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Methods to inform research towards conservation management of Australian inshore dolphins

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Contents

Table of Figures

Introduction

The 2015 Coordinated National Research Framework (2015 Framework; DoE 2015) broadened the focus and changed the objectives of the 2013 Coordinated National Research Framework (2013 Framework; DoE 2013) in response to new information and initiates an alternative approach to inshore dolphin research. Research previously directed towards assessment of the conservation status of the Australian snubfin dolphin (*Orcaella heinsohni*) under the EPBC Act was reoriented to research to inform conservation management of the three species; Australian snubfin dolphin (*Orcaella heinsohni*), Australian humpback dolphin (*Sousa sahulensis*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*).

This report reviews and updates the report 'Methods for assessment of the conservation status of Australian inshore dolphins' (2014 Methods; Brooks et al. 2014) in response to these developments. The Objectives specified in the 2015 Framework were classified as of enabling, high or medium priority. Objective 1, the enabling objective, refers to indigenous engagement. The high priority research objectives refer to national distribution data (Objective 2), long-term monitoring (Objective 3) and threat risk assessment (Objective 4).

The high priority research objectives are summarised in 2015 Framework as follows (p.6).

> **Objective 2 - National Distribution Data:** *Provide for access to and analysis of standardised national tropical dolphin data to assess distribution and underpin management and conservation.*
>
> **Objective 3 - Long-term Monitoring:** *Gather and use information over long-term timescales to determine trends, mitigate impacts from threats, and support adaptive management and conservation of tropical inshore dolphins.*
>
> **Objective 4 - Threat Risk Assessment:** *Identify, map and assess threats to tropical inshore dolphins, understand related impacts, and mitigate risks.*

This report seeks to address Objectives 2 and 3. As in the 2014 Methods document, the focus is on systematic sampling design and statistical methods for the analysis of the resulting data.

The Northern Territory Government Department of Land Resource Management (NTDLRM) conducted sampling for the broad scale distribution of coastal dolphins across the Northern Territory in 2014 and 2015. With a change of research platform from small boats to helicopters, this project implemented the sampling design specified for the 'extent of occurrence and area of occupancy of snubfin dolphins' in the 2014 methods document (2014 NT Methods; see NTDLRM 2014 for details of the NT sampling design). The experience of conducting this research and the data generated have important implications for future research on Australian inshore dolphins. Comment is made on the comparison between small boat and helicopter platforms, and results from an initial analysis of the data are presented to demonstrate alternative models and update knowledge of the distribution and relative density of the species.

A recent critique by Efford and Dawson (2012) has clarified limits on the interpretation of occupancy estimates for data collected in continuous habitat. Their critique is discussed and its implications for inshore dolphin surveys highlighted, and an alternative approach, relative density modeling, is specified for the data. Results from the planned occupancy model and the alternative model fitted to the available Northern Territory data are reported and compared. While the results reported here were generated for the purpose of comparing the alternative models, they also represent new information on the distribution of snubfin dolphins.

The proposed new model estimates relative density in the sense that true density remains unknown because the methods employed do not allow for estimating the number of dolphins missed on transect. While dual observer methods have been proposed and used for strip transect aerial surveys (Marsh and Sinclair 1989, Pollock et al. 2006) to adjust for non-detection by single observers, the sampling design was specified originally for survey from small boats and modified for survey from helicopters, and it is not possible to implement this methodology from these platforms. Use of a type of aircraft and the number of observers per unit suitable for the dual platform methodology was never envisioned for this project and half of the relevant area has now been surveyed by helicopter. As very useful results can be derived from the single observer data it is sensible to maintain methodological consistency for survey of the remaining area.

Boats versus helicopters

The 2014 Methods document included a section considering the potential of aerial survey methods (pp. 26, 27) and a pilot study to compare small boat and aerial platforms was completed by NTDLRM in Cobourg Marine Park in March/April 2014. While a detailed report of the results of that study is made in the 2014 NT Methods document, the conclusions are summarised here:

- The estimated probabilities of detection were broadly comparable for survey from boats and helicopters
- Crews reported that detection from the air is apparently less affected by the sea state than detection from the surface
- The amount of transect that can be surveyed from a helicopter in a day requires a week or more to survey from a boat
- Fewer days would be lost due to unsuitable weather for a helicopter than a boat because whole sites (320-480 km of transect in the NT) can be surveyed in one day and weather changes are less likely during a one-day than a one-week survey

- Many sites on the tropical coast (NT, Kimberley, Western Cape York) are not accessible by road and could either not be included in a sample or sampling would require either a live–aboard vessel or for camps to be set up
- Transition from one site to another is much faster for a helicopter than a boat
- Less on-site accommodation is required for a helicopter than a boat survey
- Completion of sampling on a site in a day gives a snapshot of the distribution of dolphins over the area
- Cost of wet hire of a suitable helicopter and pilot is approximately $1400 per hour. This is cost-effective relative to the cost of a boat and accommodation over a much longer period.

Efford and Dawson – occupancy in continuous habitat

Efford and Dawson (2012) set out to 'clarify the implications of home range size and plot size for the design of occupancy studies in continuous habitat' (p.3). Home range size was considered in the 2014 Methods and 2014 NT Methods documents. A plot size was chosen to be approximately the size of a group home range on the assumption, according to the state of knowledge at the time, that snubfin dolphins occurred in small, isolated populations on relatively small home ranges that may often extend over less than 50 km of coastline (2014 Methods p. 6; Cagnazzi et al. 2013). It was recognised that this assumption was based on very few data and that the actual sizes of home ranges may be variable and sample sites may overlap with home ranges to varying degrees. It was considered necessary to make some assumption of this sort, however, to provide a basis for development of a sampling design and interpretation of the resulting occupancy estimate. While this sort of consideration is unnecessary in the case of well-delimited habitat areas such as islands or ponds, Efford and Dawson (2012) make it clear that home range size, plot size and the density of animals in the area are crucial to the meaning of an occupancy estimate in continuous habitat. They use simulation to show that the estimated occupancy (ψ) is critically dependent on the ratio of plot size to home range size. Their critique concludes that 'Confounding of ψ with home-range size and plot size creates the potential for serious inferential error or loss of inferential power when ψ is used as a surrogate for density in population monitoring' (p. 11).

The Efford and Dawson (2012) critique demonstrates that occupancy is ill-defined when survey is conducted in continuous habitat and home range size is unknown. It was pointed out in the 2014 Methods document (p. 22) that the probability of occupancy of sub-sites is a measure of the rate of use of such areas rather than a measure of the proportion of them consistently used by dolphins (or in which they are 'resident'). It is now clear that this sort of interpretation of an occupancy estimate may also apply to whole sample sites when sampling is conducted in continuous habitat. Given that occupancy estimation may not clearly provide information beyond the relative rates of use of different parts of the coastal habitat, it is sensible to model this directly in a relative density model. A further benefit of such a model is that it would make use of counts of individuals rather than simply sightings of groups, particularly when sightings of groups beyond the first on a transect pass are ignored in occupancy estimation.

Review of 2014 Methods

Methods for Objective 1 of the 2013 Framework

Overview

Objective 1 of the 2013 Framework was "To conduct a broad-scale assessment of the extent of occurrence and area of occupancy of snubfin dolphins. This should include: a compilation of existing data sources; the development of an indigenous engagement and knowledge sharing strategy; the development of a temporally and spatially replicated presence/absence boat survey covering a large geographic range."

Indigenous engagement is now identified separately as Objective 1 of the 2015 Framework and was central to the recent 2014/2015 Northern Territory survey program (NTDLRM 2015). Compilation of existing data sources is an ongoing process among individual researchers (e.g., Parra & Cagnazzi 2016) but no central registry has been established.

It is now clear that the sampling design specified in 2014 Methods for a replicated presence/absence survey could not provide an estimate of the total area of occupancy because an occupancy estimate on which it might be based is ill-defined when made from data collected in continuous habitat (Efford and Dawson 2012). Consequently, while much of the material in 2014 Methods on occupancy models may now be considered redundant - or at least of secondary interest - and best replaced by new material on a relative density model, much of the material on sampling remains valid.

Sampling design considerations

The hierarchical sampling scheme of sites, zones within sites and transects within zones remains useful.

- While following naturally from an occupancy study design of sites and replicate samples, randomly distributing a sample of relatively large sites (400-600 km^2) around the coast and sampling from those is an effective way to manage a survey across the very large length of often remote coastline. This approach is more efficient than the alternative of randomly distributing transects around the coast because survey operations require re-fuelling, provisioning and accommodation and it is very inefficient to sample far from bases available or set up for this purpose.
- Although partitioning each site into zones (I 'inshore', N 'nearshore', O 'offshore') is not necessary, it serves to organise transects into coherent areas that may identify parts of the habitat that may be used at different rates. The zone types are potentially different habitat in

the different site types (A ‘estuarine’, B ‘coastal’) but may be combined with the site types to yield the five factor levels AI, AN, AO, BN and BO.

- Transects are the basic sampling units and serve as a measure of effort and on which some habitat character and all detection (sighting conditions) covariates are measured.

The 2014 Methods design restricts sampling to within 10 km from shore. This was in the interests of the safety of crews in small boats and to limit the total area to be sampled from which was very large in any case. The available knowledge at the time indicated that most inshore dolphins would be within this distance from shore most of the time even though sightings had occasionally been made further from shore. Moreover, the 10 km from shore limit to sampling was considered to have minimal impact on occupancy estimation as it was considered likely that, if a site were occupied, there was a non-zero chance of detecting at least one dolphin on this coastal strip and the presence of dolphins further offshore at the time of sampling was considered likely to affect the probability of detection rather than the probability of occupancy.

Sites were defined as 40 km long and 10 km wide plus the inshore area in estuarine sites. This was of the approximate size or slightly smaller than an expected typical snubfin dolphin home range size. Transects were run parallel to the coast and their 40 km length was in accordance with the estimated length of transect required to meet the requirements of occupancy models for detection probability per length of transect ($p>0.2$). This is also a reasonable minimum detection rate for a relative density model as it limits the number of zeros in the response distribution to a manageable level.

It was considered more practical to run transects parallel rather than orthogonal to the coast so that each was of the required minimum length while remaining within the 10 km limit; the alternative was to construct approximately 40 km long units as sums of smaller segments for analysis. As the results to be presented below show, 40 km of transect is a sensible unit of effort whether it is the standard transect length or constructed for analysis.

Whether surveys should be conducted further from shore to provide a more complete description of habitat usage deserves some consideration given that survey from a helicopter rather than a boat may ameliorate some of the safety concerns. The total amount of survey effort is already large but survey further from shore might be achieved at similar cost by limiting the length of sites along the coast to maintain the same total area to be surveyed.

This question may best be addressed keeping in mind that it remains likely that most dolphins of all inshore species are likely to be within 10 km from shore most of the time and that a large proportion of the total length of coast within the ranges of snubfin and humpback dolphins has already been sampled in the Northern Territory only out to 10 km from shore.

Future survey could follow the 10 km limit protocol specified in 2014 Methods and followed in the Northern Territory, and inference to the spatial distribution of the dolphins would remain limited a 10 km wide coastal strip. This would allow a similar intensity of sampling of the inshore, nearshore and offshore zones and serve the purpose of providing a consistent and reasonably precise description of the relative rates of use of coastal areas within the extent of the species' range. Dolphins that travel further offshore are likely to use the adjacent inshore areas relatively frequently.

Depending on the importance placed on information about the offshore spatial distribution of the species, future surveys could be conducted on say, 20 km wide x 20 km out from shore sites (or sites of some other shape of about the same total area) while maintaining the same total survey effort. However, the areas of the current inshore and offshore zones would be halved and the corresponding inferential power reduced. Should the density of dolphins be lower further from shore, the overall detection rates would be lower and overall inferential power reduced. A sensible compromise might be made by taking an experimental approach to estimating offshore spatial distribution by deliberately selecting a subset of sites with different offshore characters (e.g. water depth) for survey further offshore. Ideally, the extra offshore area would be surveyed in addition to the area within the current protocol within 10 km from shore.

Methods for Objective 2 of the 2013 Framework – relevance to Objective 3 of 2015 Framework

Objective 2 of the 2013 Framework was "To conduct dedicated multi-year studies of the distribution, abundance and habitat use of snubfin dolphins at selected sites across northern Australia with differing levels of threatening processes. The studies would provide a plausible estimate of rate of change within sites and by extension, across the entire range" (2013 Framework p. 3).

Objective 3 of the 2015 Framework is very similar: "Gather and use information over long-term timescales to determine trends, mitigate impacts from threats, and support adaptive management and conservation of tropical inshore dolphins (2015 Framework p. 6).

The methods recommended for Objective 2 of the 2013 Framework in 2014 Methods (pp. 28-35) are thoroughly described and remain appropriate in the main for Objective 3 of the 2015 Framework.

Description of Objective 3 is expanded to include Objective 3.3: "For previously unstudied locations, with a priority for impacted or likely to be impacted sites, conduct short-term assessments of abundance to further inform site selection and sampling design for longer-term studies." (2015 Framework pp. 29-30). The 2015 Framework also includes a set of criteria for selection of sites for further research (pp. 21-22).

As described in 2014 Methods (p .31), an abundance estimate may be made from the first primary sample in a robust design study, which is simply a closed population study over two or more secondary samples. It is sensible to design a capture-recapture study for a short-term assessment with the potential to continue the study as a robust design should further study on the site be justified. The capture probability that may be considered appropriate for a longer-term study however may be too low for an accurate (unbiased and reliable) one-off estimate.

An often-mentioned advantage of the robust design over other long-term study methods is that it can model heterogeneity of capture probabilities due to individual differences and behavioural response to first capture (see 2014 Methods). It requires at least four and preferably more secondary samples per primary sample to achieve this however, and these effects do not seem to have been found in existing capture-recapture studies of tropical inshore dolphins. If it were considered reasonable to assume that heterogeneity effects are unlikely to be found in the data from study on a proposed site, consideration might be given to reducing the number of secondary samples. This may make it possible to invest a limited budget more effectively towards achieving a capture probability per secondary sample that yields a suitably precise abundance estimate. Depending on the size of a population, $p > 0.2$ is a sensible target.

That study sites are generally smaller than the home ranges of the local populations under study and the implications of this for the closure assumption within a primary sample is discussed in 2014 Methods (pp. 29-30). In sum, dolphins may enter and leave the study area during a primary sample and, provided such movement is random, an abundance estimate will be unbiased if it is interpreted as an estimate of the number that used the sample area during the primary sample period. The rates of movement into and out of the sample area within a primary sample is generally unknown and cannot be modeled; temporary emigration refers to longer-term movements between primary samples. Consequently, although rates of movement are unknown, it seems likely that studies conducted over very short periods will yield lower abundance estimates than longer duration studies.

For the proposed short-term assessments then, some balance should be found between the number of samples that may yield the highest capture probability per sample and a duration over which they are taken that should ensure that most dolphins in the broader local area during a year or season are likely to visit the sample area at least once. In short, a study with only two samples may be adequate provided each sample is taken over several days or several passes over a set of transects so that there is a good chance of dolphins that were offsite for a day or so have a reasonable probability of being onsite at least once at some time during the study duration.

It is difficult to make a general recommendation for this as the best compromise will involve the size of the budget and the likelihood of poor weather. We recommend that the area searched on transect be worked out from an assumed sighting distance and transects be laid out to achieve at least 30% coverage of the study area per sample, depending on the proportion of dolphins seen that are expected to be captured in good quality photographs. Smaller populations are harder to study and a site coverage fraction of 50% per sample was chosen for a planned study of the Townsville area following a pilot study.

The precision of an initial, one-off abundance estimate on a site is crucial to its utility. If the site under study is also sampled for sightings rather than individual identification (as in an occupancy study, for example) such estimates might possibly contribute to estimation of approximate abundance over the broad area sampled in the sighting study. This possibility is subsequently discussed.

An alternative model for spatial distribution data – Objective 2 of the 2015 Framework

Overview

We describe and illustrate the proposed alternative model in terms of the data on snubfin dolphins collected by helicopter across the Northern Territory (NT) coast in 2014 and 2015. The NT sampling design (2014 NT Methods) planned to survey 40 sites (20 Type A or 'estuarine' and 20 Type B or 'coastal') with 12 replicates on each estuarine and eight on each coastal site. All transects were 40 km long. Occasional poor weather meant that 39 (20 estuarine, 19 coastal) sites were surveyed from 377 transects (233/240 of planned for 20 estuarine sites and 144/152 of planned for 19 coastal sites). The main models to be compared are the originally planned occupancy model, based on whether or not at least one dolphin group was sighted on each transect, and the alternative model, based on the number of individuals sighted on each transect. The 'number of individuals' response variable in the alternative model arises as the sum of the sizes of the groups sighted on each transect and results are also reported from models for the number and sizes of groups sighted on each transect.

Survey methods

A Bell Jet Ranger helicopter with the side doors removed and 'sighting rods' fitted was employed for the surveys. The two principal observers were seated on the sides of the aircraft, while a third observer/data recorder was seated in the front with the pilot. Transects were flown at 80 knots (~150 kmh^{-1}) and 400 feet (~ 120m). Sighting rods are devices fitted to the body of the aircraft outside the door openings that were adjusted for each observer at a height of 120m above the surface to define a sighting width of 200m on each side. The front observer and the pilot alerted the side observers to groups coming into view on their respective sides. When it occasionally occurred that a group was exactly under the line of flight, it was allocated to either the right or left side observer and the line of flight moved aside to allow them to make detailed observations. Circle back was employed to identify species and count individuals. Data for analysis comes only from the side observer records apart from the GPS locations of group sightings and observations of sighting conditions (e.g., sea state, turbidity).

The basic data for the response variable are the number and sizes of groups sighted on each transect. The number of individuals (sum of group sizes) sighted on each transect was standardised to a measure of sighting density by dividing by the observed area (km^2) and multiplying by 100 to yield a measure of the number of individuals sighted per 100 km^2. As all transects were 40 km long and the sighting width was limited to a total of 400 m the observed area on each transect was 16 km^2.

Although some data are yet to be derived from bathymetry and other records, covariates for models are in general those specified for the original occupancy model (2014 Methods and 2014 NT

Methods). There are two broad classes of covariates, those that measure the location or environmental characters of sites and transects, and those that measure variables that are thought to affect the probability of sighting a group should a group be present.

Models are fitted to the NT snubfin data to estimate five parameters reflecting habitat use: (1) site occupancy, (2) whether or not at least one group was sighted on transect, (3) the number of groups sighted on transect, (4) the sizes of the groups sighted on transect and (5) the sighting density (individuals per 100 km^2) on the area observed on each transect. A subset of potential covariates are assessed for all models. The latitude and longitude of each site (centroid of transects) and the zone type (AI, AN, AO, BN, BO) of each transect are fitted as location/environmental character covariates. Sea state (mean of several Beaufort scale estimates observed on transect), glare (mean of several percentage of area in glare estimates observed on transect, mean of both sides) and turbidity (mean of several 0,1,2,3 or 4 estimates observed on each transect) are fitted as detection covariates.

Occupancy model – initial results for snubfin dolphins in the Northern Territory

The standard (single season) occupancy model (MacKenzie et al. 2006; described in 2014 Methods) was used to estimate parameter (2); whether or not at least one group was sighted on each transect using program Presence V10.7. Preliminary analysis indicated that there may be a curvilinear relationship between group sighting rates and site latitude so a quadratic function of latitude was assessed. Site longitude and a quadratic function of site latitude were fitted as site covariates, and zone type (AI, AN, AO, BN, BO), sea state, glare and turbidity were fitted as detection covariates (called sample covariates in the occupancy literature) in the initial, full model. Note that while zone type is described as a detection covariate, the probability of detection depends on the density of dolphins in the area and variation in the probability of detection among zone types will represent the relative density (availability) of dolphins on the different zone types (see 2014 Methods p.6, p.22). Zone type was always fitted as a factor: i.e., all zone types or none. Covariates were systematically removed to compose a comprehensive set of models for comparison: an initial set of models was fitted with all site covariates included (latitude, latitude squared, longitude) with all combinations of the sample covariates (sea state, glare, turbidity, zone type). Further models were then fitted to correspond with the better-fitting (lower AIC; Burnham and Anderson 2002) of these to assess the effects of the site covariates.

Ten of the 16 models in the initial set (with site covariates latitude, latitude squared and longitude, and all possible combinations of sea state, glare, turbidity and zone type) had non-zero AIC weights. The AIC values for these models were very similar however, with AIC within a range of 5.0 and it was not clear which of the detection covariates were important or possibly not required. Sea state was present in six of the ten models with a combined AIC weight of 42%; glare was in eight of the ten models with a combined weight of 88%, turbidity was in four of the ten models with a combined weight of

56%, and zone type was in five of the ten models with a combined weight of 62%. While these results suggest an order of importance among the detection covariates of glare, zone type, turbidity and sea state it is not clear whether any could be left out of further comparisons.

The seven best-fitting (lowest AIC) of the initial 16 models (combined AIC weight 92% of the set) were refitted without the latitude squared covariate to assess the curvilinearity of the effect of latitude on the probability of occupancy. The results were equivocal with both the full set of site covariates (latitude, latitude squared and longitude) and the reduced set (latitude and longitude) being present in four of the eight best fitting of the full set of 23 models (8 models with 72 % of AIC weight in 23 models) and accounted for the same amount of total AIC weight.

The four models with the reduced set of site covariates (latitude, longitude) in the best fitting eight of 23 models were refitted without latitude (longitude only) to assess the contribution of latitude. It is clear that latitude is an important predictor of site occupancy with of none of the four models without this covariate accounting for as much as 1% of the AIC weight in the set of 27 models.

The eight best fitting models in the set of 27 models (70% of AIC weight) were refitted without longitude (latitude only or latitude + latitude squared) to assess the contribution of longitude. Site longitude is clearly an important predictor of site occupancy being present in the best fitting 14 and accounting for 84% of the AIC weight in the full set of 35 models. Model fit statistics are reported for the 35 models in Appendix 1, Table 1.

Model averaged estimates (Buckland et al. 1997) of the probabilities of occupancy and detection were obtained. The probability of occupancy decreases along a quadratic curve from north to south and increases linearly from west to east. The coefficients for a prediction function are not readily available for model-averaged estimates so the effects of individual predictors are difficult to evaluate or plot. However, the predicted probabilities of occupancy are plotted by latitude in Figure 1. The effect of longitude is also apparent in the figure: the probability of occupancy decreases from a maximum of 0.98 at around -11.2 S, 132.6 E to less than half of this at a minimum of 0.42 at around -14.9 S, 129.2 E; the top curve represents movement south and east while the bottom curve represents movement south and west. The mean estimated probability of occupancy by snubfin dolphins in the Northern Territory is 0.86 with standard deviation 0.16. Given that these data were collected from a random sample of 40 km long sites, the results imply that snubfin dolphins are widespread in the Northern Territory and may not be located in small, isolated groups.

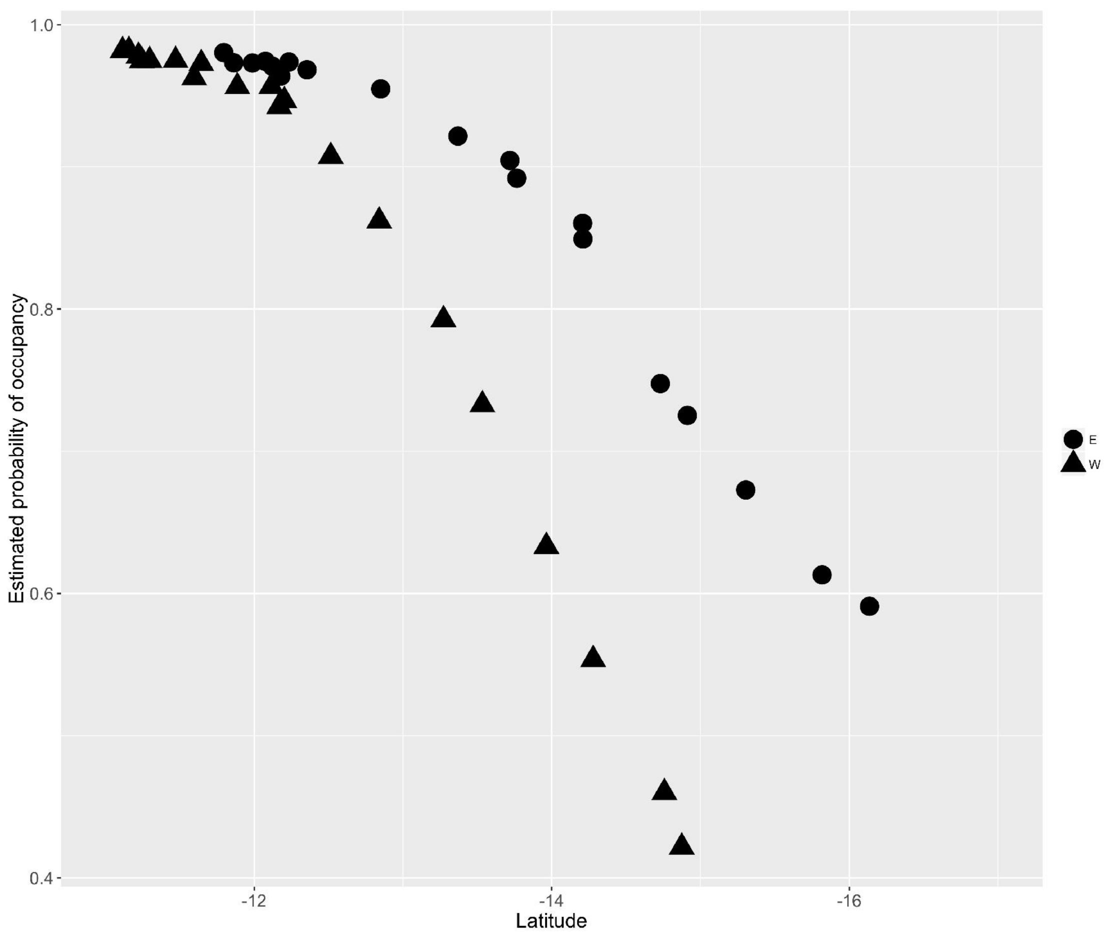

Figure 1 Predicted probability of occupancy by latitude. The effect of longitude is also apparent in the figure: the probability of occupancy decreases from a maximum at around -11.2 S, 132.6 E to around -14.9 S, 129.2 E; the top curve represents movement south and east of the maximum while the bottom curve represents movement south and west.

The model averaged estimates of the probability of detection are a function of sea state, glare, turbidity and zone type. An indication of relative rates of use of the five zone types may be represented in their mean detection estimates. Although a more in-depth analysis would be required to separate the effects of sea state, glare and turbidity from zone type, the mean probabilities of detection were 0.36 (SD=0.04), 0.44 (SD=0.04), 0.40 (SD= 0.04), 0.37 (SE=0.04) and 0.30 (SD= 0.03) for the estuarine inshore, estuarine nearshore, estuarine offshore, coastal nearshore and coastal offshore zones respectively. On the assumption that the values of the detection variables (sea state, glare and turbidity) were reasonably consistent over zone types, these results suggest that overall, snubfin dolphins occur at greater densities in estuarine than coastal sites, in the nearshore and offshore rather than the inshore zone in estuarine sites, and in the nearshore rather than the offshore zone in coastal sites. The nearshore zone (0-5 km from the estuary mouth line or coast in estuarine sites or 0-5 km from the coast in coastal sites) is better favoured than other zones in both estuarine and coastal sites.

While apparently used less frequently than the nearshore zone, the offshore zone (5-10 km offshore) appears to be used reasonably frequently suggesting that snubfin dolphins may relatively often range further than 10 km from shore.

A more comprehensive occupancy analysis of the Northern Territory coastal dolphin presence/absence data is planned for late 2016. These results are presented here for comparison with those from the proposed alternative model rather than as a complete report of an occupancy model on the data.

A relative density model

The occupancy model presented above conveys useful information about the distribution of snubfin dolphins around the Northern Territory coastline. The Efford and Dawson (2012) critique of occupancy in continuous habitat indicates however that the occupancy estimates may be biased depending on the sizes of home ranges and the background density of the species in the area. Indeed, the results suggest that snubfin dolphins are so widespread in the region that it is not clear what sense can be made of the home-range concept for this species in the Northern Territory. Nonetheless, it is possible that any bias in the estimated probability of occupancy is consistent over the sample and the estimates over the set of site latitudes and longitudes may provide a reasonably reliable indication of the distribution of snubfin dolphins around the coast.

Bias in the estimates aside, there are other reasons why an alternative model should be developed: occupancy models analyse only the presence or absence of at least one dolphin group on transect and don't make use of the available data on the number of groups, the sizes of the groups or the total number of individuals sighted on transect. Further, the available software for occupancy modeling does not allow for fitting flexible curves to covariate-response relationships which may better reflect habitat selection around a complex coastline than the polynomial functions employed above.

Generalised additive models

Anticipating the subsequent discussion, we have chosen the R package mgcv (Wood 2016) for fitting the relative density and other models. The author of package mgcv has written a book on generalised additive models (Wood 2006) that will be used as our primary reference for the statistical material to be presented. Where we do not provide them, references to other or original sources can be found there.

The generalised linear model (Nelder and Wedderburn 1972) extends the well-known general linear model (GLM; e.g., Sengupta & Jammalamadaka 2003) for normally distributed response variables to include models for categorical and other non-normal data by means of functions that link the linear predictor (the equation on the right of a GLM or multiple regression model) to the response variable. Binary logistic regression is an example of this in which a binary response (0, 1; present, absent; captured, not captured; etc.) is modeled as a function of covariates through the logit link.

Generalised additive models (GAM; Hastie and Tibshurani 1986, 1990) extend this even further to model the relationships of continuous covariates (predictors) to the response variable by means of flexible, smooth functions, rather than in terms of more rigid polynomials or other fixed functional forms. Package mgcv fits smooth functions as cubic splines (piecewise cubic polynomials that interpolate between the values, similar to a Bezier curve), 'thin plate' or other spline types (see Wood 2006 p. 222). While specific functional relational forms may be natural choices in some physical or experimental contexts, they are unlikely to be sufficiently flexible to adequately describe natural relations in environmental observational data, such the observed density of a dolphin species around a complex coastline for example.

General (and generalized) linear mixed models (GLMM; Pinheiro and Bates 2000) extend the general and generalized linear models to include random effects in addition to the fixed effects in the linear predictor. As our need for a random effect is a relatively simple case, we describe our case and the random effect we require in a relatively informal way and leave the interested reader to pursue a more formal treatment and the general case. All linear models include one random effect in the linear predictor – the residual variance. Linear mixed models include other residual variances (and sometimes covariances) in addition to those for the residual. Note that as residual variances, these effects summarise variation 'left over' after fixed effects (predictors) have been fitted and some variation in the data has been 'explained' or extracted.

The sampling design for this study generated a 'cluster sample' in which transects are grouped in sites. This follows naturally from an occupancy study on sites with replicates (samples) but, as described above, also represents an efficient way to sample an extensive, often remote coastline. To the extent that the data collected on transects within sites are more similar to each other than to data collected on different sites, the transect data will be correlated and correct inference requires an analysis for correlated data. Correlation among transect data arising from differences in the typical value among sites may be treated by fitting a random effect for site (a site level residual variance) in addition to the residual variance for transect. Although more complex structures are possible, we assume that the differences among sites are simply differences in the mean values of the data collected on the transects on each and it is only necessary to fit a residual variance for the site means (called a random intercept effect) to soak up the correlation due to the clustering of transects in sites.

While package mgcv includes methods for fitting generalized linear additive models (GAMM; Wood 2006 Ch. 6), it is possible to fit a simple random intercept effect for site with the methods used to fit GAM models. This arises as a consequence of the fact that smooths may be interpreted as mixed model components (Ruppert et al. 2003) and the methods employed to estimate smooths may also be used to estimate simple random effects such as a random intercept effect for site.

Smoothing methods

A number of different smoothing methods are available in package mgcv including thin plate regression splines. Thin plate regression splines have several advantages over conventional regression spline smoothers including that they avoid the problem of estimation of the optimal number and placement of knots (points at which segments of the curve are joined) (Wood 2006, pp.150-156). They have the additional advantage that smooths of lower rank are nested within smooths of higher rank, so that it is legitimate to use conventional hypothesis testing methods to compare models (see R documentation for mgcv; Wood 2006, pp. 154-156).

The additional flexibility of a smooth function relative to a function with determinate form is advantageous in representing complex relationships in observational data but, if taken too far, it would simply reproduce the observed data without providing a useful, parsimonious summary or the form of the general relationship. The 'wiggliness' of a regression spline curve is controlled by applying a penalty for the complexity of the shape to obtain a parsimonious good fit to the data through an iterative optimisation process. A modified version of thin plate regression splines has been developed to potentially shrink the parameter space of a curve to zero rather than to some minimum function (Wood 2006, p.156) facilitating removal of uninformative covariates from a model. Marra and Wood (2011) discuss shrinkage methods for spline fitting and present results to show that they not only facilitate elimination of spurious covariates leading to a simpler model but also 'perform significantly better than the competing methods in terms of predictive ability'.

Smooth functions can be fitted to one covariate at a time (a univariate smooth) or, in principle, any number of covariates simultaneously (a multivariate smooth and tensor product smooths; Wood 2006, pp.158-163). Tensor smooths have the advantage of being 'scale invariant' and are especially useful for representing functions of covariates measured in different units.

Mgcv employs a penalised version of the iteratively re-weighted least squares algorithm (P-IRLS; Wood 2006, pp.136, 165-166) to obtain penalised likelihood estimates of model parameters. Several alternative methods may be used to implement smoothing parameter estimation criteria, including the unbiased risk estimator (UBRE; Wood 2006, pp.168-169) for response distributions with known scale parameters and generalised cross validation (GCV; Wood 2006, pp. 129, 171-174) for response distributions for which the scale parameter must be estimated. The scale parameter of a distribution describes its variance; the binomial and Poisson and distributions have known scale parameters as specific functions of their means; the Normal distribution has an unknown scale parameter (σ^2), as do the negative binomial and Tweedie distributions (see below).

Restricted maximum likelihood (REML; Wood 2006, pp.293-295) may be used to fit GAMs whether or not the response distribution has a known scale parameter. Marra and Wood (2011) found REML to yield more precise estimates from shrinkage splines than the alternative fitting methods. We have used REML estimation in all models.

Example of GAMs on several response distributions from data on snubfin dolphins in the Northern Territory

Response variables and proposed model distributions

We propose to fit GAMs to

- Whether at least one group was sighted on each transect or not. Although this expression is used to emphasise that while sighting a group indicates its presence, not sighting a group does not indicate absence because a group may have been present but not sighted, we subsequently refer to this variable as group presence/absence.
- The number of groups sighted on each transect.
- The sizes of the groups sighted on each transect.
- The sighting density of individuals on each transect (individuals per 100 km^2).

We propose the following probability distributions for the responses

- Group presence/absence – binomial distribution.
- Number of groups – Poisson distribution.
- Group size – negative binomial distribution.
- Sighting density – Tweedie distribution.

The binomial and Poisson distributions are well known; the negative binomial distribution may be less so but knowledge of the Tweedie distribution is limited to researchers in a relatively few fields.

The Tweedie distributions are a family of distributions within which a number of better known distributions are included as special cases including the normal, Poisson, gamma and others. A salient feature of any Tweedie distribution is that the variance $var(Y)$ relates to the mean $E(Y)$ by the power law $\mathrm{var}(Y) = a[E(Y)]^p$, where a and p are positive constants. The normal distribution is a Tweedie distribution in which $p = 0$; in the Poisson distribution $p = 1$; in the gamma distribution $p = 2$. We're interested in a Tweedie distribution in which $1 < p < 2$.

The power law relationship of the mean to the variance of the Tweedie distribution is of particular relevance to ecologists who are interested in the variance of the number of individuals of a species per unit area of habitat; this is often described by Taylor's law (Smith et al. 2014). Taylor's law is an empirically derived relationship from numerous ecological studies and may be expressed as follows: $\mathrm{var}(Y) = a\mu^p$ where Y is a population count on a given area with mean μ. Kendall (2004) argues that Taylor's law arises as a consequence of a general mathematical convergence effect and does not require an animal behavioural or population dynamic account. However it might be accounted for, empirical studies have found that the clustering of animals in space can often be described by a Tweedie distribution in which $1 < p < 2$ (Engen et al. 2008).

Foster and Bravington (2012) discuss Tweedie generalized linear models for analysis of continuous, non-negative ecological data that include exactly zero observations (e.g., when no group is sighted in our case). They take advantage of the fact that a Tweedie distribution with $1 < p < 2$ is equivalent to the sum of a Poisson number of gamma random variates to extend the Tweedie model to yield estimates of both the Poisson and gamma parts from a unified model rather than simply their sum as in the normal Tweedie case. Their model has a number of potential advantages in some contexts but we expect a Tweedie GAM to provide very reasonable estimates for the present research without the extra complexity of the Foster and Bravington model.

Tests of the fit of the proposed distributions to the data

Histograms of the observed data on group presence/absence, number of groups, group size and sighting density are shown in Figure 2.

We tested the hypotheses that the data on the four response variables fitted the proposed distributions by fitting the observed data to the proposed distributions, simulating new data from the estimated parameters and comparing the observed and simulated distributions using a Komolgorov-Smirnov test.

None of the four tests indicated rejection of these null-hypotheses with p-values from the Komolgorov-Smirnov tests being 0.99, 0.99, 0.99 and 0.29 for the binomial, Poisson, negative binomial and Tweedie distributions respectively.

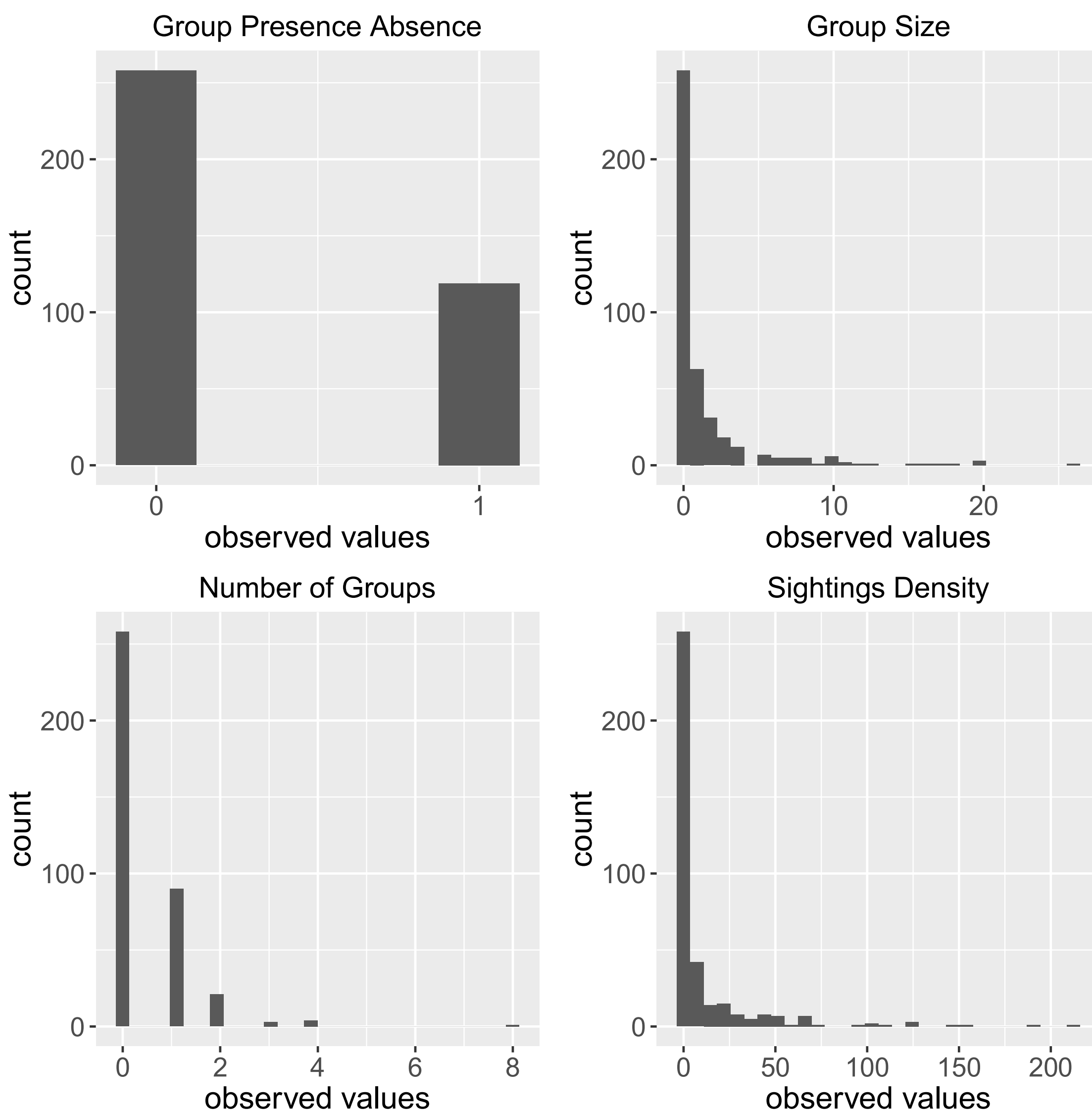

Figure 2 Histograms of the observed group presence/absence, number of groups, group size and sighting density data on snubfin dolphins in the Northern Territory

Fitting GAMS

We fitted the five-level factor for zone type (AI, AN, AO, BN, BO) and used shrinkage splines for the continuous predictors (site latitude, site longitude, turbidity, glare and sea state) and a random effect for site. Tensor product smooths were fitted for combinations of two or more variables including site latitude and longitude, and various combinations of the sighting covariates (turbidity, glare and sea state).

Fitted GAMs were checked following the methods described by Wood (2006, pp.229, 230, 234; also see pdf https://statistique.cuso.ch/fileadmin/statistique/document/part-3.pdf) using the 'gam.check' function in mgcv and included examination of residual plots. Although the 'gam.check' function routinely tests for the number of knots in spline fits, this was redundant with thin plate regression splines and shrinkage smooths. Examination of 'concurvity' is an important component of GAM checking. Concurvity in a GAM is analogous to multicollinearity in a GLM and refers to similarity between the forms of smooth functions of different variables, and leads to similar difficulty in interpreting the effects of a model. Severe concurvity can also bias estimates of residual variance (Ramsay et al. 2003). The 'concurvity' function provides measures of concurvity (scaled to a 0:1 interval) for all smooth terms in a model. Concurvity is a common problem in GAMs that include functions of spatial location (e.g., latitude and longitude) and functions of covariates that may also vary spatially.

We used differences in the explained deviance (Wood 2006, p.69) of models with different covariates and the p-values for the effects to determine which effects to include in a final model. Although the p-values are approximate and may sometimes be too small, it is safe to conclude that an effect with $p > 0.05$ is clearly not significant and might be eliminated from the model (Wood 2006, p.191). The p-values of the terms in the model are more accurate under REML than UBRE or GCV estimation: "In simulations the p-values have best behaviour under ML smoothness selection, with REML coming second. In general the p-values behave well…" (Wood, http://search.rproject.org/library/mgcv/html/summary.gam.html).

Concurvity was assessed as part of the model-fitting process and smooth functions of sighting covariates were sometimes removed and replaced with others if they induced concurvity in the location (site latitude, site longitude) covariate function. Models were assessed for univariate smooths of each, and tensor smooths of two-variable and the three-variable combinations of the sighting covariates. These functions were initially fitted separately in models to identify those with the strongest relationships with the response variables (more deviance explained, lower p-values) and then together with the location covariates (zone type and latitude and longitude) to identify those that induced unacceptable levels of concurvity.

Model fitting

Names, predictor terms included and statistics (p-values and concurvity for terms, and percentage deviance explained) are reported for a number of models fitted to each response variable in the Appendix, Table 2. Terms with p-values > 0.05 were systematically removed until a final model with only significant terms ($p < 0.05$) was identified. These final models are shown with a grey background in Table 2.

The tensor spline of the three sighting variables (turbidity, glare and sea state) invariably resulted in high concurvity on the tensor spline of site latitude and site longitude and was not further considered in order that the location (site latitude and site longitude) tensor was subject to clear interpretation. Tensor splines of any two of the sighting variables did not have this effect and were all considered in models. The tensor of turbidity and glare was always favoured over tensors of the other pairs of sighting variables with models including it having a greater percentage of deviance explained. The two-variable tensors of the sighting variables always outperformed splines of any one sighting variable and models including them are not reported.

None of the final models accounted for a large percentage of the deviance with 8.2%, 12.7%, 18.8% and 17.7% of the deviance explained by the final models for group presence/absence, number of groups, group size and sighting density respectively. No final model included a random variance for site with the site random effect always being eliminated in the model-reduction process. The relatively low percentages of explained deviance and lack of significance of the site random effect indicate that the variation in the responses among transects is large relative to the variation among sites.

Although the zone type (AI, AN, AO, BN and BO) factor was significant ($p < 0.05$) at some stage of the model-reduction process for most response variables, the evidence for differences among zone types on group presence/absence, group size and sighting density was relatively weak and the effect was absent in the final models. However, the zone type effect remained significant ($p = 0.046$) in a competitor for the final model for number of groups while the tensor of turbidity and glare was not. When the zone type effect was removed and replaced by the tensor of turbidity and glare, the latter was significant while the zone type effect was not. Both models had similar percentages of explained deviance (12.9% for the model with zone type and 12.7% for the model with the tensor of turbidity and glare) and the model with the tensor of turbidity and glare was selected for interpretation for consistency with the effects in the final models on the other response variables.

Although the Poisson distribution was found to be a good fit to the observed number of groups, examination of residuals from best fitting Poisson model indicated overdispersion and a negative binomial distribution was employed to model number of groups. The negative binomial and Poisson distributions are very similar except that the negative binomial distribution has an extra parameter for variance (Gardner et al. 1995).

The final models for all response variables except for group presence/absence had the same predictor effects: a tensor spline of site latitude and site longitude, and a tensor spline of turbidity and glare. It may be the case that, where dolphin groups are present on a transect pass, the probability of sighting at least one is not greatly affected by the sighting conditions.

Contour plots are presented to show the form of fitted functions of two variables with the estimated value of the response variable represented by colours such that higher values are represented by lighter colours. The plotted values are centred on zero and estimated at the nearest observed values to the medians of variables in the model but not shown in the plot.

Predicted values were derived from the final models (generated from the ‘basis’ functions for the spline terms) for each response variable at the latitudes and longitudes of each of the sample of sites at the values of turbidity and glare that maximised the predicted values. This was in order to estimate 'what would have been seen' had sighting conditions been ideal. The predicted values for each response variable together with their standard errors are presented for the latitudes and longitudes of the sample of sites in the Appendix, Table 3. The predicted values are ordered from west to east for comparison with the plot of sample sites in Figure 4.

Group presence/absence – binomial model

The final model for group presence/absence was relatively simple with only a tensor smooth of site latitude and site longitude surviving the model-reduction process. The tensor smooth of site latitude and site longitude was strongly significant with $p < 0.001$; the explained deviance was 8.2%. A contour plot of the predicted probability of presence from the fitted smooth is presented as Figure 3. Lighter colours indicate a higher probability of presence. The prediction only applies to the 10 km wide coastal strip and the plot may be best interpreted by reference to the associated map of the Northern Territory in Figure 4 and in terms of the predicted values in the Appendix, Table 3.

The mean predicted probability of sighting at least one group per transect over the set of sample sites (Appendix, Table 3) was 0.32 (mean SE = 0.06). Predicted values ≥ 0.4 were observed in the west between latitudes -12.8S and -13.5S, and in the east (Western Cape York; WCY) between -12.2S and -14.2S. Predicted values ≤ 0.24 were observed in the west further south than 14.3S, and around the Tiwi islands in the far north; in the east, the lowest value occurred at the most southerly and easterly site.

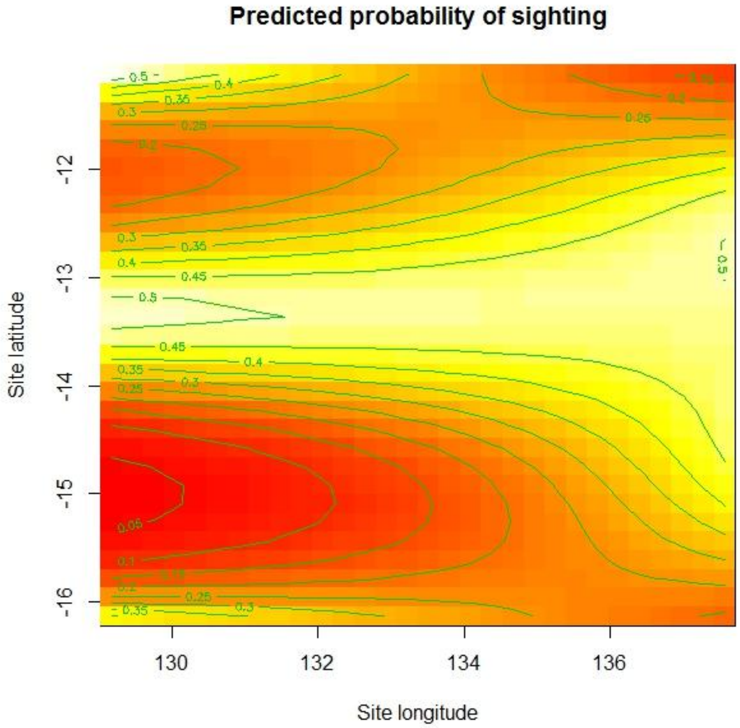

Figure 3 Contour plot of the predicted probability of sighting at least one group of snubfin dolphins by site longitude and site latitude

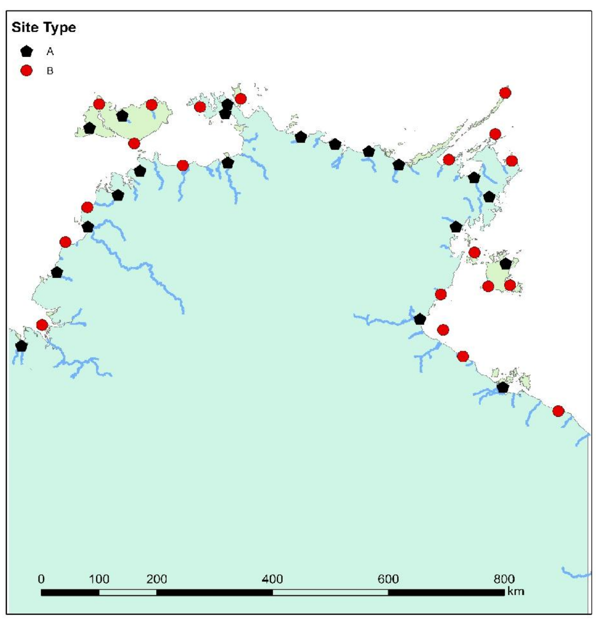

Figure 4 Map of the Northern Territory showing the locations of sample sites; the northern-most site was at -11.1S and the southern-most at -16.1S; the western-most site was at 129.1E and the eastern-most was at 137.6E.

Number of groups – negative binomial model

As described above, the residuals from a Poisson model were overdispersed and the data were estimated under a negative binomial model. The tensor smooth of site latitude and site longitude and the tensor smooth of turbidity and glare were both significant ($p \leq 0.01$); the explained deviance was 12.7%. A contour plot of the estimated number of groups sighted by site latitude and site longitude is presented as Figure 5.

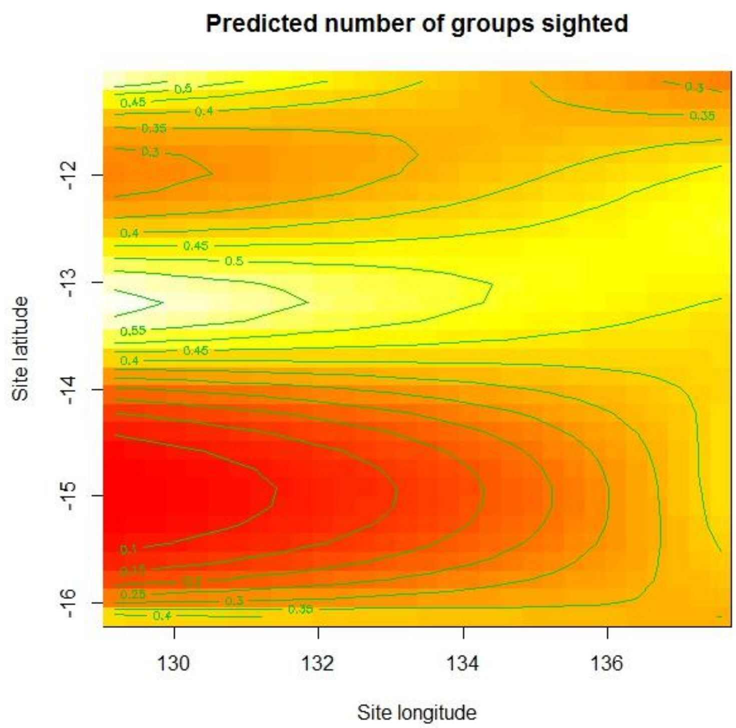

Figure 5 Contour plot of the predicted number of snubfin dolphin groups sighted by site longitude and site latitude

The mean predicted number of groups sighted over the set of sample sites (Appendix, Table 3) was 0.83 (mean SE = 0.34). Note that these estimates include transects on which no group was detected and a large number of zeros may be included in calculation of the site mean. Greater than one group was predicted to be sighted in the west between -12.8S and -13.5S, and at North Melville Island (-11.2S); in the east more than one group was predicted to be sighted between -12.2S and – 13.4S. Fewer than 0.65 groups was predicted to be sighted in the west south of -14.0S; in the east (WCY0, fewer than 0.65 groups was predicted to be sighted south of -14.7S.

Variation in the predicted number of groups sighted by turbidity and glare is shown in the contour plot, Figure 6. Predicted values are maximised at low values of turbidity and low to moderate values of glare.

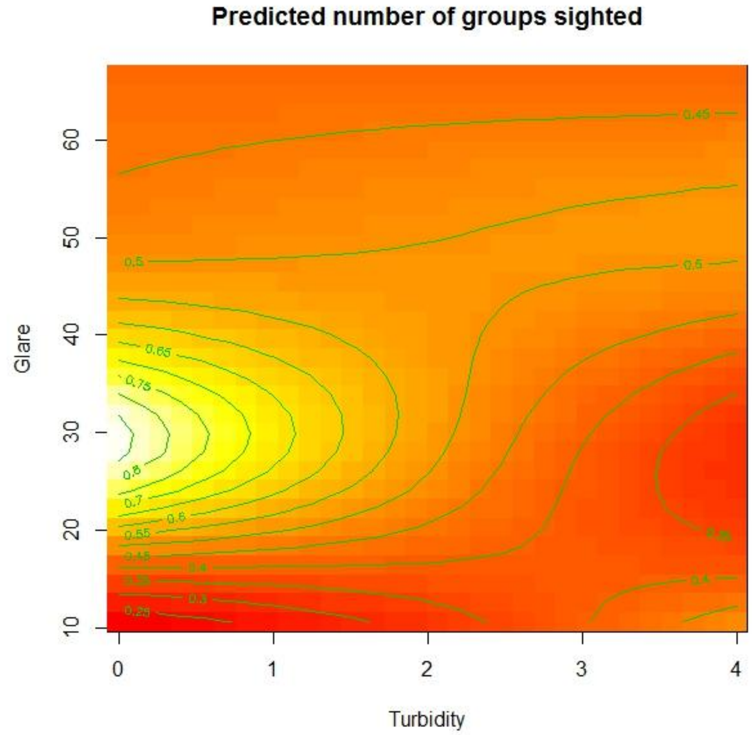

Figure 6 Predicted number of snubfin groups sighted by turbidity and glare

Group size – negative binomial model

The tensor smooth of site latitude and site longitude and the tensor smooth of turbidity and glare were both significant (lat. & long. $p \leq 0.001$: turbidity & glare $p = 0.024$); the explained deviance was 18.8%. A contour plot of the estimated mean group size by site latitude and site longitude is presented as Figure 7.

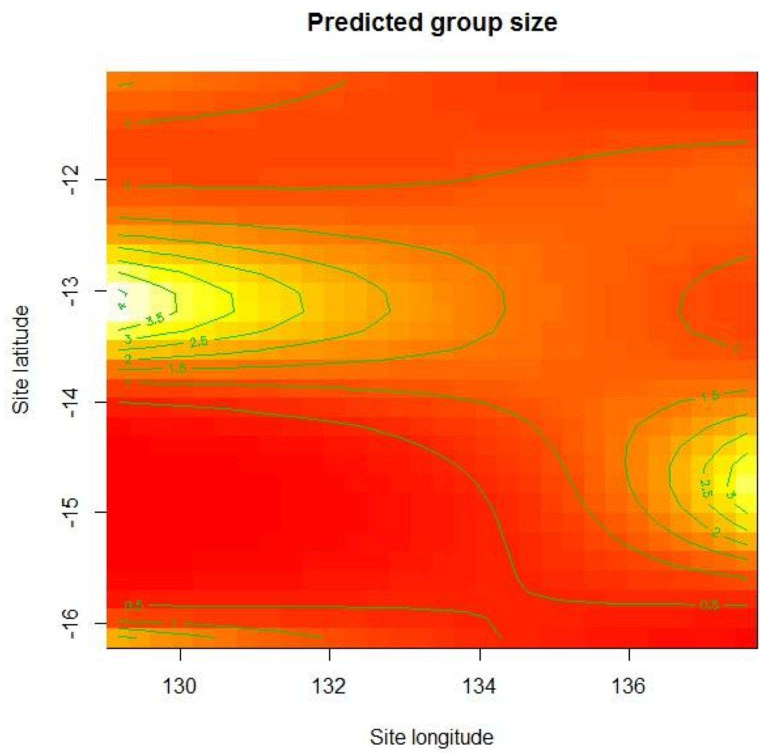

Figure 7 Predicted size of snubfin groups by site longitude and site latitude

The mean predicted snubfin group size over the set of sample sites (Appendix, Table 3) was 5.24 dolphins (SE = 4.17). Predicted group sizes greater than seven were observed in the west between -12.5S and -13.5S; in the east, group sizes greater than seven were observed at around -14.2S. Predicted group sizes of less than five were common but there were relatively few predicted group sizes of less than four. Predicted group sizes of less than four were observed in the west south of -14S; there was one estimate of less than four in the mid longitudes at around -11.6S; in the east, predicted group sizes of less than four were observed south of -15.8S.

Variation in the predicted group size by turbidity and glare is shown in the contour plot, Figure 8.

The predicted value of group size is maximised around the mid. range of turbidity values and at maximum glare values. This is counter-intuitive on the face of it but may be reasonable. The predicted value by turbidity and glare functions are discussed below.

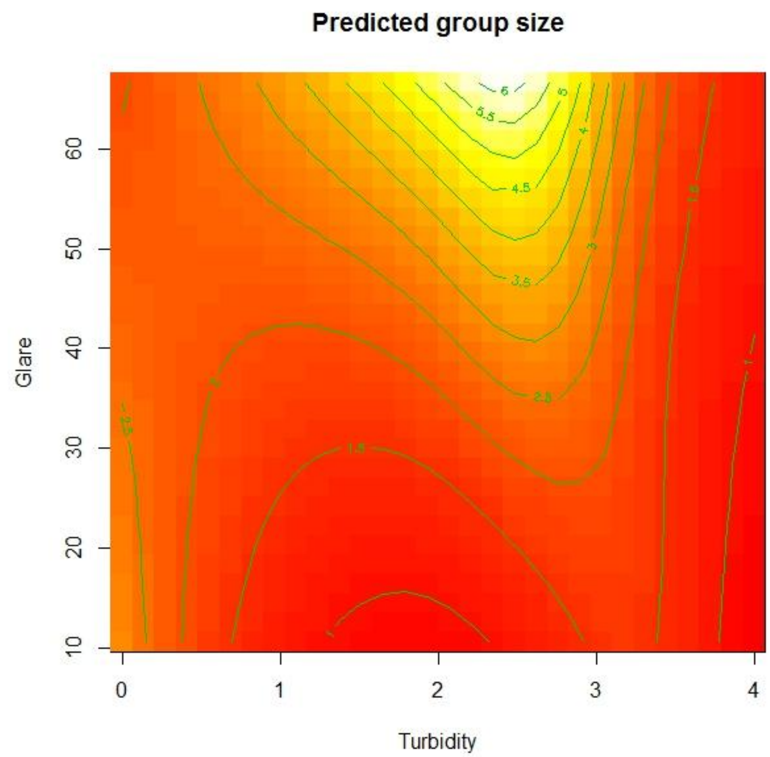

Figure 8 Predicted size of snubfin groups by turbidity and glare

Sighting density – Tweedie model

The tensor smooth of site latitude and site longitude and the tensor smooth of turbidity and glare were both significant (lat., long. $p \leq 0.001$: turbidity, glare $p < 0.020$); the explained deviance was 17.7%. A contour plot of the predicted sighting density by site latitude and site longitude is presented as Figure 9.

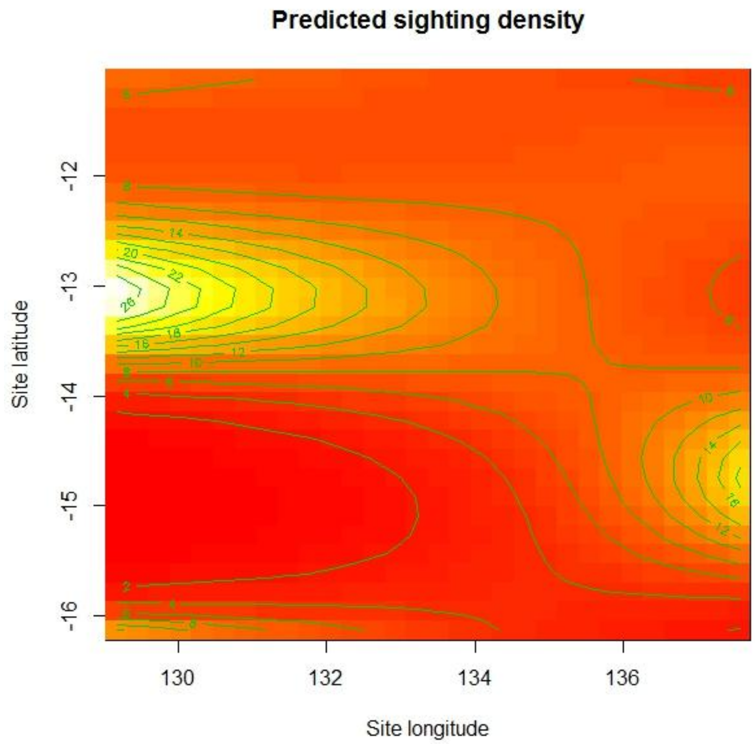

Figure 9 Predicted sighting density of snubfin dolphins by site longitude and site latitude

The mean predicted sighting density for snubfin dolphins over the set of sample sites (Appendix, Table 3) was 72.9 dolphins per 100 km^2 (SE = 65.9). Predicted sighting densities of greater than 90 snubfin dolphins per 100 km^2 were observed in the west between -12.5S and -13.5S; in the east (WCY), predicted sighting densities of greater than 90 snubfin dolphins per 100 km^2 were observed at around -14.2S. Predicted sighting densities between 60 and 90 snubfin dolphins per 100 km^2 were common but predicted sighting densities of fewer than 60 snubfin dolphins per 100 km^2 were relatively few; these low densities were observed in the west south of -14S; in the east they were observed south of -15.8S.

Variation in predicted sighting density by turbidity and glare is shown in the contour plot, Figure 10.

The turbidity by glare function predicting sighting density is very similar to the function for group size (Figure 8) and is subject to the same reservations.

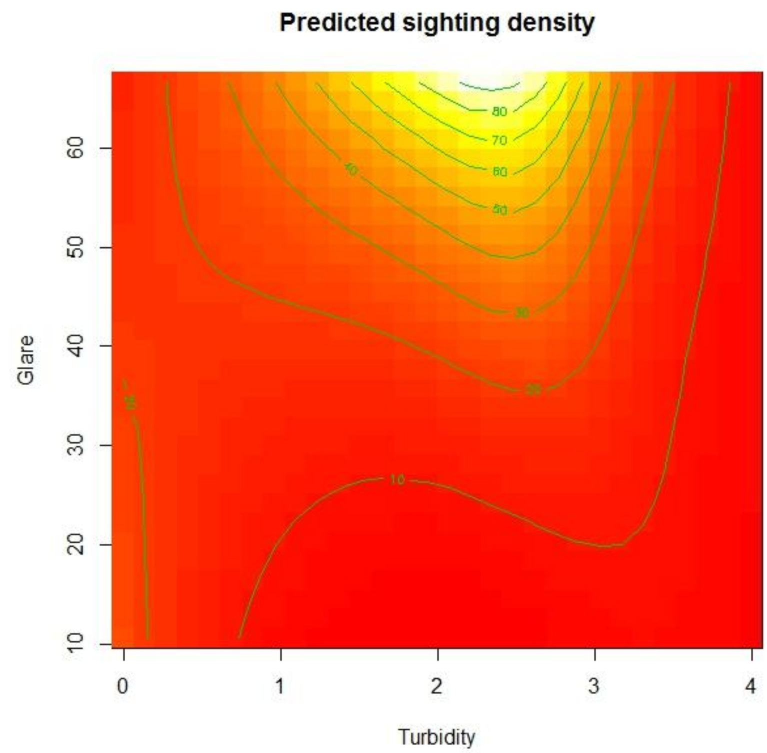

Figure 10 Predicted sighting density of snubfin dolphins by turbidity and glare

Interpretation of the smooth functions of turbidity and glare

The smooth of turbidity and glare for the number of groups sighted on transect appears reasonable being maximised at low values of the two variables. The smooths of turbidity and glare for group size and sighting density are somewhat puzzling, being maximised around the mid. range of turbidity values and at maximum glare values. The function for number of groups and the functions for group size and sighting density represent different field situations however, with circle-back being used to count dolphins in groups and with group size apparently dominating number of groups in the sighting density function. Although circle-back was not always used, when single individuals or a very small group was sighted for example, it was typically used when larger groups were sighted. Circle-back moves the aircraft off the transect line for which turbidity and glare were calculated and to a position in which sighting conditions are more optimal for counting individuals.

It should also be recognised that the smooths of turbidity and glare are partial functions representing the unique contribution of these variables given the presence of the smooth for site latitude and site longitude in the model. Despite the different situations in which groups are sighted on transect and individuals within groups counted during circle-back, and the partial nature of the smooths, we remain somewhat suspicious of the functions of turbidity and glare in the group size and sighting density models.

Smooths of spatial variables are sometimes subject to edge effects such that they 'curl up at the edges', i.e., at values near the ends of the variable distributions (Miller et al. 2013). If this has happened, it appears to have affected glare greater than turbidity. Field observers have noted that sometimes glare can be advantageous because it glints off wet dorsal fins and there may be some sort of interaction between this sighting effect and a potential edge effect in the smooth.

We have not had time to fully investigate the possibility of edge effects in the smooths of turbidity and glare in models on data that involve counting individuals during circle-back and our enquiries are ongoing.

While doubt remains about the appropriateness of the smooths of turbidity and glare for response variables on data that involve counting individuals in groups, the predicted values for group size and sighting density tabled in the Appendix (Table 3) and reported above should be treated as provisional.

Relationship of response variable predicted values

As may be discerned in a general sense from the contour plots shown above (Figures 3, 5, 7 and 9), the predicted values of the several response variables display a similar spatial pattern. The predicted values from the Appendix, Table 3 are plotted together in Figure 11. The scale of sighting density has been changed from individuals per 100 km^2 to individuals per 10 km^2 for display. Figure 11 makes it clear that the probability of sighting at least one group, the number of groups sighted, the sizes of groups and the sighting density of individuals all follow a similar spatial pattern: i.e., the predicted values of all response variables tend to be greater where there are more dolphins.

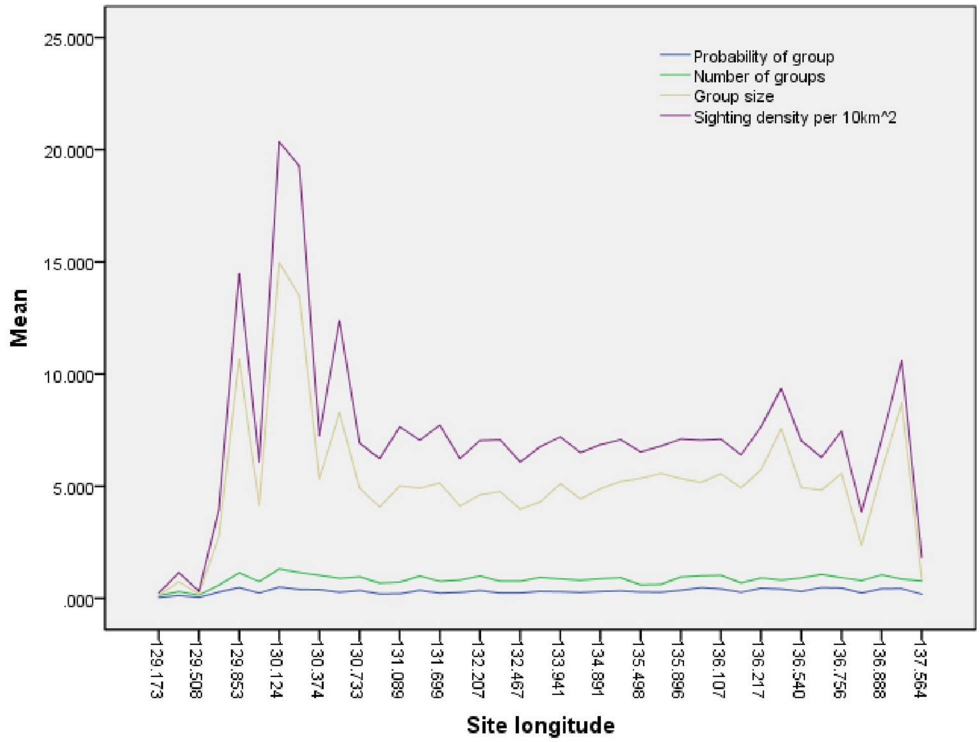

Figure 11 Probability of group detection, number of groups, group size and sighting density by site longitude

Summary of example GAMs

The objective of the exercise of fitting GAMs to the response variables (probability of sighting at least one group, number of groups sighted, group size and the sighting density of individuals) was to demonstrate an alternative to modeling the probability of occupancy. A pragmatic and robust approach has been taken to GAM fitting: tensor product smooths, thin plate shrinkage smoothing splines and REML estimation are chief features of this approach. There are many options that might be explored to estimate a more optimal model however.

Tensor product functions have the useful feature of being invariant to scaling of the variables so that they do not need to be measured on the same scales. This may come at some cost to flexibility however, and a more optimal fit to site latitude and site longitude might be achieved by rescaling site latitude and site longitude to a Euclidean grid (to make the x and y scales the same) and fitting a normal bivariate thin plate smooth. Similarly, the turbidity and glare variables might be standardised prior to fitting.

The main concern with the fitted models for group size and sighting density is the possibility of edge effects particularly in the sighting covariate function of turbidity and glare (Miller et al. 2013). We have not had time to fully explore this and our investigations are continuing. Although the sampling methods employed do not allow for estimating the proportions groups or individuals missed as a dual sampling protocol might, making predictions from the models at optimal values of covariates that affect sighting conditions allows for some adjustment of the observed estimates to 'what would have been seen' had sighting conditions been optimal. This is the approach taken here but the accuracy of the predictions depends strongly on the appropriateness of the functions fitted to the sighting covariates.

Overall, although we cannot claim that the models fitted in the examples are optimal, we think they've served the purpose of identifying a viable alternative to occupancy modeling for the data. Moreover, the estimates produced go well beyond analysis of whether nor not at least one group was sighted on transect to include information on the number and sizes of groups sighted, and the sighting density of individuals. Moreover, relative to the sorts of fixed-form curves that might be implemented in the occupancy modeling program Presence, the flexible curves that may be implemented using a GAM program like mgcv offer a much more accurate description of the distribution of dolphins around a complex coastline.

Provided there is reasonable confidence in the fitted functions of sighting covariates, the predicted values offer a basis for estimation of the minimum population size by expansion of the sighting density predictions to the whole sampled area. Such an estimate would inevitably be a minimum as it could only apply to the sampled 10 km wide coastal strip and the sampling protocols employed cannot allow for a full account of dolphins that were present but not sighted. Nonetheless, as coastal development usually occurs within this strip, the models provide a very useful description of coastal habitat usage and the relative conservation values of different parts of the coast. In addition, it seems likely that groups of these dolphin species that use areas further offshore are likely to also use and be dependent on this coastal strip.

Further comment on Objective 2 – National distribution data

The full statement of Objective 2 (2015 Framework p. 27) is:

"Objective 2 - National Distribution Data: Provide for access to and analysis of standardised national tropical dolphin data to assess distribution and underpin management and conservation.

2.1 Undertake a national synthesis of all available distribution, abundance and related data (e.g. habitat, ecology) of Australian snubfin dolphins and Australian humpback dolphins, and of Indo-Pacific bottlenose dolphins within the ranges of the other two species, and manage as a centralised, accessible data repository with associated metadata.

2.2 Conduct an expert workshop to consider and address issues surrounding methodologies, such as survey techniques (e.g. boat, aerial), underpinning statistical approaches, and comparability of data amd produce best practice guidelines

2.3 Conduct systematic occupancy (replicated presence/absence) surveys, using agreed techniques, to describe the spatial distribution of important habitats over each species' range.

2.4 Investigate the feasibility of using various species to estimate the detection rate and abundance at a small sample of sites for use together with detection rate data from presence/absence surveys (2.3) to better estimate abundance over the each species' range.

2.5 Identify tropical dolphin habitats at ecologically appropriate scales and develop spatial habitat models, evaluate models, and investigate transferability of model results to unstudied areas.

2.6 Identify Biologically Important Areas for Australian's tropical dolphins in accordance with the established protocol for inclusion in the Conservation Values Atlas."

We are not aware of any initiative to establish a central repository for tropical inshore dolphin data (2.1).

The proposed expert workshop (2.2) has not yet been convened.

The conduct of systematic occupancy (replicated presence/absence) surveys (2.3) was a major focus of 2014 Methods and described in detail in this report. It is contended that the methods described herein offer a systematic approach and highly informative description of the spatial distribution of the species. The results apply however at a relatively broad scale although the sensitivity of the smooth functions provides a level of detail not envisaged under an occupancy modeling approach. The example models presented here did not make use of all potential covariates and, although the results did not include significant differences among the zone types. The effect was however reasonably close to significant and it is possible that factors that distinguished between estuarine and coastal sites, or the nearshore and other zones would be significant. The inclusion of further covariates (see 2014 Methods) may account for more of the residual variance and increase the power to detect such finer-scaled habitat use effects.

Water depth is an effect that may be of interest but it is not possible to estimate this directly in any model based on data at the transect level because depth varies widely over the lengths of transect required to achieve suitable detection rates. The data collected following a transect design include the specific locations of each group sighting and water depth at these locations might be derived from bathymetry maps. An alternative modeling strategy (e.g., Bagchi and Illian 2015) would be needed to assess such highly spatially variable covariates.

It is not clear until the sorts of broad scale results demonstrated here are available that sensible judgments about what ecologically appropriate scales (2.5) are. The approach taken here to the question of transferability of model results to unstudied areas has been to use standard sampling theory to link the gaps between sample sites through functions of spatial covariates.

The sorts of results described here might be used to identify biologically important areas (2.6) for inclusion in the Conservation Values Atlas.

The possibility of using abundance estimates on a sub-sample of sites studied in a broad scale sighting survey (2.4) is considered directly.

Abundance estimation by ratio estimation with double sampling

It may be possible to derive an estimate of total abundance on the area sampled for counts of individuals from two kinds of data: 1) the number of individuals sighted per unit area (sighting density) on the sample sites in the broad scale study and 2) the number of individuals estimated from capture-recapture data on individuals on a subset of those sample sites.

The underlying principle of the proposed method, ratio estimation with double sampling, is described by Thompson (2002, pp.158-160). Following Thompson, where $\hat{y}_i$ represents the estimates of abundance and x_i represents the sighting densities from the subsample of n sites on which both were measured, the ratio r is calculated as $r = \frac{\sum_{i=1}^{n} \hat{y}_i}{\sum_{i=1}^{n} x_i}$.

From the full sample n' of sites in the sighting study, the population total $\hat{\tau}_x$ of densities x_i is estimated as $\hat{\tau}_x = \frac{N}{n'} \sum_{i=1}^{n'} x_i$ where N is the population of sites from which the sample of n' sites was selected.

The ratio estimator of the population total $\hat{\tau}_r$ of the abundance is then $\hat{\tau}_r = r\hat{\tau}_x$.

The estimated variance of the ratio estimator $\hat{\tau}_r$ of the total abundance, is written as follows:

$\hat{V}ar(\hat{\tau}_r) = N(N - n')\frac{s^2}{n'} + N^2 \frac{n' - n}{n'n(n-1)} \sum_{i=1}^{n} (y_i - rx_i)^2$, where s^2 is the sample variance of the abundance estimates $\hat{y}_i$.

Calculation of the sample variance of the abundance estimates would need to account for the variance associated with the estimates themselves because they *are* estimates rather than observed data.

The variances associated with the estimates of sighting density in the Appendix, Table 3, are large relative to the estimates (mean CV = 0.92). However these variances are due to estimation at the transect level and the variation among transects is wide representing how a local group is distributed on its range at the time of sampling. It is reasonable, however, to calculate the observed sighting density on whole sites which may more closely represent the mean density on a site over time for the purpose of estimating total abundance by the proposed method.

The population N of sites in the sighting study could be estimated as the total number of sites of the size of each sample site in the area sampled from.

Ratio estimation with double sampling relies on a strong linear correlation between the paired variables, $\hat{y}_i$ and x_i, in the ratio: in the present case, between the abundance estimates and the sighting densities. It is by no means clear how strong this relationship is likely to be as it would depend on two unknown proportions – 1) the proportion of the number dolphins that regularly use the sighting survey site that are present there at the time of survey and 2) the proportion of the number dolphins that were present on the sighting survey site that visit the capture-recapture subsite during sampling (at some time during the period on which the abundance estimate is based).

The proportion of the number dolphins that regularly use the sighting survey site that are present there at the time of survey is related to the size of the group home range and what part of that is within the survey site. If the survey site included the whole home range, then the proportion would be 1.00, but little is known about home range sizes or about how sample sites might be located within them.

The proportion of the number dolphins that were present on the sighting survey site that visit the capture-recapture subsite during a sampling session there depends on both the duration of the sampling session and the rate at which dolphins enter and leave the sample site. While it seems reasonable to assume that dolphins move about widely within their range and are likely to visit a well-chosen subsite relatively frequently, there is little information on the small-scale movements of coastal dolphins.

Without a stronger basis for making judgements about these two factors, it is not possible to make a reasonable estimate of the probable strength of the correlation between capture-recapture estimates of abundance from data from subsites and sighting densities observed on broader sites that include the subsites. If it were the case that 1) most of the dolphins that regularly use the sighting survey site are likely to be present there at any time and 2) most of the dolphins that are present on a sighting survey site at the time of survey are likely to visit the capture-recapture subsite during a sampling session there, then a suitably strong correlation between the two variables in the ratio of abundances to sighting densities might be expected.

There is too much uncertainty about the probable reliability of the ratio to recommend investment of funds in this proposal. It remains interesting nonetheless and it would be worthwhile to investigate it further were data to become available at time goes by.

General conclusions

The alternative of sampling from a helicopter rather than a boat was evaluated and several advantages of the helicopter platform described. Although the hourly cost of hiring a helicopter is relatively high, the overall cost of conducting a broad scale survey in a remote area by helicopter is competitive and may be cheaper than by boat.

The Efford and Dawson (2012) critique of occupancy in continuous habitat was described and it was concluded that an occupancy estimate on sightings of coastal dolphins is ill-defined. Although variation in the probability of occupancy over a large length of coastline is informative of their relative abundance, it does not provide greater insight into the spatial distribution of the dolphins than a model based on the probability of detecting a group.

An alternative approach to analysis of data collected on transect in the course of an ‘occupancy’ study was described and illustrated using data on snubfin dolphins in the Northern Territory. A set of generalized additive models (GAMs) was fitted to the data on whether or not at least one group was sighted on transect, the number of groups sighted, group sizes and the density of sighted individuals. The set of models is not only more informative in terms of the number of groups sighted, group sizes and the density of sighted individuals but the results are based on smooth functions of the covariates with much greater flexibility to describe the distribution of the dolphins around a complex coastline than the sorts of fixed form functions that might be fitted with the available software for modeling the probability of occupancy. The GAM approach is very flexible and there are many options to be considered in specifying and evaluating models. The example models presented here represent a first approach and may be subject to improvement; in particular, the smooth functions fitted may be subject to edge effects and this should be further investigated before the estimates presented here are treated as definitive.

The material presented in 2014 Methods on long-term monitoring on selected sites was briefly reviewed and found to remain appropriate under the revised Framework. The additional objective to conduct short term assessments of abundance was discussed and comment made on matters to be considered in designing studies to meet this objective.

The proposal to enhance the data on relative density to yield an approximate estimate of total abundance over the range of the species was considered under the heading ‘abundance estimation by ratio estimation with double sampling’. The underlying principal of a method by which this might be done was described and the feasibility of the proposed method considered. It was concluded that there were too many unknowns to anticipate the reliability of the method to invest in this approach specifically, although the proposal is interesting and could be further assessed as suitable data are accumulated.

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Appendix 1: Model results – supplementary tables

Table 1 Model fit statistics for 35 occupancy models on Northern Territory snubfin dolphin data

Model	AIC	AIC change	AIC weight	Model likelihood	Number of parameters	-2Log likelihood
psi(lat, latsq, long), p(glare, zone)	447.60	0.00	0.10	1.00	9	429.60
psi(lat, long), p(glare, turbidity)	447.69	0.09	0.09	0.96	4	439.69
psi(lat, latsq, long), p(glare, turbidity, zone)	447.86	0.26	0.08	0.88	10	427.86
psi(lat, latsq, long), p(glare, turbidity)	447.88	0.28	0.08	0.87	5	437.88
psi(lat, long), p(glare, tubidity, zone)	447.95	0.35	0.08	0.84	9	429.95
psi(lat, long), p(glare, zone)	448.00	0.40	0.08	0.82	8	432.00
psi(lat, long), p(sea state, glare, turbidity)	448.38	0.78	0.06	0.68	5	438.38
psi(lat, latsq, long), p(sea state, glare, turbidity)	448.54	0.94	0.06	0.63	6	436.54
psi(lat, latsq, long), p(sea state, glare, zone)	449.52	1.92	0.04	0.38	10	429.52
psi(lat, latsq, long), p(sea state, zone)	449.54	1.94	0.04	0.38	9	431.54
psi(lat, long), p(sea state, zone)	449.56	1.96	0.04	0.38	8	433.56
psi(lat, latsq, long), p(sea state, glare, turbidity, zone)	449.57	1.97	0.04	0.37	11	427.57
psi(lat, long), p(sea state, glare, turbidity, zone)	449.67	2.07	0.03	0.36	10	429.67
psi(lat, long), p(sea state, glare, zone)	449.95	2.35	0.03	0.31	9	431.95
psi(lat, latsq), p(glare, turbidity)	450.20	2.60	0.03	0.27	4	442.20
psi(lat, latsq), p(glare, zone)	450.71	3.11	0.02	0.21	8	434.71
psi(lat, latsq), p(glare, turbidity, zone)	450.72	3.12	0.02	0.21	9	432.72
psi(lat, latsq, long), p(sea state)	450.78	3.18	0.02	0.20	4	442.78
psi(lat, latsq), p(sea state, glare, turbidity)	450.99	3.39	0.02	0.18	5	440.99
psi(lat, latsq, long), p(glare)	451.90	4.30	0.01	0.12	4	443.90
psi(long), p(glare, zone)	452.58	4.98	0.01	0.08	7	438.58
psi(lat, latsq, long), p(sea state, glare)	452.62	5.02	0.01	0.08	5	442.62
psi(long), p(glare, turbidity)	452.79	5.19	0.01	0.07	3	446.79
psi(long), p(glare, turbidity, zone)	453.14	5.54	0.01	0.06	8	437.14
psi(long), p(sea state, glare, turbidity)	453.71	6.11	0.00	0.05	4	445.71
psi(lat), p(glare, zone)	454.59	6.99	0.00	0.03	7	440.59
psi(lat), p(glare, turbidity)	454.94	7.34	0.00	0.03	3	448.94
psi(lat), p(glare, turbidity, zone)	455.25	7.65	0.00	0.02	8	439.25
psi(lat), p(sea state, glare, turbidity)	455.88	8.28	0.00	0.02	4	447.88
psi(lat, latsq, long), p(turbidity)	475.34	27.74	0.00	0.00	4	467.34
psi(lat, latsq, long), p(.)	475.87	28.27	0.00	0.00	4	467.87
psi(lat, latsq, long), p(turbidity, zone)	476.15	28.55	0.00	0.00	9	458.15
psi(lat, latsq, long), p(zone)	476.79	29.19	0.00	0.00	8	460.79
psi(sietlat, latsq, long), p(sea state, turbidity)	477.15	29.55	0.00	0.00	5	467.15
psi(lat, latsq, long), p(sea state, turbidity, zone)	477.64	30.04	0.00	0.00	10	457.64

Table 2 Model fit statistics for GAMs

Symbols: SFG snubfin group presence/absence; SFNg snubfin number of groups; SFGs snubfin group size; SFSd snubfin sighting density
Zt zone type (parametic factor); te(LL) tensor smooth of site latitude and site longitude; s(Site): random effect for site
te(Tb,Gl) tensor smooth of turbidity and glare; te(Tb,Ss) tensor smooth of turbidity and sea state; te(Gl,Ss) tensor smooth of glare and sea state

Model name	**Terms/stat.**	**Zt**	**te(LL)**	**s(Site)**	**te(Tb,Gl)**	**te(Tb,Ss)**	**te(Gl,Ss)**	**te(Tb,Gl,Ss)**	**Deviance Explained %**
Group P/A - Binomial									
SFG.Zt.LL.Site.TBGlSs	Terms	X	X	X				X	13.2
	P-value	0.032	0.000	0.566				0.074	
	Concurvity		0.975	1.000				1.000	
SFG.Zt.LL.Site.TBGl	Terms	X	X	X	X				11.8
	P-value	0.052	0.000	0.686	0.074				
	Concurvity		0.41	0.996	0.474				
SFG.Zt.LL.Site.TBSs	Terms	X	X	X		X			10.8
	P-value	0.052	0.000	0.985		0.226			
	Concurvity		0.41	0.995		0.504			
SFG.Zt.LL.Site.GlSs	Terms	X	X	X			X		10.4
	P-value	0.064	0	0.885			0.408		
	Concurvity		0.386	0.992			0.440		
SFG.Zt.LL.Site	Terms	X	X	X					10.4
	P-value	0.064	0.000	0.885					
	Concurvity	0.97	0.085	0.988					
SFG.Zt.LL	Terms	X	X						10.4
	P-value	0.064	0.000						
	Concurvity	0.833	0.014						
SFG.LL	Terms		X						8.22
	P-value		0						
	Concurvity		0						

Model name	Terms/stat.	Zt	te(LL)	s(Site)	te(Tb,Gl)	te(Tb,Ss)	te(Gl,Ss)	te(Tb,Gl,Ss)	Deviance Explained %
N. Groups – Poisson									
SFNg.Zt.LL.Site.TbGlSs	Terms	X	X	X				X	22.8
	P-value	0.072	0.000	0.887				0.000	
	Concurvity		0.975	0.887				0.000	
SFNg.Zt.LL.Site.TbGl	Terms	X	X	X	X				18.7
	P-value	0.072	0.001	0.61	0.002				
	Concurvity		0.41	0.996	0.474				
SFNg.Zt.LL.Site.TbSs	Terms	X	X	X		X			14.5
	P-value	0.118	0.001	0.133		0.561			
	Concurvity		0.41	0.995		0.504			
SFNg.Zt.LL.Site.GlSs	Terms	X	X	X			X		12.7
	P-value	0.017	0.000	0.327			0.262		
	Concurvity		0.386	0.993			0.440		
SFNg.Zt.LL.Site	Terms	X	X	X					14.5
	P-value	0.118	0.001	0.133					
	Concurvity		0.085	0.988					
SFNg.Zt.LL	Terms	X	X						12.3
	P-value	0.011	0.000						
	Concurvity	0.833	0.014						
SFNg.Zt.LL.TbGl	Terms	X	X		X				14.6
	P-value	0.045	0.001		0.011				
	Concurvity		0.369		0.458				
re-fitted as negbin									
SFNg.Zt.LL.TbGl.negbin	Terms	X	X		X				16.2
	P-value	0.034	0.000		0.077				
	Concurvity		0.369		0.458				
SFNg.Zt.LL.negbin	Terms	X	X						12.9
	P-value	0.046	0.002						

Model name	Terms/stat.	Zt	te(LL)	s(Site)	te(Tb,Gl)	te(Tb,Ss)	te(Gl,Ss)	te(Tb,Gl,Ss)	Deviance Explained %
	Concurvity	0.836	0.000						
SFNg. LL.TbGl.negbin	Terms		X		X				12.7
	P-value		0.005		0.010				
	Concurvity		0.343		0.434				
Group size - Neg.bin.									
SFGs.Zt.LL.Site.TbGlSs	Terms	X	X	X				X	30.2
	P-value	0.017	0.000	0.004				0.000	
	Concurvity		0.978	1.000				0.000	
SFGs.Zt.LL.Site.TbGl	Terms	X	X	X	X				19.3
	P-value	0.508	0.000	0.193	0.012				
	Concurvity		0.409	0.997	0.488				
SFGs.Zt.LL.TbGl	Terms	X	X		X				21.3
	P-value	0.116	0.000		0.007				
	Concurvity		0.371		0.464				
SFGs.LL.Site.TbGl	Terms		X	X	X				19.5
	P-value		0.000	0.116	0.273				
	Concurvity		0.361	0.958	0.445				
SFGs.LL.TbGl	Terms		X		X				18.8
	P-value		0.000		0.024				
	Concurvity		0.347		0.439				
SFGs.Zt.LL.Site.TbSs	Terms	X	X	X		X			20.5
	P-value	0.158	0.000	0.634		0.005			
	Concurvity		0.409	0.994		0.516			
SFGs.Zt.LL.TbSs	Terms	X	X			X			20.5
	P-value	0.158	0.000			0.005			
	Concurvity		0.387			0.497			
SFGs.LL.TbSs	Terms		X			X			17.3
	P-value		0.000			0.032			

Model name	Terms/stat.	Zt	te(LL)	s(Site)	te(Tb,Gl)	te(Tb,Ss)	te(Gl,Ss)	te(Tb,Gl,Ss)	Deviance Explained %
	Concurvity		0.370			0.446			
SFGs.Zt.LL.Site.GlSs	Terms	X	X	X			X		20.3
	P-value	0.351	0.000	0.335			0.010		
	Concurvity		0.370	0.992			0.444		
SFGs.Zt.LL.GlSs	Terms	X	X				X		20.3
	P-value	0.351	0.000				0.010		
	Concurvity		0.324				0.416		
SFGs.LL.GlSs	Terms		X				X		18.2
	P-value		0.000				0.023		
	Concurvity		0.299				0.380		
Sighting density - Tweedie									
SFSd.Zt.LL.Site.TbGlSs	Terms	X	X	X				X	26.5
	P-value	0.186	0.000	0.021				0.000	
	Concurvity		0.978	1.000				0.000	
SFSd.Zt.LL.Site.TbGl	Terms	X	X	X	X				21.8
	P-value	0.080	0.000	0.007	0.000				
	Concurvity		0.410	0.996	0.474				
SFSd.LL.Site.TbGl	Terms		X	X	X				17.7
	P-value		0.000	0.698	0.018				
	Concurvity		0.360	0.957	0.441				
SFSd.Zt.LL.TbGl	Terms	X	X		X				16.1
	P-value	0.762	0.000		0.045				
	Concurvity		0.386		0.488				
SFSd.LL.TbGl	Terms		X		X				17.7
	P-value		0.000		0.018				
	Concurvity		0.343		0.434				
SFSd.Zt.LL.Site.TbSs	Terms	X	X	X		X			16.1
	P-value	0.762	0.000	0.981		0.045			

Model name	Terms/stat.	Zt	te(LL)	s(Site)	te(Tb,Gl)	te(Tb,Ss)	te(Gl,Ss)	te(Tb,Gl,Ss)	Deviance Explained %
	Concurvity		0.410	0.995		0.504			
SFSd.Zt.LL.TbSs	Terms	X	X			X			16.1
	P-value	0.762	0.000			0.045			
	Concurvity		0.386			0.488			
SFSd.LL.Site.TbSs	Terms		X	X		X			14.8
	P-value		0.000	0.482		0.082			
	Concurvity		0.377	0.963		0.457			
SFSd.LL.TbSs	Terms		X			X			14.8
	P-value		0.000			0.082			
	Concurvity		0.367			0.445			
SFSd.Zt.LL.Site.GlSs	Terms	X	X	X			X		17.1
	P-value	0.897	0.000	0.493			0.036		
	Concurvity		0.386	0.993			0.44		
SFSd.LL.Site.GlSs	Terms		X	X			X		16.5
	P-value		0.000	0.992			0.037		
	Concurvity		0.327	0.969			0.396		
SFSd.Zt.LL.GlSs	Terms	X	X				X		17.1
	P-value	0.897	0.000				0.036		
	Concurvity		0.333				0.419		
SFSd.LL.GlSs	Terms		X				X		16.5
	P-value		0.000				0.037		
	Concurvity		0.309				0.384		

Table 3 GAMs: Predicted probability of group presence/absence (pG), number of groups (Ng), group size (Gs) and sighting density (Sd) with estimated standard errors (SE). Sites are ordered from west to east for map reference.

Site Name	Site Latitude	Site Longitude	pG	SEpG	Ng	SENg	Gs	SEGs	Sd	SESd
Victoria River	-14.874	129.173	0.036	0.024	0.130	0.085	0.146	0.162	2.476	3.002
Wadeye	-14.278	129.380	0.132	0.053	0.310	0.165	0.747	0.708	11.540	12.317
Fitzmaurice River	-14.757	129.508	0.046	0.028	0.152	0.093	0.198	0.210	3.296	3.836
Hyland Bay	-13.964	129.626	0.289	0.075	0.599	0.291	2.774	2.452	39.768	40.137
Cape Ford	-13.534	129.853	0.487	0.089	1.143	0.542	10.666	9.270	144.685	143.815
Bathurst Island	-11.596	130.123	0.244	0.051	0.754	0.332	4.150	3.505	60.905	58.838
Anson Bay	-13.272	130.124	0.508	0.085	1.316	0.603	14.958	12.829	203.516	199.245
Fog Bay	-12.840	130.195	0.400	0.073	1.162	0.516	13.492	11.437	192.812	186.504
North Melville Island	-11.245	130.374	0.395	0.080	1.034	0.472	5.325	4.532	72.607	70.990
Bynoe Harbour	-12.515	130.534	0.282	0.060	0.898	0.397	8.292	6.989	123.800	118.909
Snake Bay	-11.297	130.733	0.356	0.064	0.964	0.416	4.914	4.053	69.203	65.664
Sth Melville Island	-11.886	130.988	0.204	0.044	0.690	0.297	4.079	3.376	62.375	58.748
Vernon Islands	-12.168	131.089	0.217	0.049	0.730	0.318	5.017	4.165	76.495	72.199
NE Melville Island	-11.222	131.256	0.368	0.063	0.999	0.423	4.919	3.990	70.599	66.040
Point Stuart	-12.203	131.699	0.239	0.046	0.767	0.318	5.148	4.143	77.283	70.658
Van Diemans Gulf 1	-11.471	131.942	0.275	0.038	0.822	0.322	4.122	3.225	62.342	55.848
Port Essington	-11.115	132.207	0.356	0.069	0.999	0.423	4.619	3.730	70.430	65.553
Kakadu	-12.115	132.371	0.248	0.041	0.773	0.306	4.761	3.721	70.725	62.694
Van Diemans Gulf 2	-11.644	132.467	0.248	0.035	0.771	0.297	3.988	3.083	60.810	53.530
Croker Island	-11.158	132.640	0.323	0.067	0.941	0.395	4.303	3.472	67.689	62.642
Sth Goulburn Island	-12.179	133.941	0.310	0.041	0.871	0.319	5.120	3.775	72.069	60.141
Maningrida	-11.862	134.078	0.275	0.039	0.817	0.303	4.435	3.277	65.037	54.449
Blythe River	-11.988	134.891	0.313	0.045	0.879	0.321	4.896	3.533	68.578	56.037
Ramingining	-12.122	135.136	0.344	0.049	0.925	0.336	5.220	3.739	70.821	57.421
Limmen Bight	-14.731	135.498	0.290	0.069	0.614	0.224	5.352	4.090	65.336	55.488
Maria Island	-14.912	135.715	0.285	0.073	0.628	0.232	5.576	4.287	67.910	57.977

Site Name	Site Latitude	Site Longitude	pG	SEpG	Ng	SENg	Gs	SEGs	Sd	SESd
Buckingham Bay	-12.076	135.896	0.363	0.058	0.959	0.355	5.346	3.805	71.074	57.254
Blue Mud Bay	-13.369	136.056	0.486	0.077	1.017	0.354	5.176	3.955	70.603	60.725
Arnhem Bay	-12.355	136.107	0.423	0.064	1.034	0.377	5.556	3.970	71.036	57.291
Rosie Creek	-15.305	136.121	0.278	0.070	0.695	0.234	4.933	3.806	63.998	55.202
Bickerton Island	-13.765	136.217	0.458	0.075	0.914	0.309	5.739	4.392	76.606	65.872
South Point (Groote Eylandt)	-14.210	136.419	0.416	0.073	0.820	0.279	7.572	5.732	93.601	79.151
English Company	-11.795	136.540	0.320	0.073	0.913	0.366	4.943	3.675	70.316	58.914
Caledon Bay	-12.850	136.657	0.489	0.074	1.074	0.381	4.833	3.565	62.877	52.158
Port Langoon (Groote Eylandt)	-13.719	136.756	0.468	0.083	0.928	0.323	5.570	4.319	74.603	64.845
Pellew Islands	-15.818	136.832	0.249	0.074	0.796	0.258	2.359	2.023	38.574	37.437
Nhulunbuy	-12.233	136.888	0.432	0.077	1.056	0.407	5.659	4.072	70.665	57.321
Cape Beatrice (Groote Eylandt)	-14.208	136.911	0.440	0.080	0.867	0.304	8.697	6.658	106.012	90.442
Seven Emu	-16.136	137.564	0.193	0.097	0.783	0.380	0.880	0.939	18.374	22.040
Mean			**0.320**	**0.062**	**0.834**	**0.335**	**5.243**	**4.171**	**72.858**	**65.932**