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Migration of green turtles (*Chelonia mydas*) from Australasian feeding grounds inferred from genetic analyses

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Abstract. Coastal seagrass habitats in tropical and subtropical regions support aggregations of resident green turtles (*Chelonia mydas*) from several genetically distinct breeding populations. Migration of individuals to their respective dispersed breeding sites provides a complex pattern of migratory connectivity among nesting and feeding habitats of this species. An understanding of this pattern is important in regions where the persistence of populations is under threat from anthropogenic impacts. The present study uses mitochondrial DNA and mixed-stock analyses to assess the connectivity among seven feeding grounds across the north Australian coast and adjacent areas and 17 genetically distinct breeding populations from the Indo-Pacific region. It was hypothesised that large and geographically proximate breeding populations would dominate at nearby feeding grounds. As expected, each sampled feeding area appears to support multiple breeding populations, with two aggregations dominated by a local breeding population. Geographic distance between breeding and feeding habitat strongly influenced whether a breeding population contributed to a feeding ground ($w_i = 0.654$); however, neither distance nor size of a breeding population was a good predictor of the extent of their contribution. The differential proportional contributions suggest the impact of anthropogenic mortality at feeding grounds should be assessed on a case-by-case basis.

Additional keywords: dispersal, Indo-Pacific, migratory connectivity, mixed-stock analysis, mtDNA.

Introduction

Long-distance migration is a characteristic trait of most large marine species (e.g. whales, white sharks and turtles). It is driven by ecological and biogeographic processes, such as the spatial and temporal distribution of resources (Boyd 2004) and habitat (Weng *et al.* 2007), seasonal variation in temperature and currents (Luschi *et al.* 2003), reproductive needs and differential survival across regions (Craig *et al.* 2003). The geographic extent and direction of oceanic migration within a species can vary among populations and among individuals within a population (Alerstam *et al.* 2003). The green turtle (*Chelonia mydas*) is a classic example of a migratory species. Migrations during early life-history phases can involve dispersal within an entire ocean gyre and adult breeding migrations between feeding and nesting habitat may encompass thousands of kilometres (Limpus *et al.* 1992). Some populations also have a developmental migration phase, in which immature turtles leave one feeding ground to migrate to another where they mature and remain as adults (Whiting and Miller 1998; Bjorndal *et al.* 2000). Despite a large number of studies, gaps remain in understanding the mechanisms behind selection and recruitment of individual turtles to a feeding ground. Knowledge of the connectivity between turtles in nesting and feeding habitats is required to allow quantification of the impact of threats (e.g. the geographic extent of anthropogenic mortality) with more precision, thereby enhancing the successful management of green turtles.

The green turtle is a large, long-lived, herbivorous reptile that grazes on seagrass and selected marine macroalgae in shallow tropical and temperate waters throughout the world (Bjorndal *et al.* 1997). Several studies have found that aggregations of turtles at a feeding ground are derived from several genetically distinct breeding populations (Lahanas *et al.* 1998; Bass and Witzell 2000; Luke *et al.* 2004). Each such foraging population can be referred to as a ‘mixed stock’. In addition, studies of adult

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females have shown that individuals faithfully migrate between their breeding areas and resident feeding areas (Limpus *et al.* 1992; Balazs 1994; Troëng *et al.* 2005). Knowledge concerning the contributions of breeding populations to feeding grounds in Australia and the region comes from tagging studies (Limpus and Reed 1985*a*; Limpus *et al.* 1992, 2005) and satellite telemetry of post-nesting females (Spring and Pike 1998; Kennett *et al.* 2004). These studies have confirmed the overlap of different breeding populations at feeding grounds in Australia and showed a large variation in the extent of dispersal of turtles from breeding grounds to feeding grounds (e.g. from <8 km to >2000 km, Limpus *et al.* 1992). However, interpretation of tag recoveries to determine the contribution of the respective breeding populations to any one feeding ground is difficult when there is uneven tagging effort at the breeding grounds and uneven capture effort at the feeding areas. In addition, such an imbalance in mark–recapture efforts complicates investigation of factors that influence the relative contributions. For example, contributions from populations nesting in close proximity to the feeding ground are generally expected to be higher than those from distant populations, and larger populations are expected to contribute more than smaller populations.

In Australasia, most green-turtle populations experience anthropogenic mortality on the feeding grounds to various degrees. The harvest of green turtles in northern Australia, Papua New Guinea (PNG) and eastern Indonesia is believed to represent the greatest threat to the green-turtle stocks in this region (Limpus and Chatto 2004). Commercial green-turtle harvests take large numbers of turtles at feeding grounds to be sold on regional markets in PNG (Limpus and Parmenter 1985), Indonesia (Dethmers 2000) and the Philippines (R. Cruz, pers. comm.). There are also non-commercial harvests of green turtles through much of Australasia, including harvest by local indigenous communities in Australia (Kowarsky 1982; Johannes and MacFarlane 1991), PNG, Indonesia (Suarez and Starbird 1996) and Melanesia (e.g. the Solomon Islands; Broderick 1997). In principle, an assessment of the genetic composition of turtle feeding populations can provide insights into the identity of genetically distinct populations affected and the extent to which each is affected by such harvests. Understanding the composition of feeding grounds in this region is made possible because of surveys of mitochondrial-DNA (mtDNA) variation that included 27 green-turtle rookeries within the Australasian region, and identified 17 genetically distinct breeding populations, including seven in Australia (Dethmers *et al.* 2006).

In the present study, we use mtDNA variation and mixed-stock analysis to examine the relative contributions of green-turtle breeding populations to assemblages at multiple feeding grounds across the northern Australian coast and adjacent areas. On the basis of the mark–recapture studies, we expect that haplotype diversity and frequencies at each of the feeding grounds result from the contributions from a combination of breeding populations. Using the relative stock contributions, we test the extent to which breeding population size or proximity to feeding grounds predicts population representation at feeding grounds in Australasia, to better understand the geographic extent of possible threatening processes affecting green-turtle populations in the region.

Methods and materials

Sampling

Seven green-turtle feeding grounds were selected across the northern region of Australia and south-eastern Indonesia to represent an east–west sampling transect (Fig. 1). Three of these feeding grounds are adjacent to significant nesting beaches of known genetic composition: Ashmore Reef (AR), Aru Islands (AI) and the Sir Edward Pellew Islands (SEP). Feeding grounds at Cobourg Peninsula (CP), Field Island (FI) and Cocos (Keeling) Islands (CK) are adjacent to beaches that have only sporadic nesting and are thus considered remote feeding grounds. Fog Bay (FB) is remote from green-turtle nesting beaches and supports only immature turtles; thus, it is considered a developmental feeding ground (Whiting and Guinea 1998). Turtles were captured with drift nets, barramundi gill-nets, by hand while walking on reef flats and by the rodeo method (Limpus and Reed 1985*b*). Once captured, turtles were tagged with a unique, numbered titanium tag to prevent double-sampling. Skin biopsies were taken from the dorsal surface of the shoulder and stored in a sodium chloride (NaCl)-saturated solution of 20% dimethylsulfoxide (DMSO). Curved carapace length (CCL) was measured along the midline from the junction of the skin and carapace at the neck to the posterior margin of the carapace. We used a CCL of 84.3 cm as a cut-off point to distinguish between adult and juvenile turtles, on the basis of the smallest turtle observed (Dethmers 2010) to be nesting on Aru. This is a conservative size limit for the present study; subadult green turtles of larger size classes have been observed in eastern Australia (e.g. Heron Reef; Limpus and Reed 1985*b*) and the average size observed in female green turtles preparing to breed for the first time at a feeding ground in eastern Australia (Shoalwater Bay) is 97.9 cm (minimum 87.8 cm CCL; Limpus *et al.* 2005).

Molecular methods

Methods for DNA extraction and genotyping followed those used in a regional study of breeding populations (Dethmers *et al.* 2006). DNA was extracted from small amounts of tissue using the 'salting out' procedure (Millar 1987) and resuspended and stored in a 1× TE buffer and 5% chelex solution. A 384-bp segment of the mtDNA control region was amplified using TCR5 (5′ TTGTACATCTACTTATTTACCAC) and TCR6 (5′ CAAGTAAAACTACCGTATGCC) primers (modified after Norman *et al.* (1994), with the latter primer containing a 41-bp GC clamp). Typically, 1–2 μL of template was used in 25-μL PCR reactions under standardised conditions of denaturing at 94°C for 10 s, annealing at one-cycle, 1°C touchdown temperatures from 59 to 56°C for 30 s and extension at 72°C for 40 s for 32 cycles. Haplotypes were identified using denaturing gradient gel electrophoresis (DGGE; Myers *et al.* 1987) as described in Dethmers *et al.* (2006). The sensitivity of the DGGE screening protocol was increased through in-group and out-group heteroduplex analysis and targeted sequencing, thus reducing the possibility of missing new haplotypes with denaturing profiles similar to those of the known haplotypes. Selected samples were sequenced in both directions on a CEQ2000 capillary sequencer (Beckman Coulter, Sydney, Australia) for haplotype confirmation with the use of M13-tailed TCR5 and TCR6 (without the GC-clamp) primers (Dethmers *et al.* 2006).

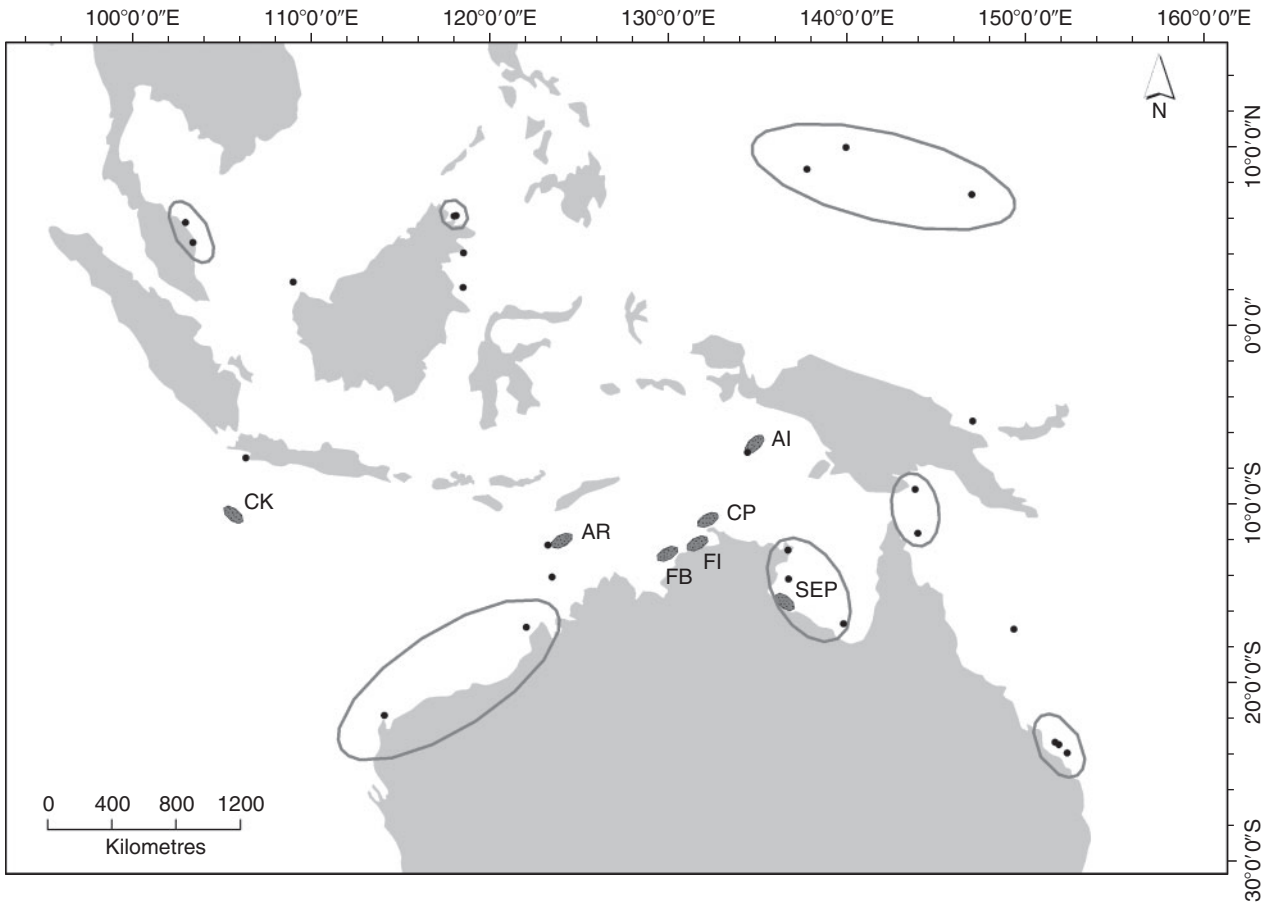

Fig 1. Location of samples from foraging grounds (larger filled-in circles) of green turtle (*Chelonia mydas*) aggregations in Australasia, relative to genetically distinct breeding populations (solid dots, adapted from Dethmers *et al.* (2006)). Feeding and nesting symbols for Ashmore and Aru overlap because these habitats are separated by less than 50 km. Foraging grounds are abbreviated as follows; CK, Cocos Keeling; AR, Ashmore Reef; FB, Fog Bay; FI, Field Island; CP, Cobourg Peninsula; AI, Aru Islands; and SEP, Sir Edward Pellew Islands. Several of the contributing stocks are abbreviated as follows: PNG, Papua New Guinea; nGBR, northern Great Barrier Reef; sGBR, southern Great Barrier Reef; GoC, Gulf of Carpentaria; and NW Shelf, North-west Shelf.

Statistical methods

Complementary reverse sequences were checked against forward sequences in Sequencher 4.1.4 (Gene Codes, Inc., Arundel, Queensland, Australia) and final sequences were aligned by using Clustal X (Thompson *et al.* 1997). These sequences were compared with those found among nesting populations in the Australasian region and if unique, compared against haplotypes provided in GenBank and at the Archie Carr Centre for Sea Turtle Research (http://accstr.ufl.edu/cmmtdna.html, verified 26 December 2009). Estimates of nucleotide (π) and haplotype (h) diversity, Exact tests of population differentiation (100 000 replicates; Raymond and Rousset 1995), pairwise F_{ST} tests, and AMOVA (10 000 replicates; Excoffier *et al.* 1992) were performed in Arlequin 3.01 (Schneider *et al.* 2000) and used to examine genetic structure across the feeding grounds. For estimates of sequence divergence, the Tamura and Nei (1993) model of nucleotide substitution was used.

Proportional contributions of each breeding stock to each of the feeding grounds were determined by using a computational Bayesian mixed-stock analysis (MSA) approach as developed by Pella and Masuda (2001). The Bayesian model gives the option to use prior information to distinguish more accurately among source populations. Therefore, we ran two models for each feeding ground; in the first, we used weighted priors using the relative size of each rookery to assign greater probability to larger rookeries, and in the second model we used uniform priors to give equal probability to all rookeries regardless of their size. The use of prior information can be particularly helpful when rookeries share common and widespread haplotypes and when there are large differences in the relative size of those rookeries (Bolker *et al.* 2007). We ran 17 chains for each of the contributing stocks and for each model and 50 000 Markov Chain Monte Carlo (MCMC) runs for every chain. Each chain was started with 95% contribution from one of the potential rookeries of origin and a burn-in of 25 000 runs was used to calculate the posterior distribution of all chains combined. To test whether all chains had convergence, we used the Gelman and Rubin shrink factor. Convergence was verified if the shrink factor was <1.2 for each chain (Pella and Masuda 2001). Confidence intervals for estimated contributions in each of the mixed stocks were kept at 95%. New haplotypes, not previously detected at the contributing stocks, were removed from these analyses.

As potential contributors, we used the 17 genetically distinct breeding populations or groups of populations (hereafter

referred to as stocks) in Australasia, with distribution and genotypic frequencies described in Dethmers *et al.* (2006). Although sampling of these stocks was designed to cover all of the known major and historically important rookeries ($n = 27$) throughout South-east Asia, Australia, the Western Pacific and Eastern Indian Oceans (see Dethmers *et al.* 2006), it is possible that some genetically unsampled, but regionally significant, rookeries exist. Therefore, the baseline dataset is potentially not complete and additional unstudied stocks might be represented in the mixtures.

We used the output from the model with uniform priors to test for the hypothesised influence of geographic distance and population size on the distribution of stocks across the feeding grounds. In multiple stepwise regression tests, with percentage contribution (transformed to $\sin^{-1}\sqrt{0.01^{*}p}$, where p is the percentage contribution) as the response variable and distance ($D_{\text{stock-FG}}$) and population size (N_{stock}) as the predicting factors, the assumption that the errors are normally distributed was not met. We instead used generalised linear models (GLMs) to provide an alternative approach in which the regression is not carried out on the response variable, y, but on a linearised version of the link function applied to y (Crawley 2002). The statistical evidence for correlations between the contribution and $D_{\text{stock-FG}}$ and N_{stock} were evaluated by an evidence-ratio approach using Akaike weights in Program R (version 2.6.0, R Development Core Team 2005). Binomial GLM models (equivalent to ANOVA and ANCOVA) with logit-link functions were used to determine the statistical relationship between contribution (breeding population present or absent) and (1) distance ($D_{\text{stock-FG}} = \approx$0–500, 500–2000, $\geq$2000 km), (2) population size ($N_{\text{stock}} = \approx$0–500, 500–5000, 5000–10 000, $\geq$10 000 individuals), as well as (3) size class of individuals in the feeding ground sample (N_{CCL}: all <84.3, majority <84.3, majority $\geq$84.3 cm). Shortest sea distances between nesting beaches of the contributing stocks and the feeding grounds were calculated by using the great-circle distance equation that incorporates the curvature of the earth and by estimating the shortest distance to rerouted migratory pathways around major landmasses. Population sizes were derived from the marine-turtle database maintained by C.J.L., and previously published in Dethmers *et al.* (2006).

To determine whether individuals with CCL < 84.3 cm ($\text{Ind}_{\text{small}}$) and those with CCL $\geq$ 84.3 cm ($\text{Ind}_{\text{large}}$) at a single feeding ground were recruiting from different stocks, pairwise Exact tests were repeated at three of the feeding grounds (CP, AI and SEP). These were selected because sample sizes in both size classes were sufficiently large (CP: $\text{Ind}_{\text{large}} = 57$, $\text{Ind}_{\text{small}} = 34$; AI: $\text{Ind}_{\text{large}} = 20$, $\text{Ind}_{\text{small}} = 20$; SEP: $\text{Ind}_{\text{large}} = 55$, $\text{Ind}_{\text{small}} = 47$) to allow for statistical inferences.

Results

Molecular diversity

The analyses across all feeding grounds revealed 30 distinct haplotypes (Table 1). Of these, 14 haplotypes were previously identified among the Australasian nesting populations (Dethmers *et al.* 2006) and they represented >95% of sampled individuals. The origin of the remaining 16 newly detected (novel) haplotypes (GenBank Accession Numbers EF156419–EF156434), comprising 22 individuals and 4.75% of all observations, is not known. These new haplotypes were most prevalent (up to 15%) at feeding grounds in the Northern Territory, and varied by one or two base pairs from the most similar haplotypes previously observed. All fell within the five clades identified in Dethmers *et al.* (2006). Comparison of haplotype frequencies at feeding grounds and regional stocks (Table 1) revealed that feeding grounds other than Aru (AI) were dominated by the C1 and C3 haplotypes, which are widely distributed across stocks from northern Australia, the Sunda Shelf and Indian Ocean, but are rare in Pacific Ocean stocks. Conversely, the haplotypes that dominate the eastern Australian rookeries (southern Great Barrier Reef (sGBR), northern GBR; Haplotypes A2, B1, B3) were rare in the sampled feeding grounds. Likewise, the C4, C5 and D2 variants that (along with C3) characterise the central Sunda Shelf (Peninsula Malaysia and Borneo) stocks were at low to moderate frequencies in the sampled feeding grounds. Overall haplotype diversity was 0.75 (Table 2) and it was relatively uniform across all feeding grounds, with lower values observed for SEP ($h = 0.64$), AR ($h = 0.61$) and particularly CK ($h = 0.45$). By comparison, overall haplotype diversity among the stocks was 0.88, with a wide variation, ranging from $h = 0.07$ to $h = 0.82$ (Dethmers *et al.* 2006). Nucleotide diversity among the feeding grounds was quite variable, ranging from 0.001 (CK) to 0.037 (AI) and an overall diversity of 0.013, which is considerably lower than the overall nucleotide diversity found among the stocks ($\pi = 0.041$).

Results of the AMOVA indicated significant partitioning of genetic variance among the feeding aggregations ($F_{\text{ST}} = 0.090$, $P < 0.001$), although the majority of the variation (91%) was explained by within-population variation. Exact tests for population differentiation based on haplotype frequencies (Table 3) indicated that the four feeding aggregations at CP, AI, SEP and CK had significantly different haplotype frequencies, whereas the AR, FB and FI feeding grounds were statistically homogeneous after sequential Bonferroni correction of α values. Analyses of adult (including residents and potential migrants) versus non-adult (resident) turtles at CP, AI and SEP did not reveal any significant shifts in the genetic compositions; Exact tests for size-class differentiation based on haplotype frequencies gave no significant results within each of the feeding grounds ($P = 0.92$, 0.84 and 0.83, respectively).

Stock representation at feeding grounds

Results of the mixed-stock analyses showed that the two models (using weighted and uniform priors) gave similar results (see Accessory Publication to this paper, available on the web). However, for feeding grounds dominated by the C1 and C3 haplotypes, a slightly higher contribution was estimated for larger rookeries when using priors based on rookery size. In addition, narrower confidence intervals (CIs) surrounded estimates when using weighted priors. In the following, we refer to results from the Bayesian model using weighted priors only. Overall, the results from the MSA showed that green-turtle aggregations at each of the feeding grounds were derived from multiple breeding stocks (Table 4). The origin of the stocks and the range of possible proportional contributions varied among the sites. Mixed-stock estimates at four of the feeding grounds

Table 1. Frequencies of green turtle (*Chelonia mydas*) mtDNA haplotypes at 17 Australasian management units (MUs; as described in Dethmers *et al.* 2006) and at seven foraging grounds across the northern Australian coastline and south-eastern Indonesia

MUs represent the contributing stocks to the foraging grounds. N_f is the estimated total number of breeding females (Dethmers *et al.* 2006) and is given for each contributing stock. Year is given for each foraging ground. The mean size range of foraging turtles is expressed as the curved carapace length (CCL). nGBR, northern Great Barrier Reef; sGBR, southern Great Barrier Reef

Parameter	N_f or year	*n*	CCL (cm)	Familiar haplotype																								Novel haplotype															
				A1	A2	A3	A4	A6	B1	B3	B4	B5	C1	C2	C3	C4	C5	C7	C8	C9	C12	C13	C14	D2	E1	J1	J2	A7	B6	B7	C15	C16	C17	C18	C19	C20	C21	C22	C23	C24	C25	D5	K1
Contributing stock																																											
nGBR	133 500	52		–	2	–	–	–	42	2	–	–	–	–	–	1	–	–	–	–	2	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coral Sea Platform	15 500	41		–	30	–	–	–	–	9	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
sGBR	36 500	102		–	94	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
New Caledonia	?	10		–	2	–	–	–	4	2	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Micronesia	7000	49		7	2	26	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Papua New Guinea	4500	18		–	–	16	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gulf of Carpentaria	36 500	132		–	–	1	–	–	–	–	–	–	65	–	45	–	–	–	20	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aru	5500	28		–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Berau Islands	39 000	29		–	–	–	–	1	–	–	–	–	–	–	7	–	9	–	–	–	–	–	5	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SE Sabah	1500	30		–	–	–	–	–	–	–	–	–	–	–	18	–	3	–	–	–	–	–	1	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sulu Sea	76 500	67		–	–	–	–	–	–	–	–	–	–	–	13	–	1	–	–	–	–	–	–	53	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sarawak	1500	22		–	–	–	–	–	–	–	–	2	–	–	2	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Peninsular Malaysia	2000	27		–	–	–	–	–	–	3	–	–	–	–	22	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ashmore Reef	3500	20		–	1	9	–	–	–	–	–	–	3	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scott Reef	1500	19		–	1	–	–	–	–	–	–	–	5	–	11	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
West Java	1500	23		–	–	–	–	–	–	–	–	–	–	–	17	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
North-west Shelf	690 000	45		–	1	–	–	–	–	–	1	–	36	1	3	–	–	–	–	2	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Foraging ground																																											
Cocos Keeling Islands	2004	36	63.2 (40–113.6)	–	–	–	–	–	–	–	–	–	10	–	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Ashmore Reef Feeding	1996	65	60.3 (38.7–96.6)	–	1	2	–	–	1	–	–	–	37	–	17	1	1	1	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
Fog Bay	1996	67	46.3 (33.7–78.2)	–	–	5	–	–	–	–	–	–	28	–	14	6	1	–	3	5	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	1	1	–	–	–
Field Island	2002	62	57.1 (39.5–92)	–	2	1	–	–	2	–	–	–	29	–	12	2	–	1	1	1	–	–	1	1	–	–	–	2	–	–	–	–	–	–	2	1	1	1	–	–	2	–	–
Cobourg Peninsula	2002	91	84.7 (66.6–103)	1	1	8	–	–	9	–	–	–	33	–	24	1	1	–	–	3	–	–	–	5	–	–	–	–	1	–	–	1	1	1	–	–	–	–	–	–	–	1	–
Aru Island Feeding	2000	40	82 (39.4–112.4)	–	–	9	–	–	4	–	–	–	3	–	2	–	1	–	–	–	–	–	19	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sir Edward Pellew Islands	2002	102	79.7 (38.7–133.5)	–	1	–	–	–	4	1	–	–	53	–	27	1	–	–	15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 2. Genetic diversity (± s.d.) within the foraging grounds
n, sample size; *h*, haplotype diversity; π, nucleotide diversity

Region	Foraging ground	*n*	*h*	π
Indian Ocean	Cocos Keeling	36	0.452 ± 0.070	0.001 ± 0.001
Timor Sea	Ashmore Reef	65	0.614 ± 0.054	0.012 ± 0.007
	Fog Bay	67	0.771 ± 0.040	0.016 ± 0.008
Arafura Sea	Cobourg Peninsula	91	0.785 ± 0.029	0.027 ± 0.014
	Field Island	62	0.747 ± 0.051	0.017 ± 0.009
	Aru Islands	40	0.722 ± 0.059	0.037 ± 0.019
Gulf of Carpentaria	Sir Edward Pellew Islands	102	0.643 ± 0.035	0.008 ± 0.005
Combined foraging grounds		463	0.749 ± 0.015	0.013 ± 0.007

Table 3. *P*-values of pairwise comparisons among foraging grounds, based on Exact tests of population differentiation derived from haplotype frequencies
Significant values ($P < 0.05$) are indicated with asterisks

Foraging ground	Cocos Keeling	Ashmore Reef	Fog Bay	Field Island	Cobourg Peninsula	Aru Islands	Sir Edward Pellew Islands
Cocos Keeling	–						
Ashmore Reef	0.0009*	–					
Fog Bay	0.0001*	0.0817	–				
Field Island	0.0008*	0.8127	0.0878	–			
Cobourg Peninsula	0.0029*	0.0431*	0.0012*	0.0218*	–		
Aru Islands	0.0000*	0.0000*	0.0000*	0.0000*	0.0000*	–	
Sir Edward Pellew Islands	0.0001*	0.0014*	0.0000*	0.0012*	0.0000*	0.0000*	–

(AR, FI, AI and SEP) revealed a dominance of a single stock, with a mean contribution of 50% or more. For AI and SEP, this involved the geographically most proximate breeding stock at Aru (mean = 63.2, 95% CI = 36.8–85.6) and the Gulf of Carpentaria (GoC; mean = 85.1, 95% CI = 64.9–95.7), respectively, both within a distance of 200 km. However, at the Ashmore Reef feeding ground, 75.4% (95% CI = 46.2–95.8) of the contributions were assigned to the North-west Shelf stock, 960 km from this feeding ground. Interestingly, the Ashmore Reef stock (at <50-km distance) had little representation at AR (mean = 1.2, 95% CI = 0.0–18.3). In contrast, 11.2% (95% CI = 0.0–43.2) of turtles at the Cobourg Peninsula feeding grounds were estimated to have originated from the Ashmore Reef stock, 950 km away. The SEP feeding ground had the lowest genetic diversity, with 85.1% of its population nesting within the Gulf of Carpentaria. FB, FI and CP supported the highest diversity of stocks, with five or more represented at each of the feeding grounds. These feeding grounds also had the highest proportion of novel haplotypes (4, 6 and 5, respectively).

The estimates for the CK feeding ground were surrounded by a larger CI and several chains had not converged after 50 000 runs (shrink factor >1.2). This feeding ground was dominated by the widespread and thus largely uninformative C1 and C3 haplotypes (Table 1), which, in combination with the CK's relatively small sample size, are likely to have contributed to the uncertainty. In addition, the East Indian Ocean contains many as-yet unsampled rookeries, which further erodes our confidence in the estimation of contributing stocks. For these reasons, we exclude the CK estimates from further analyses and discussion.

The most parsimonious model to explain the contribution of stocks to feeding grounds revealed contribution as a factor of distance ($D_{\text{stock-FG}}$; $w_i = 0.654$). There was less support for modelling contribution as a factor of distance as well as population size (contribution = distance + population size; $\Delta_i = 1.99$; $w_i = 0.242$). There was little support for the global model (contribution = distance + population size + size class: $\Delta_i = 3.68$; $w_i = 0.104$) and no support for the null model (contribution = population size and contribution = size class: $w_i < 0.001$).

Discussion

Spatial structure and connectivity

This first mixed-stock analysis of green-turtle feeding ground compositions across an east–west transect in the Indo-Pacific suggests a complex network of connectivity among nesting and feeding habitats in this region. Different stocks are not randomly distributed across the available feeding grounds, as indicated by the observed genetic structure among the feeding grounds. In a pattern of diffuse migratory connectivity, individuals from a single stock migrate to several different feeding grounds. Additionally, nearly all feeding grounds were shown to contain multiple stocks, and include adjacent or neighbouring stocks (e.g. SEP–GoC, AI–ARU) at <500 km or stocks at >500 km away from the feeding ground. Because of these varied patterns, no clear relationship became immediately apparent, indicating that contribution to a feeding ground depends on the stock's proximity or on its size.

Mark–recapture and satellite-telemetry studies provide valuable information about movements of individual adult turtles that can be used in conjunction with genetic data to reveal the magnitude and complexity of the migratory connectivity within

Table 4. Estimated proportional stock contributions to six individual foraging grounds, using weighted priors (rookery size)

Contributions are expressed as the mean and the median of likely proportional contributions within a 95% confidence interval. Estimates are based on the Pella and Masuda model (2001). Zero-contributions are indicated as a dash. nGBR, northern Great Barrier Reef; sGBR, southern Great Barrier Reef

Rookery	Foraging ground																							
	Ashmore Reef				Fog Bay				Cobourg Peninsula				Field Island				Aru Islands				Sir Edward Pellew Islands			
	Mean	Median	2.5%	97.5%	Mean	Median	2.5%	97.5%	Mean	Median	2.5%	97.5%	Mean	Median	2.5%	97.5%	Mean	Median	2.5%	97.5%	Mean	Median	2.5%	97.5%
nGBR	1.6	0.9	–	7.0	–	–	–	1.8	11.4	11.2	4.6	19.4	4.9	4.1	–	14.7	9.1	8.7	–	21.1	5.5	5.4	–	11.3
Coral Sea	–	–	–	0.5	–	–	–	0.2	–	–	–	0.2	0.1	–	–	1.9	0.1	–	–	0.3	0.1	–	–	1.5
sGBR	0.1	–	–	1.5	–	–	–	0.6	0.1	–	–	0.8	0.3	–	–	4.1	0.1	–	–	0.9	0.1	–	–	1.7
New Caledonia	0.2	–	–	2.0	–	–	–	0.1	0.1	–	–	0.5	0.6	–	–	8.7	0.3	–	–	3.5	0.5	–	–	6.9
Micronesia	–	–	–	0.1	0.2	–	–	3.7	3.5	–	–	15.3	–	–	–	0.2	0.3	–	–	0.9	–	–	–	–
Papua New Guinea	3.8	3.2	–	12.6	0.2	–	–	17.6	1.6	–	–	13.8	2.1	–	–	10.5	7.4	–	–	34.6	–	–	–	–
Peninsular Malaysia	2.2	–	–	26.5	0.2	–	–	–	–	–	–	–	0.8	–	–	15.9	–	–	–	–	–	–	–	–
Sarawak	–	–	–	–	6.7	–	–	21.0	–	–	–	–	0.3	–	–	4.7	–	–	–	–	–	–	–	–
Sulu Sea	0.2	–	–	1.8	0.1	–	–	1.9	0.9	–	–	9.4	0.9	–	–	6.7	1.1	–	–	8.9	0.1	–	–	0.9
Berau Island	0.6	–	–	6.8	0.8	–	–	6.7	0.2	–	–	2.4	0.5	–	–	6.1	2.9	–	–	16.9	0.1	–	–	0.5
SE Sabah	9.4	5.5	–	32.1	2.0	–	–	14.6	23.9	25.1	–	41.8	5.1	0.8	–	25.4	3.9	0.9	–	17.1	0.2	–	–	1.8
Aru	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	63.2	64.7	36.8	85.6	–	–	–	–
Gulf of Carpentaria	2.4	–	–	36.2	29.7	29.2	–	58.8	0.4	–	–	4.7	26.2	24.6	–	63.8	0.5	–	–	6.7	85.1	86.9	64.9	95.7
Ashmore Reef	1.2	–	–	18.3	7.3	–	–	36.5	11.2	–	–	43.2	0.1	–	–	0.1	2.2	–	–	30.7	–	–	–	–
Scott Reef	1.0	–	–	15.5	0.1	–	–	3.2	0.8	–	–	8.8	0.3	–	–	–	–	–	–	–	–	–	–	–
West Java	1.8	–	–	24.6	0.2	–	–	1.6	0.1	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–
North-west Shelf	75.4	75.9	46.2	95.8	49.1	48.4	22.1	79.9	45.8	45.8	28.5	62.5	57.6	58.8	23.0	86.6	9.1	8.4	0.6	21.5	8.3	5.9	–	28.4

a geographic region. For example, marked turtles from both the North-west Shelf and nGBR stocks have been captured at the Aru feeding grounds in Indonesia (Prince 1993; Schulz 1996; Limpus *et al.* 2003; K. Dethmers, pers. obs.) and results of mixed-stock analysis implied that these stocks each make modest contributions to this feeding ground. Tag-recovery data from throughout the region are consistent with the finding that most feeding grounds comprise significant contributions from multiple stocks (e.g. De Silva 1986; Prince 1997; Limpus *et al.* 2005). Importantly, the modelling output that indicated a relationship in which stock contribution to feeding grounds decreases with distance is also consistent with the more extensive tag-recovery data in eastern Australia. Long-term studies in the GBR have suggested that although tag-recovery data are widely dispersed, the majority of turtles nesting at the nGBR and sGBR stocks use feeding grounds within ~500 km of their respective rookeries (Limpus *et al.* 2003, 2005).

In addition to tag-recovery data, aspects of the genetic analysis have been supported by various satellite-telemetry studies on adult green turtles in the region. In particular, all of the 25 post-nesting turtles that were tracked by satellite telemetry from their nesting beaches within the western GoC stock migrated ~150 km south to their residential feeding ground at SEP within the Gulf (Kennett *et al.* 2004). Again, these data supported the notion that feeding grounds in the south-western GoC are composed primarily of GoC nesters. Migrations beyond the nearest feeding grounds were demonstrated by a green turtle nesting on Ashmore Reef that was tracked travelling to the Tiwi Islands, adjacent to CP, on completion of her breeding season (Spring 1990; Spring and Pike 1998) and green turtles from the Scott Reef stock were tracked to Cobourg Peninsula (R. I. T. Prince, pers. comm.). In Indonesia, one of three green turtles receiving a satellite transmitter at the rookery on Piai Island (West Papua) travelled to the Aru feeding grounds (at ~1000 km) and remained there (Gearheart 2005), as did two individuals that received a transmitter while nesting at one of the Palau Islands, Micronesia (at 1500 km, Klain *et al.* 2007). Preliminary genetic characterisation of the Piai Island nesting population (X. Velez-Zuazo, pers. comm.) indicated a grouping with the PNG stock, consistent with the contribution of this stock to the Aru feeding ground. Green turtles that nest in Peninsular Malaysia were found to migrate into Indonesian waters across nearly 2000 km (van de Merwe *et al.* 2009). Satellite-telemetry studies in other regions have found various post-nesting migration distances. The largest mean distance travelled (1968 km) was reported for individuals from Ascension Island tracked by satellite while migrating to residential feeding habitat along the Brazilian coast (Luschi *et al.* 1998). Green turtles from WanAn Island in the East China Sea migrated on average 687 km (Cheng 2000) and from the Tortuguero rookery in Costa Rica, turtles travelled on average 512 km (Troëng *et al.* 2005) to their respective feeding grounds.

Uncertainty

The ranges of possible proportional contributions to a mixture within the 95% confidence intervals are broad for most of the studied feeding grounds and the results in the present study allowed only general inferences on migratory connectivity among nesting and foraging habitat. The uncertainty can be attributed to any one or to a combination of the following limitations: (1) reduced analytical power associated with shared common haplotypes, (2) the use of a single molecular marker, (3) relatively small sample sizes of both the contributing and the mixture populations and (4) the presence of novel haplotypes.

The presence of a large diversity of haplotypes (Dethmers *et al.* 2006), although with very few regionally diagnostic ones, and some that are widely distributed (e.g. C1 and C3), reduces the ability to differentiate among the feeding aggregations and nesting populations. This is especially a problem in the eastern Indian Ocean, where there is low among-stock divergence in mtDNA haplotype frequencies. Such lack of divergence may have led to erroneous estimates of stock contributions from distant rookeries such as Peninsular Malaysia, Sulu Sea and Micronesia. By contrast, information content of mtDNA is much higher across the central and eastern Sahul Shelf because of major frequency shifts, manifest as a high frequency of private alleles in the sGBR, nGBR, GoC and Aru breeding populations (Dethmers *et al.* 2006). To better understand the missing links, future genetic analyses will need to increase the sampling effort and should aim to increase the power of analyses by employing more complex, hierarchical Bayesian models (e.g. Pella and Masuda 2006; Bolker *et al.* 2007) and by sequencing longer regions of the mtDNA to add resolution to the genetic data (Abreu-Grobois *et al.* 2006).

Unfortunately, preliminary analyses of microsatellite data from two of the feeding grounds, SEP and FI, by using assignment tests produced very low levels of assignment to the nesting populations (M. McCann and N. FitzSimmons, unpubl. data). This suggested a limited usefulness of microsatellite data to analyse feeding-ground compositions for these populations, which we suspect is due to relatively low levels of differentiation among nesting populations (FitzSimmons *et al.* 1997) and homoplasy across this broad geographic scale.

Incomplete sampling of nesting populations in some areas may have biased the results, particularly by reducing the capacity to detect contributions from more distant rookeries. The region encompassing the stocks included in the present study covers a vast expanse of habitats suitable for feeding turtles, as well as a widespread distribution of nesting activity. Sampling and genetic characterisation of breeding populations is strong across western, northern and eastern Australia, Borneo and the eastern Sunda Shelf, in comparison to the northern Indian Ocean, south China Sea, southern Sunda Shelf, Papua and the adjacent western Northern Pacific Ocean. However, much of the nesting activity in these areas is currently at low density, and some areas have been influenced by recent, severe population declines (Limpus 1996). Thus, limited sampling of rookeries in these areas could confound mixed-stock estimates, particularly for the Cocos (Keeling) Islands, Aru and Ashmore Reef foraging aggregations. Small sample sizes for some of the sampled stocks would have precluded the detection of haplotypes at low frequencies and may also have contributed a bias to the results. However, recent analysis of an additional 21 samples collected at the Ashmore Reef nesting area did not produce shifts in haplotype frequencies in space or time, thus confirming adequate genetic

characterisation of a sampled stock in this region with a sample-size of 20 (M. Jensen, pers. comm.).

Identifications of novel haplotypes is common in studies of mixed sea-turtle stocks and range from 0.7% of observations at a single feeding area (Bass *et al.* 2004) to 5% of observations at two feeding areas (Roberts *et al.* 2005). Although novel haplotypes are rare, the contributing stocks that they represent are not necessarily rare. Such haplotypes could possibly reflect remaining individuals of one or several severely depleted stocks that are influencing the analysis. For example, the AR stock was heavily exploited before the declaration of the Ashmore Reef National Nature Reserve in 1983 (Russell 2005). Ashmore Reef is a small stock that had an estimated marginal representation (mean = 11.2, 95% CI = 0.0–43.2) at only the Cobourg Peninsula feeding ground. However, a tag recovery from the AR stock at Weipa, in the eastern GoC and well beyond Cobourg Peninsula (at a distance of 2050 km, QTC turtle research database), indicates the need for further investigation of the feeding range for this stock. Further research into the origin of these unidentified contributions would not only improve our evaluation of the foraging aggregations but would also provide insight into the status of some breeding stocks.

Migration and dispersal

The constraints have limited our ability to draw robust conclusions and emphasised the importance of the use of both genetic and field-based methodologies to better understand the origins of turtles at feeding grounds and reveal the magnitude and complexity of migratory connectivity within a geographic region. We have shown that the relationship between distance and contribution is particularly strong for the SEP and ARU feeding grounds. In this analysis, the south-western GoC feeding ground (SEP) is dominated by GoC nesting turtles (from <500-km distance), with a relatively small contribution from nGBR (from ~1000-km distance) and a negligible proportion of turtles coming from sGBR (from ~2500-km distance). This result supports the tag-recovery data. Of the tens of thousands of nesting females tagged at the nGBR and sGBR stocks, 12 and 3, respectively, have been recaptured at SEP whereas two migrants from the few thousand tagged while nesting within the GoC stock have been recaptured there (Limpus *et al.* 2003; C. Limpus, unpubl. data, from the Queensland Turtle Research database). At Aru, the genetic conclusions appeared robust, given that they were largely based on a high frequency (86%) of a haplotype (C14) that was found in 96% of the Aru nesting turtles, 29% of the Berau stock and <10% in some Malaysian and Australian stocks (Dethmers *et al.* 2006). However, Schulz (1996) reported a recapture at the Aru feeding grounds from a turtle nesting within the Sulu Sea stock, and this stock was not detected at a significant level in the genetic analysis because of large standard errors. In the northern Atlantic region, the relative importance of distance and population size of stocks to their contribution appears to vary among feeding grounds and species. Lahanas *et al.* (1998) found that the size of green-turtle populations was a strong predictor of estimated contributions to a feeding ground in the Bahamas, whereas the influence of distance was insignificant. Contributions of juvenile hawksbill turtle (*Eretmochelys imbricata*) populations to various feeding grounds in the Caribbean were significantly correlated with both factors (Bowen *et al.* 2007), whereas neither of these factors correlated with juvenile green-turtle contributions to a Barbados feeding ground (Luke *et al.* 2004).

In theory, the connection between the breeding sites and the foraging areas is established via the oceanic pelagic dispersal of the small post-hatchling green turtles from their respective natal beaches via ocean currents (Bolten *et al.* 2003; Bass *et al.* 2006; Blumenthal *et al.* 2009). However, the details regarding the temporal and spatial distribution of the post-hatchlings as they move with the currents is poorly understood (but see Bass *et al.* 2006; Blumenthal *et al.* 2009), especially for the stocks of northern and western Australia (Walker 1990). Even less is known regarding the age and size structure and behaviour of the large post-hatchlings as they return to coastal waters and recruit to the benthic foraging populations of the region within this present study. The present study has demonstrated that small immature turtles from one stock can recruit to multiple foraging areas within several thousand kilometres of a breeding area. The gyre of the Arafura Sea–Gulf of Carpentaria (Wolanski 1993) and the Indonesian Throughflow (Verschell *et al.* 1995; Bray *et al.* 1996) are likely to have an influence on the dispersal patterns of post-hatchlings from rookeries across northern Australia and South-east Asia, although it is unknown where these turtles travel before recruiting to feeding grounds along the Sahul Shelf and Gulf of Carpentaria. However, the present study suggests that individuals from the North-west Shelf and Scott Reef stocks have recruited in feeding areas to the north-east of the breeding sites, apparently against the predominant currents, including the southern-flowing Leeuwin current off Western Australia (Verschell *et al.* 1995; Bray *et al.* 1996). Similarly, the relatively minor contribution of the very large nGBR stock to feeding grounds to the west suggests the role of seasonal eastward-flowing currents through Torres Strait in transporting post-hatchlings during the monsoon months (Saint-Cast and Condie 2006) into other current systems. Thus, the contributing factors for post-hatchling dispersal and eventual recruitment by juvenile turtles throughout the region are not obvious at this time. Once recruited, however, the similarities between the origins of subadult versus adult turtles at the feeding grounds may reflect a lack of developmental migration, with the exception of Fog Bay (Whiting and Guinea 1998).

The southern Gulf of Carpentaria presents an interesting management scenario for green turtles because the data indicated that few individuals from stocks other than the GoC stock migrate into the south-western Gulf. Although tagged individuals from the GBR stocks have been recaptured within the GoC, the genetic analysis showed that their overall contribution to the SEP feeding aggregation is estimated to be proportionally small (mean = 5.5, 95% CI = 0.0–11.3) for the nGBR (from ~1000 km) and undistinguishable for the sGBR (from ~2500 km). With the GoC stock estimated to be almost the sole contributor of the SEP aggregation, a potential reduction of the foraging aggregation such as the through the loss of seagrass habitats as reported by Indigenous hunters in the region (R. Kennett, pers. comm.) or cyclones (Limpus and Reed 1985*a*) would have a direct impact on the GoC stock. Any decline in the feeding aggregation would be poorly compensated because of minimal recruitment from other stocks. Conversely, management actions directed at green turtles within the Gulf of

Carpentaria have a greater chance of success because the stock is less affected by other unmanaged impacts outside the Gulf of Carpentaria (Kennett *et al.* 2004). This scenario is well suited for coordinated management actions focussed on both rookeries and feeding grounds as is currently being planned and implemented by Aboriginal organisations within the Gulf of Carpentaria.

Conclusion

The methodology explored in the present study has provided a broad indication of stocks that are represented in a feeding aggregation and thus a preliminary insight into the potential geographic extent of the impact associated with anthropogenic mortalities. For example, a high level of mortality at Cobourg Peninsula could have a negative impact on multiple breeding populations, whereas a similar level of mortality in the Sir Edward Pellew Islands is likely to primarily affect the Gulf of Carpentaria stock. Similarly, the North-west Shelf and Aru stocks can be expected to be heavily affected by exploitation pressure at the Ashmore and Aru feeding grounds, respectively. Although the results at this stage do not provide a solid basis for firm management decisions, management can be guided to focus on obtaining missing data and information on the stocks of concern. Ultimately, the severity of the impact or the success of potential management actions depends on the following three variables: (1) the level of representation of each of the stocks at a single feeding ground, (2) the total population size of affected stocks and (3) the distribution of affected stocks over (potentially) multiple feeding grounds. For green turtles in Australasia, it is not possible to predict the proportional representation of breeding stocks at feeding grounds, owing in part to the interrelationship between the timing of post-hatchling migration, geography and oceanic currents. It is expected that connectivity between breeding and feeding grounds will be similarly complex for the other species of marine turtles that utilise this region. Our findings also suggest the possible biological importance of counter currents or seasonal currents in influencing post-hatchling dispersal, comparable, for example, to that for hawksbill turtles in the Caribbean (Blumenthal *et al.* 2009), and this is likely to be true for the dispersal of other marine organisms that are influenced by currents in this region. Further work needs to be carried out to understand the fine-scale current patterns throughout the region (e.g. Saint-Cast and Condie 2006) and how this affects other dispersing organisms.

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