Journal of Experimental Marine Biology and Ecology 471 (2015) 77–83

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Improving in-water estimates of marine turtle abundance by adjusting aerial survey counts for perception and availability biases

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ARTICLE INFO

Article history:
Received 3 December 2014
Received in revised form 3 May 2015
Accepted 4 May 2015
Available online xxxx

Keywords:
Abundance estimation
Aerial surveys
Availability bias
Detection bias
Detection probability
Marine turtles
Perception bias

ABSTRACT

Aerial surveys are often used to estimate wildlife abundance. The probability of detecting an animal during a survey involves two processes: (1) availability bias when animals present in the search area are not available for detection and (2) perception bias, when some animals potentially visible to observers are missed. Estimating these two sources of bias can lead to improved abundance estimates. However, to date, no marine turtle aerial survey has quantified both biases. To improve in-water marine turtle abundance estimates from aerial counts we estimated: (1) perception bias using independent tandem observers and mark recapture models, and (2) availability bias by quantifying the effect of turtle diving behaviour and environmental conditions on the detection probability of turtles. We compared unadjusted and adjusted abundance estimates to evaluate the effects of these detection biases in aerial surveys. Adjusted data produced a substantially higher estimate of turtles than the unadjusted data. Adjusting for availability bias increased the estimates 18.7 times; adjusting for perception bias resulted in a further 5% increase. These results emphasize the need to consider availability and perception corrections to obtain robust abundance estimates. This approach has application for aerial surveys for other marine wildlife including marine mammals and large sharks.

1. Introduction

All species of marine turtles are listed as threatened (IUCN, 2014) and are subject to active conservation programs in many parts of the world. Reliable information on the abundance and distribution of marine turtles is important for their successful management and conservation (Eguchi et al., 2007; Thomson et al., 2013). Such information can enable population trends to be assessed, provide a context for evaluating anthropogenic and natural threats, including the risks of population collapse, and assist in identifying priority areas for management (Hamann et al., 2010; National Research Council, 2010; Roos et al., 2005).

Marine turtle abundance has been estimated using a variety of techniques (e.g., capture–mark–recapture, nesting beach monitoring, tagging and in-water surveys) from a range of platforms (e.g., land, aerial or boat-based) (e.g.,(Chaloupka and Limpus, 2001; Broderick et al., 2002; Seminoff et al., 2014). However, most work to date has estimated abundance from counts of nesting female turtles (Stokes et al., 2014). Nesting animals are accessible, and studying turtles on land is logistically easier and less expensive than when they are at sea (Seminoff et al., 2003; Stokes et al., 2014). However, female marine turtles spend most of, and male turtles all of, their lives at sea. In-water surveys are thus essential to ensure that abundance estimates cover both male and female turtles across a broad range of age classes and in feeding as well as breeding habitats (Chaloupka and Musick, 1997; Seminoff et al., 2003).

Aerial surveys enable the abundance of subadult and adult turtles to be estimated over large tracts of sea (Cardona et al., 2005; Epperly et al., 1994; Gómez de Segura et al., 2003; McDaniel et al., 2000; Seminoff et al., 2014). However, aerial surveys of in-water marine wildlife fail to meet a fundamental assumption of line transect sampling: that all animals on the transect line are detected (Buckland et al., 1993). This limitation can be mitigated by correcting abundance estimates to compensate for this reduced probability of detection. Nevertheless, it remains challenging to obtain defensible estimates of detection

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http://dx.doi.org/10.1016/j.jembe.2015.05.003
0022-0981/

probability, particularly for animals such as marine turtles that only spend a small proportion of their time at the surface (Marsh and Sinclair, 1989a; Okamura et al., 2006). Earlier studies have estimated detection probability as a single constant, using diverse methods, including multiple independent observers, concurrent aerial and ship surveys, and estimates of breathing rates (obtained external to the survey) for the target species (Buckland and Turnock, 1992; Laake et al., 1997).

Marsh and Sinclair (1989a) recognised that the probability of detection of marine wildlife involves two processes: (1) availability bias, which occurs when submerged animals, although present in the survey area, are not available for detection due to environmental conditions (e.g., water turbidity, sea state, cloud cover, surface glare) and animal characteristics (e.g., group size, body colour, body size, diving patterns); and (2) perception bias, which results from observers missing animals that are available for detection. Availability and perception biases interact and are not mutually exclusive.

Estimating these two sources of bias at the level of animal sighting leads to improved abundance estimates (see Pollock et al., 2006; Hagihara et al., 2014). Most efforts along these lines have been directed at improving abundance estimates for marine mammals. Refinements have been achieved by deploying telemetry devices to record diving and surfacing patterns of individual animals and using the resultant data to estimate the proportion of time that animals are available for detection across various environmental conditions and for different animal characteristics (e.g., life stage, pod composition, sex; see (Hagihara et al., 2014). In contrast, aerial surveys of marine turtles have only recently addressed availability bias by incorporating information on animal diving and surfacing patterns (e.g., Gómez de Segura et al., 2006; Seminoff et al., 2014). To our knowledge, no marine turtle aerial surveys have quantified both perception bias and availability bias or compensated for the heterogeneous environmental conditions typical of coastal environments.

To address these issues for an aerial survey of turtles, we (1) corrected for perception bias following the method of Pollock et al. (2006); (2) developed correction factors to compensate for availability bias at the level of individual sighting by (a) conducting experimental trials with a 'marine turtle Secchi Disk' to identify the depth of detection zones below the water surface where turtles are visible to aerial observers under different environmental conditions and (b) estimating the proportion of time that turtles spend in these detection zones by analysing time-depth recorder data from devices deployed on free-living turtles; (3) applied the resultant correction factors to aerial survey counts to improve abundance estimates; and (4) compared unadjusted and adjusted abundance estimates to evaluate the effects of failing to account for availability and perception biases in aerial surveys of subadult and adult marine turtles. The approach considered here and our suggestions for future improvements of in-water marine turtle abundance are widely applicable to abundance data from aerial and vessel surveys of other marine wildlife.

2. Materials and methods

2.1. Study site

Torres Strait (S 10° 29.59″, E 142° 10.44″), between Australia and Papua New Guinea, is mainly shallow (<20 m) with more than 200 islands, cays, and sandbanks (Harris et al., 2008) scattered over ~45,000 km^2 (~150 km north–south and ~300 km east–west, Fig. 1). Torres Strait provides foraging grounds for immature and adult turtles and acts as a corridor for turtles that migrate from eastern Indonesia, the Arafura Sea region, and the Gulf of Carpentaria to breeding sites in eastern Torres Strait and the northern Great Barrier Reef (nGBR) (Limpus and Parmenter, 1986). Three species of marine turtles nest and forage in Torres Strait: the green turtle, *Chelonia mydas*; the hawksbill turtle, *Eretmochelys imbricata*; and the flatback turtle, *Natator depressus* (Miller and Limpus, 1991). The loggerhead turtle, *Caretta caretta*, the olive ridley turtle, *Lepidochelys olivacea*, and the leatherback turtle, *Dermochelys coriacea*, are also found in Torres Strait waters. Nonetheless, green turtles dominate the Torres Strait marine turtle community; the other five species occur at much lower densities (Miller and Limpus, 1991). Consequently, green turtle behavioural data (obtained external to the survey) were used for estimating availability bias.

2.2. Standard aerial survey

A systematic aerial survey was conducted in central and western Torres Strait between 11 and 28 November 2013. Eastern Torres Strait, an area with important green turtle nesting grounds, was not surveyed (Fig. 1) because the survey was part of a long-term time series for dugongs, which occur there only at very low densities. The survey occurred at the beginning of green turtle nesting in the region (Limpus et al., 2003).

The survey was conducted using a 6-seat, high-wing, twin-engine Partenavia 68B flown 500 feet (152 m) above sea level along predetermined transects as close as possible to a ground speed of 100 knots (Fig. 1; Sobtzick et al., 2014). A strict ceiling was imposed on environmental conditions (no precipitation, sea state <4); 97% of the survey was conducted in Beaufort sea state <4.

The strip transect technique (a form of distance sampling that assumes constant likelihood of detection across a defined strip) was developed experimentally by Marsh and Sinclair (1989a,b) and Pollock et al. (2006) for the dugong, *Dugong dugon*, a species that generally surfaces for only a few seconds. A tandem teams of two independent, trained observers sat on each side of the aircraft and scanned a transect 200 m wide demarcated using fibreglass rods attached to artificial wing struts on the aircraft. Each transect was divided into four horizontal substrips (very high, high, medium, and low) by marks on the wing struts.

The two members of each tandem team operated independently and could neither see nor hear each other when on transect. Each observer recorded sightings onto separate tracks of an audio recorder. The recording of the sightings in the four substrips enabled the survey team to decide when reviewing the recordings if simultaneous sightings by tandem team members were of the same group of animals. This protocol was used instead of an inclinometer as the sighting rate was often very high and an inclinometer requires the observer to take their eyes off the water to read it, potentially resulting in missed animals.

All sea turtle sightings were recorded (but not to species), including those that did not fall within the transect strip. In such cases, the animals were recorded as 'inside' (below) or 'outside' (above) the transect strip to reduce the likelihood of an observer recording a sighting as in the transect when it was just outside. Sightings outside the transect were not used in the analyses.

Three combinations (teams) of tandem observers were used during the survey for logistical reasons. The survey leader collected data on environmental conditions at the beginning of each flight (cloud cover, cloud height, wind speed and direction, and air visibility) and for each transect (cloud cover). Sea state, water visibility, and glare (each side of the aircraft) were recorded every few minutes during each transect and whenever conditions changed using standard categories (Sobtzick et al., 2014). The survey area was divided into spatial blocks of varying sampling intensity with transects of varying lengths (Fig. 1 and Supplementary Table 1).

The aerial survey data were used to estimate the relative abundance of marine turtles following the methodology of Pollock et al. (2006). This method corrects for (1) sampling fraction, (2) perception bias, and (3) availability bias (*sensu*; Marsh and Sinclair, 1989a). Corrections for the biases were applied separately for each turtle sighted as an individual, and for each group of turtles (turtles seen in quick succession).

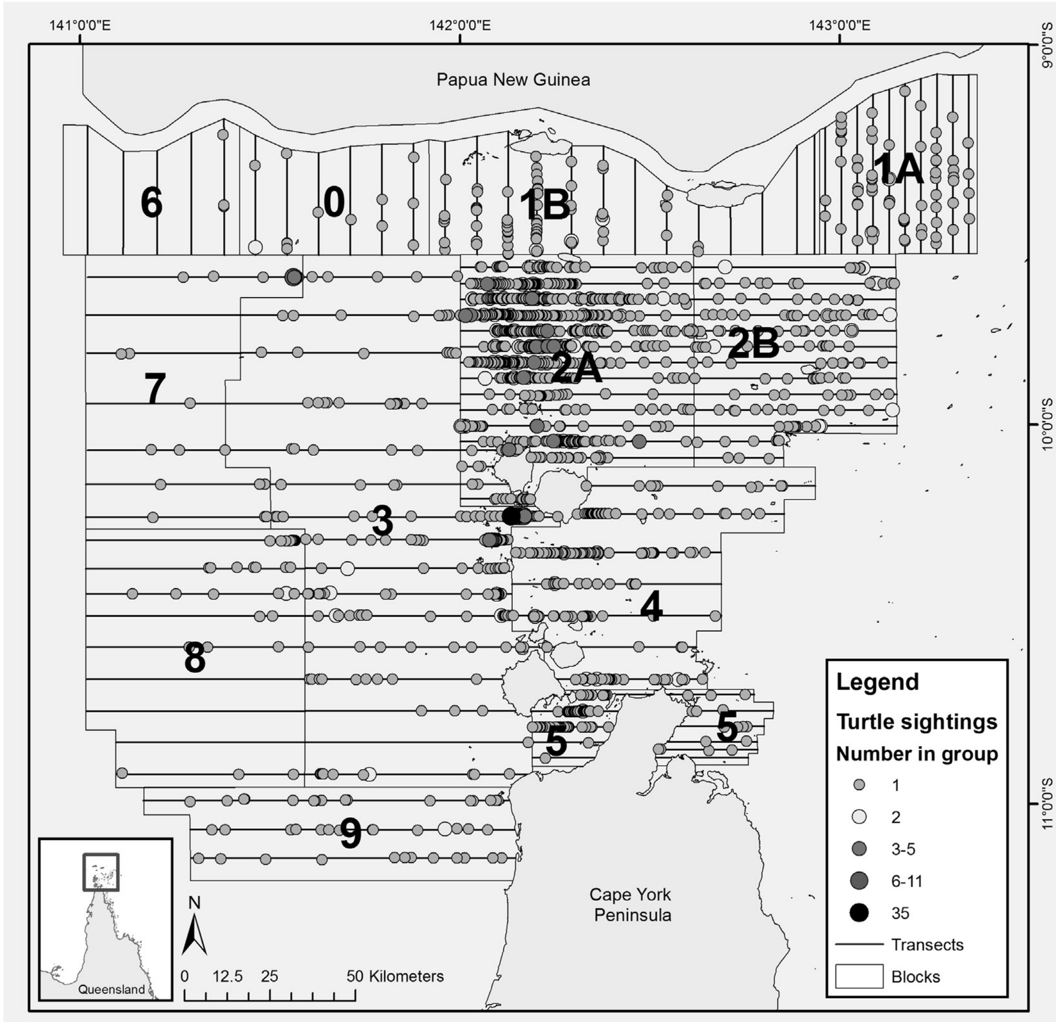

Fig. 1. Spatial extent of the 2013 aerial survey in Torres Strait, Australia; transects and blocks utilised for surveys and marine turtles sighted.

2.3. Estimating perception bias

The probability of aerial observers sighting marine turtles, given that the turtles were available for detection, was estimated using the methodology of Pollock et al. (2006), which calculated the probabilities of each observer (front and rear port and front and rear starboard) and each tandem observing team (port and starboard) (Marsh and Sinclair, 1989a; Pollock et al., 2006). Probability estimates were calculated by fitting a generalized Lincoln–Petersen model to the data set using Program MARK as per Pollock et al. (2006). Using the probability estimates from the model of best fit, the probability of detection (*Pd*) by ≥1 observer on 1 side of the aircraft is as follows:

$$Pd_{(\mathrm{port,starboard})} = 1 - (1 - p1)\,(1 - p2)$$

where $p1$ (probability of a turtle being sighted by the front seat observer) and $p2$ (probability of a turtle being sighted by the rear seat observer) are the values obtained from the model of best fit according to Program MARK. This approach also allowed us to quantify the improvement in detecting available turtles from using two tandem teams of observers rather than a single observer on each side of the aircraft.

2.4. Estimating availability bias for subadult and adult green turtles

Availability bias was estimated for various environmental conditions as follows: (1) a 'green turtle Secchi Disk' was deployed experimentally to estimate the depth of the zone beneath the surface of the water in which subadult/adult green turtles are visible to trained observers at the aerial survey height of 500 feet under different conditions, and (2) estimates of turtle availability within the experimentally determined detection zones were calculated from Timed-Depth Recorders (TDRs) deployed on free-living green turtles.

2.4.1. Experiments to estimate detection zones for subadult and adult green turtles

A 'green turtle Secchi Disk' (100 cm of CCL) (hereafter Secchi Disk) was constructed from marine plywood and fibreglass and painted to resemble a green turtle as sighted by highly experienced aerial observers from an aerial survey height of 500 feet. The Secchi Disk was balanced to be slightly positively buoyant and fitted with a Timed-Depth recorder (TDR) (DST milli-F manufactured by Star-Oddi) synchronised to the GPS time and set to record depth every second. The Secchi Disk was attached by rope to a pulley system and a counter weight on the sea floor. The free end of the rope was controlled by an operator on an anchored boat. Before each experimental trial, the Secchi Disk was lowered to a depth where it was not visible to observers in an R44 helicopter hovering at 500 feet (aerial survey height). On receipt of radioed instructions from the lead observer, a vessel-based operator began raising the Secchi Disk. Each observer independently recorded the GPS time when the Secchi Disk became recognisable as a turtle. The two observers could not communicate as they were acoustically isolated during the experiment. The trial was repeated at least eight times for each

Table 1
Environmental Conditions scale used for aerial surveys and the green turtle Secchi Disk experiment. The depth below the water surface at which the Secchi Disk was visible in experimental trials is also presented. Note the experiment was conducted in Beaufort sea states <4.

Environmental Conditions[1] class	Water quality	Depth range	Visibility of the sea floor/bottom	Average Secchi Disk depth ± (SE) (m)[2]	Detection zone (m) below surface
1	Clear	Shallow	Clearly visible	n/a	All depths
2	Variable	Variable	Partially visible	1.13 ± 0.63	0 to 1
3	Clear	Deep	Not visible	2.29 ± 0.73	0 to 2.5
4	Turbid	Variable	Not visible	0.67 ± 0.53	0 to 1

[1] Environmental Conditions is a composite index of water turbidity, sea state, glitter on the surface of the water, and water depth.
[2] Depth below surface at which turtle Secchi Disk was sighted from air

Environmental Conditions classes 2–4 as defined in Table 1. Environmental Conditions class 1 occurs when the water is shallow and the seafloor clearly visible. By definition, a large juvenile or adult turtle is available when the Environmental Conditions are class 1, and the availability bias must be 1 (full detection). Thus, this situation was not tested experimentally.

The experiment was carried out on several days between April 2013 and April 2014. Detection zones were rounded to the nearest 0.5 m to reflect the ±0.5 m resolution of the TDRs.

2.4.2. Estimating availability bias for subadult and adult green turtles

Behavioural data for green turtles at diverse life stages were obtained from four research projects, conducted external to this study, at widely dispersed locations (Table 2). External data were used since it is logistically difficult to retrieve time-depth recorders (TDRs) from turtles in remote Torres Strait. At each location, TDRs were deployed on study turtles and subsequently recovered for data download. Zero offset corrections were applied to correct small baseline discrepancies that are typical of depth recorders, thereby ensuring the minimum recorded depth was zero. The subset of records covering hours from 08:00 to 16:00 each day (the timeframe for aerial surveys) was extracted for each turtle. Data for periods when substrate depth could have been <2.5 m were excluded because in that situation, a turtle would necessarily spend 100% of the time within 2.5 m of the surface. Substrate depth was inferred by visual scrutiny of daily depth trajectories depicted by TDR data, on the rationale that dives extending below 2.5 m confirmed that a turtle was not constrained by a substrate <2.5 m. The same inference could not be made when dives did not extend below 2.5 m, and such periods were excluded.

The depth data were then used to calculate the proportion of time (within survey hours and substrate depths >2.5 m) that each turtle had spent in each of the detection zones of interest. These zones were identified by the Secchi Disk experiment described above. Resulting values (log-transformed) were assessed for potential differences between the four study locations using one-way ANOVA, and for potential relationship with sea temperature using Pearson correlation.

2.5. Calculation of population estimates and sensitivity analysis

The abundance of turtles was estimated separately for each survey block (±standard errors and coefficient of variation) and then for the whole survey area (Supplementary Table 1). The standard error estimates incorporated the errors associated with each of the correction factors (described above) and was calculated using simulation as per Pollock et al. (2006).

To explore the influence that different values for perception and availability biases may have on abundance estimates, we calculated turtle abundance for four scenarios: (1) unadjusted for both of the potential biases; adjusted for (2) availability bias and (3) perception bias, and (4) adjusted for both biases. All scenarios were adjusted for sampling fraction using the method of Pollock et al. (2006).

2.6. Estimating the number of subadult and adult green turtles

To estimate the number of adult and large subadult green turtles, we considered the relative proportion of nesting turtles in the region for each species occurring in Torres Strait (green turtles, flatback, and hawksbill turtles; see (Limpus et al., 1993, 2003; Limpus, 2007) and the fact that flatback turtles tracked in Torres Strait moved outside the survey region (Hamann, unpublished data). Consequently, we assumed that 97% of sighted turtles were green, 2.5% were flatback, and 0.5% other species (hawksbill, olive ridley and loggerhead turtles).

3. Results

3.1. Perception bias

The perception probability of each tandem team of observers was best described by the model that assumed that all observers were different (Table 3). The probability of observers sighting turtles, that were available for detection, was high, with the tandem observer teams sighting 81–96% and single observers sighting between 37% and 93% of turtles that were available (Table 3). Rear observers who were less

Table 2
Data used to estimate turtle availability for the aerial surveys. The sex of the study animals is indicated as M = male, F = female, U = undetermined.

Location	Study turtles (sex)	Turtle life stage	TDR devices	Sampling interval (s)	Deployment duration (d)
Gulf of California, Mexico 28° 58′N, 113° 33′W (Seminoff et al., 2004)	Immature and adult (U), $n = 14$	Foraging	Wildlife Computers TDR Mk 7	5 to 15	1 to 4
Raine Island, Queensland, Australia 11° 35′ S 144° 02′ E (Bell et al., 2009)	Adult (F), $n = 6$	Inter-nesting	Vemco Minilog	20 to 30	1 to 7
Toolakea, Queensland, Australia 19° 09′ S 146° 35′ E (Huth, 2014)	Immature (U), $n = 3$	Foraging	Star-Oddi DST Milli-F	2	8 to 15
Moreton Bay, Queensland, Australia 27° 28′ S 153° 13′ E (Hazel et al., 2009b)	Immature and adult (U, F, M), $n = 11$	Foraging	Star-Oddi DST Milli	15	1 to 7

Table 3
Details of the best model to calculate perception bias for each tandem team of observers. Potential models included the following: the same for all observers, varied according to experience (primary or secondary observers), varied according to side of the aircraft (port or starboard), or different for every observer.

Survey team	Best fit model*	Probability estimates from the model of best fit** (±SE)	Probability of detection of an available turtle for each tandem team (±SE)
1	All observers different	Port front 0.83 ± 0.06 Port rear 0.56 ± 0.06 Starboard front 0.82 ± 0.04 Starboard rear 0.75 ± 0.05	Port = 0.94 ± 0.06 Starboard = 0.95 ± 0.04
2	All observers different	Port front 0.84 ± 0.01 Port rear 0.65 ± 0.01 Starboard front 0.82 ± 0.01 Starboard rear 0.59 ± 0.01	Port = 0.94 ± 0.01 Starboard = 0.93 ± 0.01
3	All observers different	Port front 0.93 ± 0.05 Port rear 0.37 ± 0.09 Starboard front 0.56 ± 0.08 Starboard rear 0.56 ± 0.08	Port = 0.96 ± 0.05 Starboard = 0.81 ± 0.08

* The generalised Lincoln–Petersen model of best fit according to Akaike's Information Criterion using the MARK program (White and Burnham, 1999).
** Probability estimates provided by the model using the MARK program.

experienced had a lower probability of sighting a turtle than front seat observers.

3.2. Availability bias

The depths beneath that water surface at which the Secchi Disk was visible to the aerial observers during the experimental trails are summarized in Table 1. These depths were rounded to the nearest 0.5 m to allow for TDR resolution, resulting in a detection zone of 1 m below the surface for Environmental Conditions classes 2 and 4 and 2.5 m for Environmental Conditions class 3 (all turtles were available at Environmental Conditions class 1 by definition). Rounding the detection depth of Environmental Conditions class 4 to the nearest 0.5 m resulted in a 0.5 m detection zone. In view of the TDR resolution of 0.5 m and the location of the TDR attached to a turtle body (measured depths vary depending on orientation of a body), we decided that a more conservative detection zone of 1 m for Environmental Conditions class 4 was more appropriate. For free-living green turtles (data averaged across four different locations), 5% (SE ±1%) of their time was spent at depths 0 to 1 m, and 18% (SE ±2%) of time was spent at depths 0 to 2.5 m (Table 4). Differences between locations were not statistically significant (0 to 1 m: $F_{(3, 30)} = 2.141$, $p = 0.12$; 0 to 2.5 m: $F_{(3, 30)} = 1.57$, $p = 0.22$), and there was no significant correlation between sea temperature and time spent in either of the detection zones (0 to 1 m: $r = 0.08$, df = 27, $p = 0.68$; 0 to 2.5 m: $r = -0.16$, df = 27, $p = 0.42$).

3.3. Marine turtle abundance

A total of 1896 individuals (1639 groups) of marine turtles was sighted during the aerial survey, which covered an area of 41,643 km^2. Adjusting for sampling fraction only resulted in an estimate of 30,885 ± SE 4,040 large juvenile and adult turtles in the survey area (Table 5 and Supplementary Table 2). Correcting the estimates for availability bias only increased this estimate ~18.7 times (Table 5 and Supplementary Table 2). Correcting estimates for perception bias only using two tandem teams of observers increased the estimate by 5% (Table 5 and Supplementary Table 2). Using a tandem team of observers rather than a single observer improved the correction for perception bias from 3% to 250% and was observer dependent. When corrections for both perception and availability bias were incorporated, a total of 617,209 (±SE 83,717) (95% CI, 441,505–1,025,552) large juvenile and adult turtles were estimated for the survey area (Table 5 and Supplementary Table 2) of which 598,692 (95% CI; 428,259 to 994,785) were estimated to be green turtles, based on their proportion of the region's overall adult sea turtle nesting population size.

4. Discussion

Our in-water abundance estimates of juvenile and adult marine turtles are the first to correct for the effects of both perception bias and the heterogeneous nature of availability bias on detection probability during an aerial survey. The estimates corrected for both availability and perception bias are about 20 times higher than the uncorrected estimates (617,209 ± SE 83,717 vs. 30,885 ± SE 4,040; Table 5). Most of this difference was due to the correction for availability bias. The probability of a tandem team of observers sighting turtles that were available for detection was relatively high (0.81–0.95, Table 3). However, a high proportion of turtles was unavailable for detection, and this proportion varied with environmental conditions from 0.05 to 1 (Table 4). Our results emphasize the need to improve abundance estimates of in-water marine turtles based on aerial surveys by incorporating corrections for (1) the heterogeneous nature of availability bias and (2) the perception bias based on a tandem team of observers.

Failure to account for these biases will lead to misleading abundance estimates, which may result in misinterpretation of threats, especially in places like Torres Strait where green turtles are legally harvested as a traditional fishery under the Torres Strait Treaty between Australia and Papua New Guinea. To determine sustainable green turtle catch values for Torres Strait, robust information on the size of both the green turtle population and the catch is required (Marsh et al., 2004).

Table 4
Proportion of time that free-living green turtles spent in detection zones of 0 to 1m (Environmental Conditions class 2 and 4) and 0 to 2.5m (Environmental Conditions class 3) within survey hours (08:00 to 16:00) and substrate depths >2.5 m. These proportions were estimated from TDR data collected in the studies summarised in Table 2. All turtles were available in Environmental Conditions class1 by definition.

Location	Study turtles (n)	Data (h) per turtle (median [range])	Sea temperature (°C) (median [range])	Time at 0 to 1m (mean ± SE)	Time at 1 to 2.5m (mean ± SE)
Gulf of California, Mexico*	14	12 [7 to 35]	26 [22 to 27] *	0.06 ± 0.02	0.23 ± 0.05
Raine Island, Australia	6	12 [4 to 61]	28 [27 to 28]	0.06 ± 0.01	0.11 ± 0.03
Toolakea, Australia	3	38 [12 to 41]	28 [27 to 28]	0.08 ± 0.01	0.16 ± 0.03
Moreton Bay, Australia	11	8 [2 to 53]	23 [17 to 27]	0.03 ± 0.00	0.16 ± 0.02
Average across locations	8.5	17.5	26.25	0.05 ± 0.01	0.18 ± 0.02

* Mexico study collected temperature data for 9 turtles only.

Table 5
Abundance estimates of all turtles (±SE, CV) for the different scenarios.

	Unadjusted perception bias (100% probability of detection)	Adjusted perception bias
Unadjusted availability bias (100% probability of availability)	30,885 ± 4,040 (0.13)	32,553 ± 4,623 (0.13)
Adjusted availability bias (5% probability of availability in visibility 1 and 4, and 18% in visibility 3)	576,776 ± 80,331 (0.13)	617,209 ± 83,717 (0.13)

We obtained important insights into green turtle abundance in Torres Strait, even though our survey did not include eastern Torres Strait. The aerial surveys coincided with the green turtle nesting season, when mating or nesting turtles may have already migrated to nesting beaches in eastern Torres Strait or the northern Great Barrier Reef (e.g., Raine Island) (Harris et al., 1992), further contributing to the likelihood that our estimates are underestimates. Estimates of marine turtle abundance in Torres Strait would be improved by (1) redesigning the survey to include all the turtle habitats in Torres Strait and (2) timing this expanded survey outside the nesting season; (3) conducting separate helicopter surveys in circling mode in the same season as the surveys to identify the species and sex of a large sample of turtles to enable the sex ratio and species composition of sightings in subsequent aerial surveys conducted in passing mode to be estimated; (4) conducting additional turtle Secchi Disk experiments to determine the minimum size at which turtles are visible to an observer at aerial survey height; and (5) accounting for the effect of water depth on turtle diving behaviour as has been done for dugongs by Hagihara et al. (2014). The last requires marine turtles to be fitted simultaneously with satellite telemetry units and time-depth recorders or the use of satellite relayed data loggers (Godley et al., 2008; Myers et al., 2006). Only a few studies have simultaneously obtained detailed marine turtle diving behaviour and relatively precise location data (for examples see (Sale et al., 2006; McMahon et al., 2007; Hamel et al., 2008; Gaos et al., 2012). Unfortunately, these studies have not analysed depth-specific surfacing and diving patterns in a way that could inform our study. It would also be desirable to estimate turtle abundance in areas with zero counts, which is theoretically possible but challenging (see Martin et al., 2014).

Marine turtle diving patterns, at some locations, are affected by temperature and turtle size (Hazel et al., 2009a; Hochscheid, 2014), and such variation could influence the probability of marine turtles being detected during aerial surveys (Thomson et al., 2013). The effect of habitat depth and seasonal water temperature on the availability of turtles was recently explored for boat surveys (Thomson et al., 2012, 2013). Estimates of turtle density were found to be underestimated during the cold season if the extended dive times during cooler periods were not considered (Thomson et al., 2013). We found no significant difference in the proportion of time that turtles spend within each examined detection zone across the four study sites from which data were available, despite these studies including turtles of different sizes and from regions with varying temperatures. This finding strengthens our untested assumption that the diving patterns from elsewhere hold true in Torres Strait, suggesting that regardless of population, size, or habitat that green turtles adhere to a common surfacing pattern, likely related to their universal physiology and breathe holding potential. This finding warrants further investigation of the effects of environmental variables on the probability of detecting marine turtles from the air and the potential of determining species-specific availability bias.

As availability correction factors for marine turtles are highly heterogeneous (Thomson et al., 2012), a greater understanding of the depth-specific surfacing patterns and diving behaviour of green turtles at a range of coastal and offshore habitats and for a variety of environmental conditions (e.g., sea states, tides) is necessary to improve existent detection probability correction factors. The availability to aerial and vessel-based observers of other marine wildlife taxa (e.g., minke whales, manatees, and sharks) is also likely to be heterogeneous as a result of environmental factors (Langtimm et al., 2011; Southall et al., 2005; Stockin et al., 2001). Thus, the approach considered here and our suggestions for future improvements should be widely applicable to abundance data from aerial and vessel surveys of marine wildlife.

Acknowledgements

We thank the National Environmental Research Program, the Australian Marine Mammal Centre, and the Torres Strait Regional Authority for funding this research. We are a grateful for our dedicated aerial survey team members, including Helen Penrose, Shane Preston, Alvaro Berg Soto, Jasmine Roberts, Kelly Cates, Jessica Riggin, Kym Collins, Erin Wyatt, Milena Kiatoski-Kim, and Kah Leng Cherh, as well as our ground support staff Jimmy White and the pilots Michael Harper and Robert Gillies for all their efforts in the field. We also thank the Torres Strait Regional Authority, in particular, Stan Lui and Damian Miley, for their support, as well as Herbert Warusam (Saibai Ranger) and Frank Nona (Badu Ranger) for sea state and weather updates for the Torres Strait. The Secchi Disk experiments were conducted under permits G13/36292.1 (Great Barrier Reef Marine Park) and QS2013/MAN213 (Moreton Bay Marine Park). Staff of the Moreton Bay Filed Station provided support for the Secchi Disk experiments. **[SS]**

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2015.05.003.

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