a vessel's position is an oil spill from an offshore installation such as a platform or drilling rig. The NWS study area is host to a number of installations; however, they were not considered as part of the hazard analysis because of the following reasons: (1) A review of oil spill incidents on the NWS showed low historical incidence from offshore installations (Swan et al. 1994); (2) Kagi (1983) determined that oil produced from the NWS is generally light in nature and that if an incident did occur and oil was released, the oil would likely dissipate rapidly; and (3) studies suggested that the highest risk of an oil spill occurring on the NWS is from shipping activity resulting in the release of the heavier and more persistent bunker oil (Flood 1992, May 1992). Vessel positions were therefore considered appropriate to represent the location of an oil spill that would be of greatest hazard to internesting flatback turtles.

We found that 35% of areas with a high suitable internesting habitat overlapped spatially with cumulative resource sector impact areas. This indicates that there is potential for flatback turtles to interact with resource sector activities when internesting in parts of the study area. This is particularly notable in areas offshore from the Gorgon LNG development at Barrow Island and the existing port at Port Hedland, where areas of high cumulative impact overlap with suitable habitat areas.

Our results provide a platform for developers to assess the likelihood of interaction between future development activities and internesting flatback turtles situated in the NWS study area, and inform one of two components needed before the overall level of risk from an activity can be quantified in a developments EIA and environmental protection measures considered. The second component of the EIA process is to predict the consequence of the development activity on the species or their habitat. Predicting a likelihood of interaction alone is therefore of little use for quantifying the level of risk and supporting the need for environmental protection measures, as this needs to be combined with a confident prediction that the interaction will result in a consequence (Osenberg and Schmitt 1996). Increasing this confidence can be achieved by retrospectively comparing both the likelihood and consequence predictions featured in a developments EIA with the actual effect of the completed activity on the species/habitat. Until these comparisons are routinely completed, uncertainty surrounding the consequence of the predicted interactions, and an inability to anticipate future anthropogenic impact, will remain. It is therefore recommended that likelihood and consequence predictions that feature in EIAs and relate to the likelihood of an impact from offshore activities, that is, dredging, on internesting flatback turtles, are compared with the realized effect or impact following the completion of the activity, that is, marine turtle mortality records. Identifying the actual effect of a development's activity on internesting flatback turtles and how they react to the activity will also help to develop an understanding of how vulnerable flatback turtles are to specific activities, potentially allowing for further emphasis to be placed on the requirement for protection.

It is not often feasible for developers or regulators to consider the potential spatial extent of internesting flatback turtle movement from rookeries situated nearby to a development during the environmental approval process. This is primarily due to short timescales involved with development proposals, the high cost involved with identifying the spatial extent of internesting flatback turtles, and logistical constraints involved with accessing remote sites. One advantage of using ENMs in this study is that the full spatial extent of internesting movement from each rookery has been considered and all areas within the region have been assessed for their suitability as internesting habitat. The generated habitat suitability map also provides developers and regulators with a capability to identify areas in proximity to a proposed development that may or may not host internesting flatback turtles (Fig. 4). This is important as it addresses a recognized gap in providing effective protection from development activities within the NWS region as internesting flatback turtles can move up to 63 km away from their nesting site, often passing in close proximity to other developments that may not have considered their potential presence or protection (Whittock et al. 2014).

It is of concern that a number of flatback turtle rookeries within the NWS study area (and rookeries within the Dampier Archipelago) are exposed to resource sector hazards (this study and Whittock et al. 2014). Marine turtle species are considered particularly vulnerable when internesting, as areas of suitable habitat can host large aggregations of individual turtles within a relatively small area. Resource sector hazards that overlap with these habitat areas therefore have the potential to cause realistic effects on the overall population; particularly as reproductively active female turtles are considered to contribute disproportionately to sustaining the overall population compared to non-reproductively active turtles (Heppell et al. 1999, Gerber and Heppell 2004). Overlap of resource sector activities with other phases of the flatback life cycle may also occur, for example, during the phase of postnesting migration to their foraging grounds located in the Kimberley region further north from the study area (Pendoley et al. 2014*a*), providing further pressure on individuals and the overall population.

Conclusion

This study provides valuable information for managers, policymakers, and developers on the spatial distribution and habitat preferences of flatback turtles from multiple rookeries within the NWS region of Western Australia. An ecological niche-based modeling technique was used to determine areas of habitat suitability, along with the environmental variables that contributed to its suitability. Areas of high habitat suitability were integrated with resource sector hazards to identify the potential for interaction between flatback turtles and resource sector activities in the region. The development of a greater understanding of resource sector interaction, influential environmental variables, and typical properties of suitable internesting habitat should enable appropriate, effective, and targeted mitigation measures for future developments within the region.

Acknowledgments

Chevron Australia (D. Moro & R. Lagdon), BHP Billiton (S. Mavrick), and URS provided funding and logistical support for this project. Satellite attachment was conducted under the Department of Parks and Wildlife license numbers: SF005670, SF006705, SF006706, SF007088, SF007143, SF007144, SF007641, and SF007643. We thank C. Bell and R. Kamrowski for their comments on this manuscript. MH is funded by the Australian Governments NERP. This manuscript forms part of PAW's Ph.D. research at James Cook University.

Literature Cited

Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160.

Araujo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42–47.

Bailey, H., G. Shillinger, D. Palacios, S. Bograd, J. Spotila, F. Paladino, and B. Block. 2008. Identifying and comparing phases of movement by leatherback turtles using state-space models. Journal of Experimental Marine Biology and Ecology 356:128–135.

Basille, M., C. Calenge, E. Marboutin, R. Andersen, and J. M. Gaillard. 2008. Assessing habitat selection using multivariate statistics: some refinements of the ecological-niche factor analysis. Ecological Modelling 211:233–240.

Bellamy, C., C. Scott, and J. Altringham. 2013. Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. Journal of Applied Ecology 50:892–901.

Chevron Australia. 2013. Gorgon gas development and Jansz Feed gas pipeline: long-term marine turtle management plan. http://www.chevronaustralia.com/docs/default-source/default-document-library/gorgon_long-term_marine_turtle_management_plan.pdf?sfvrsn=0

Colwell, R. K., and T. F. Rangel. 2009. Hutchinson's duality: the once and future niche. Pages 19651–19658 *in* D. B. Wake, editor. Proceedings of the National Academy of Sciences, Irvine, California, December 12–13, 2008. American Society of Civil Engineers, Irvine, California, USA.

Commonwealth of Australia. 2003. Recovery plan for marine turtles in Australia. Marine Species Section, Approvals and Wildlife Division, Canberra, Australian Capital Territory, Australia.

Condie, S. A., and J. R. Andrewartha. 2008. Circulation and connectivity on the Australian North West Shelf. Continental Shelf Research 28:1724–1739.

CSIRO (The Commonwealth Scientific and Industrial Research Organisation). 2007. North West Shelf Joint Environmental Management Study Final Report. http://www.cmar.csiro.au/nwsjems/reports/NWSJEMS_final.pdf

Degraer, S., E. Verfaillie, W. Willems, E. Adriaens, M. Vincx, and V. Van Lancker. 2008. Habitat suitability modelling as a mapping tool for macro benthic communities: an example from the Belgian part of the North Sea. Continental Shelf Research 28:369–379.

Dickerson, D. D., J. I. Richardson, J. S. Ferris, A. L. Bass and M. Wolff. 1991. Entrainment of sea turtles by hopper dredges in cape canaveral and kings bay ship channels. Environmental effects of dredging. Vol D-91-1. U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi, USA.

Dickerson, D. D., M. S. Wolters MS, C. T. Theriot and C. Slay. 2004. Dredging impacts on sea turtles in the Southeastern USA: a historical review of protection. Proceedings of World Dredging Congress XVII, Dredging in a Sensitive Environment, September 27–October 1, 2004. Central Dredging Association, Delft, The Netherlands.

Dobbs, K. 2001. A compendium of information and basis for the development of policies and strategies for the conservation of marine turtles. Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia.

Falcucci, A., P. Ciucci, L. Maiorano, L. Gentile, and L. Boitani. 2009. Assessing habitat quality for conservation using an integrated occurrence-mortality model. Journal of Applied Ecology 46:600–609.

Flood, P. G. 1992. Management of oil drilling in Australian Waters. Marine Pollution Bulletin 25:143–146.

Fossette, S., G. Schofield, M. K. S. Lilley, A. Gleiss, and G. C. Hays. 2012. Acceleration data reveals the energy management strategy of a marine ectotherm during reproduction. Functional Ecology 26:324–333.

Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19:474–499.

Galparsoro, I., A. Borja, J. Bald, P. Liria, and G. Chust. 2009. Predicting suitable habitat for the European lobster (*Homarus gammarus*), on the Basque continental shelf (Bay of Biscay), using ecological-niche factor analysis. Ecological Modelling 220:556–567.

Gerber, L. R., and S. S. Heppell. 2004. The use of demographic sensitivity analysis in marine species conservation planning. Biological Conservation 120:121–128.

Gomes, L., C. Grilo, C. Silva, and A. Mira. 2009. Identification methods and deterministic factors of owl roadkill hotspot locations in Mediterranean landscapes. Ecological Research 24:355–370.

Grech, A., G. J. Parra, I. Beasley, J. Bradley, S. Johnson, S. Whiting and H. Marsh. 2014. Local assessments of marine mammals in cross-cultural environments. Biodiversity and Conservation 23: 3319–3338.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Hamann, M., T. S. Jessop, C. J. Limpus, and J. M. Whittier. 2002. Interactions among endocrinology, seasonal reproductive cycles and the nesting biology of the female green sea turtle. Marine Biology 140:823–830.

Hays, G. C., C. R. Adams, A. C. Broderick, B. J. Godley, D. J. Lucas, J. D. Metcalfe, and A. A. Prior. 2000. The diving behaviour of green turtles at Ascension Island. Animal Behaviour 59:577–586.

Hays, G. C., F. Glen, A. C. Broderick, B. J. Godley, and J. D. Metcalfe. 2002. Behavioral plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two Green Turtle (*Chelonia mydas*) populations. Marine Biology 141:985–990.

Hazel, J., I. R. Lawler, H. Marsh, and S. Robson. 2007. Vessel speed increases collision risk for the green turtle *Chelonia mydas*. Endangered Species Research 3:105–113.

Heppell, S. S., L. B. Crowder, and T. R. Menzel. 1999. Life table analysis of long-lived marine species with implications for conservation and management. Pages 137–146 *in* J. Musick, editor. Life in the slow lane: ecology and conservation of long-lived marine animals. American Fisheries Society, Bethesda, Maryland, USA.

Hijmans, R. J. and J. Van Etten. 2014. raster: package for reading, writing, and manipulating raster (grid) type geographic (spatial) data. http://cran.r-project.org/web/packages/raster/index.html

Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? Ecology 83:2027–2036.

Hirzel, A. H., B. Posse, P. A. Oggier, Y. Crettenand, C. Glenz, and R. Arlettaz. 2004. Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. Journal of Applied Ecology 41:1103–1116.

Houghton, J. D. R., A. C. Broderick, B. J. Godley, J. D. Metcalfe, and G. C. Hays. 2002. Diving behaviour during the inter-nesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. Marine Ecology Progress Series 227:63–70.

Johnsen, S., and K. J. Lohmann. 2005. The physics and neurobiology of magnetoreception. Nature Reviews Neuroscience 6:703–712.

Kagi, R. I. 1983. A Report of the Behaviour Prediction for Spills of Number 2 Fuel Oil (Gas Oil) and North Rankin Condensate in Mermaid Sound. Report for Woodside Report WENV 0039.

Keevin, T. M. and G. L. Hempen. 1997. The environmental effects of underwater explosions with methods to mitigate impacts. U.S. Army Corps of Engineers, St. Louis, Missouri, USA.

Limpus, C. J. 2007. A biological review of Australian marine turtle species 5 Flatback turtle, *Natator depressus* (Garman). Environmental Protection Agency, Brisbane, Queensland, Australia.

Lohmann, K. J. 1991. Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). Journal of Experimental Biology 155:37–49.

Lohmann, K. J., and C. M. F. Lohmann. 1993. A light-independent magnetic compass in the leatherback sea turtle. Biological Bulletin 185:149–151.

Lutcavage, M. E., P. L. Lutz, G. D. Bossart, and D. M. Hudson. 1995. Physiologic and clinicopathologic effects of crude oil on loggerhead sea turtles. Archives of Environmental Contamination and Toxicology 28:417–422.

May, R. F. 1992. Marine conservation reserves, petroleum exploration and development, and oil spills in coastal waters of Western Australia. Marine Pollution Bulletin 25:147–154.

McCauley, R. D., J. Fewtrell, A. J. Duncan, C. Jenner, M. N. Jenner, J. D. Penrose, R. I. T. Prince, A. Adhitya, J. Muchdoch and K. McCabe. 2000. Marine seismic surveys—a study of environmental implications. Australian Petroleum Production and Exploration Association Journal 2000:692–708.

McKinney, J., E. Hoffmayer, W. Wu, R. Fulford, and J. Hendon. 2012. Feeding habitat of the whale shark *Rhincodon typus* in the northern Gulf of Mexico determined using species distribution modelling. Marine Ecology Progress Series 458:199–211.

Meager, J. J. and C. J. Limpus. 2012. Marine wildlife stranding and mortality database annual report 2011. III. Marine turtle: conservation technical and data report. Department of Environment and Heritage Protection, Brisbane, Queensland, Australia.

Minamikawa, S., Y. Naito, K. Sato, Y. Matsuzawa, T. Bando, and W. Sakamoto. 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. Journal of Experimental Biology 203:2967–2975.

Osenberg, C. W., and R. J. Schmitt. 1996. Detecting ecological impacts caused by human activities. Pages 3–16 *in* R. J. Schmitt and C. W. Osenberg, editors. Detecting ecological impacts: concepts and applications in coastal habitats. Academic Press, San Diego, California, USA.

Ottaviani, D., G. J. Lasinio, and L. Boitani. 2004. Two statistical methods to validate habitat suitability models using presence-only data. Ecological Modelling 179:417–443.

Pendoley, K. L., C. D. Bell, R. McCracken, K. R. Ball, J. Sherborne, J. E. Oates, P. Becker, A. Vitenbergs, and P. A. Whittock. 2014*b*. Reproductive biology of the flatback turtle *Natator depressus* in Western Australia. Endangered Species Research 23: 115–123.

Pendoley, K., G. Schofield, P. A. Whittock, D. Ierodiaconou, and G. C. Hays. 2014*a*. Multi-species use of a coastal migratory corridor connecting marine protected areas. Marine Biology 161:1455–1466.

Pendoley, K. L., P. A. Whittock, A. Vitenbergs and C. D. Bell. 2016. Twenty years of turtle tracks: marine turtle nesting activity at remote locations in the Pilbara, Western Australia. Australian Journal of Zoology 64:217–226.

Phillips, S. J., M. Dudik and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Pages 655–662 *in* Proceedings of the 21st International Conference on Machine Learning, Banff, Alberta, 2004. Association for Computing Machinery, New York, New York, USA.

Phillips, R. A., J. R. D. Silk, J. P. Croxall, and V. Afanasyev. 2006. Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. Biological Conservation 129:336–347.

Pikesley, S. K., et al. 2013. On the front line: integrated habitat mapping for olive ridley sea turtles in the southeast Atlantic. Diversity and Distributions 19:1518–1530.

Pittman, S. J., J. D. Christensen, C. Caldow, C. Menza, and M. E. Monaco. 2007. Predictive mapping of fish species richness across shallow-water seascapes in the Caribbean. Ecological Modelling 204:9–21.

Poiner, I. R., and A. N. M. Harris. 1996. Incidental capture, direct mortality and delayed mortality of sea turtles in Australia's Northern Prawn Fishery. Marine Biology 125:813–825.

Prince, R. I. T., S. Whiting, H. Raudino, A. Vitenbergs and K. Pendoley. 2013. Proceedings of the First Western Australian Marine Turtle Symposium, Perth, Western Australia, Australia, August 28–29, 2012. Science Division, Department of Parks and Wildlife, Perth, Western Australia, Australia.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org.

Rangel, T. F., and R. D. Loyola. 2012. Labeling ecological niche models. Natureza & Conservacao 10: 119–126.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

Robins, J. B. and D. G. Mayer. 1998. Monitoring the impact of trawling on sea turtle populations of the Queensland East Coast. DPI Project Report Series Q098012. Fisheries Research and Development Corporation, Canberra, Australian Capital Territory, Australia.

Sato, K., Y. Matsuzawa, H. Tanaka, T. Bando, S. Minamikawa, W. Sakamoto, and Y. Naito. 1998. Internesting intervals of loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are effected by temperature. Canadian Journal of Zoology 76:1651–1662.

Sattler, T., F. Bontadina, A. H. Hirzel, and R. Arlettaz. 2007. Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. Journal of Applied Ecology 44:1188–1199.

Schofield, G., C. M. Bishop, K. A. Katselidis, P. Dimopoulos, J. D. Pantis, and G. C. Hays. 2009. Microhabitat selection by sea turtles in a dynamic thermal marine environment. Journal of Animal Ecology 78:14–21.

Schofield, G., V. J. Hobson, M. K. S. Lilley, K. A. Katselidis, C. M. Bishop, P. Brown, and G. C. Hays. 2010. Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. Biological Conservation 143:722–730.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10:1115–1123.

Sperling, J. B. 2007. The behaviour and physiology of the gravid flatback turtle. Dissertation. University of Queensland, Brisbane, Queensland, Australia.

Sutur, G. 1993. Ecological risk assessment. Lewis Publishers, Chelsea, Michigan, USA.

Swan, J. M., J. M. Neff, and P. C. Young. 1994. Environmental implications of offshore oil and gas development in Australia. First edition. Australian Petroleum Exploration Association, Sydney, New South Wales, Australia.

Thuiller, W., D. Georges and R. Engler. 2013. Biomod2: ensemble platform for species distribution modeling. http://cran.univ-lyon1.fr/web/packages/biomod2/biomod2.pdf

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araujo. 2009. BIOMOD—a platform for ensemble forecasting of species distributions. Ecography 32: 369–373.

UNEP (United Nations Environment Programme). 2012. The Fifth Global Environmental Outlook Report. http://www.unep.org/geo/pdfs/geo5/GEO5_report_full_en.pdf

Veevers, J. J., J. W. Tayton, and B. D. Johnson. 1985. Prominent magnetic anomaly along the continent-ocean boundary between the northwestern margin of Australia (Exmouth and Scott Plateaus) and the Argo Abyssal Plain. Earth and Planetary Science Letters 72:415–426.

Walker, T. A. 1991. Juvenile flatback turtles in proximity to coastal nesting Islands in the Great Barrier Reef province. Journal of Herpetology 25:246–248.

Wallace, B. P., A. D. DiMatteo, A. B. Bolten, M. Y. Chaloupka, B. J. Hutchinson, F. A. Abreu-Grobois, and R. B. Mast. 2011. Global conservation priorities for marine turtles. PLoS ONE 6:e24510.

Wallace, B. P., et al. 2010. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLoS ONE 5:e15465.

Whittock, P. A., K. Pendoley, and M. Hamann. 2014. Inter-nesting distribution of flatback turtles (*Natator depressus*) and industrial development in Western Australia. Endangered Species Research 26: 25–38.

Wiltschko, R., and W. Wiltschko. 1995. Magnetic orientation in animals. Springer-Verlag, Berlin, Germany.

Woodhams, J., S. Vieira and I. Stobutzki. 2012. Fishery status reports 2011: Status of fish stocks and fisheries managed by the Australian Government. Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra, Australian Capital Territory, Australia.

Zaniewski, A. E., A. Lehmann, and J. M. Overton. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. Ecological Modelling 157:261–280.

Zbinden, J. A., A. Aebischer, D. Margaritoulis, and R. Arlettaz. 2008. Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: Satellite tracking corroborates findings from potentially biased sources. Marine Biology 153:899–906.

Zuur, A. F., E. N. Leno, and C. S. Elphick. 2009. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1551/full