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Ensemble modelling of southern Australian bottlenose dolphin *Tursiops* sp. distribution reveals important habitats and their potential ecological function

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ABSTRACT: Modelling dolphin distribution is key for understanding their ecology and for their conservation and management. Information on the distribution and preferred habitats of southern Australian bottlenose dolphins *Tursiops* sp. is lacking, particularly in metropolitan areas where the species is under threat from anthropogenic activities. Here, we used boat-based surveys and an ensemble modelling approach that combined results from 6 modelling techniques (generalised additive models, generalised boosted models, classification tree analysis, flexible discriminant analysis, random forest and maximum entropy) to identify areas of high probability of southern Australian bottlenose dolphin occurrence along the metropolitan coast of Adelaide, South Australia. We used kernel density estimation to identify core and representative areas according to behaviour and investigated the importance and potential ecological function of areas of high dolphin occurrence. The ensemble predictions of dolphin distribution performed better than the corresponding single models. Results indicate that depth, benthic habitat type and slope influenced dolphin occurrence along Adelaide's coast. Dolphins favoured shallow nearshore areas and temperate reefs in summer, shallow nearshore areas in autumn and deep waters further offshore in winter. In comparison to other observed behaviours, core feeding areas overlapped considerably with areas of high probability of dolphin occurrence. Thus, we suggest that prey availability is an important driver influencing the seasonal variation in dolphin distribution along Adelaide's metropolitan coast. Our predictions identify priority areas for dolphin conservation and for the implementation of boating and fishing regulations. Continued monitoring is needed to assess potential changes in preferred habitat under increasing anthropogenic pressures.

KEY WORDS: Species distribution modelling · Seasonal distribution · Gulf St Vincent · Biomod2 · Conservation planning · Coastal dolphins · Marine mammals

INTRODUCTION

The need to identify critical habitats and priority conservation areas for coastal marine mammals has accelerated dramatically in recent times due to increasing human activities (e.g. fishing and coastal zone development) in coastal areas (Halpern et al. 2008, Bulleri & Chapman 2010). Increasing human activities and developments (industrial, commercial and residential) in coastal areas have resulted in a wide variety of anthropogenic threats to dolphins, particularly for populations that live in close proximity to urbanised areas (Jefferson et al. 2009, Pirotta et al. 2013, 2015). As urbanisation increases along the world's coastlines, identifying areas that are biologically relevant to coastal dolphins has become

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increasingly important as a tool to manage and mitigate the cumulative impacts of anthropogenic activities (Ashe et al. 2010, Hoyt 2011). However, one of the challenges in identifying such areas for coastal dolphins is the lack of understanding of species distribution, their preferred habitats and the relevance of these areas (Salm et al. 2000, Hoyt 2011).

Understanding species–environment relationships is essential for identifying areas of biological importance and to prioritize areas for conservation, zoning design, impact assessment and resource management decisions (Guisan & Thuiller 2005, Elith & Leathwick 2009). Numerous studies have identified preferred habitat by linking dolphin presence to a variety of abiotic and biotic factors over various spatial and temporal scales (reviewed in Cribb et al. 2015). Species distribution models (SDMs) have been used widely to model species distributions (Guisan & Zimmermann 2000, Elith & Leathwick 2009) and are increasingly being used to predict dolphin distribution and suitable habitats (de Boer et al. 2014, Ferro de Godoy et al. 2015, Marini et al. 2015). However, due to the wide array of methods, data types and modelling algorithms available, there are discrepancies among outputs of single-model techniques, and the best-performing models tend to vary across studies and species (Guisan & Zimmermann 2000, Elith & Graham 2009, Marmion et al. 2009, Thuiller et al. 2009). One method to overcome these variations is to combine single-model predictions through a process known as ensemble modelling (Araújo & New 2007, Franklin 2010). Ensemble modelling often provides more robust estimates of species distributions because the combined model predictions yield higher accuracies and less bias than separate single models (Marmion et al. 2009, Grenouillet et al. 2011, Scales et al. 2016). While ensemble modelling has previously been employed for some marine species (e.g. Riul et al. 2013, Pikesley et al. 2015), to our knowledge it is yet to be used widely to model dolphin distribution (but see Moura et al. 2012, Pérez-Jorge et al. 2015).

Bottlenose dolphins *Tursiops* sp. are found throughout coastal waters of southern Australia (Bilgmann et al. 2007, Möller et al. 2008, Charlton-Robb et al. 2015). Bottlenose dolphins using this coastal area may belong to a new species endemic to southern Australia (*Tursiops australis*, Charlton-Robb et al. 2011), but its taxonomic status remains under debate (Perrin et al. 2013), and thus we refer to them here as the southern Australian bottlenose dolphin (*Tursiops* sp.). The coastal distribution of southern Australian bottlenose dolphins puts them at risk from a range of anthropogenic threats. These threats include dolphin-targeted tourism (Peters et al. 2012, Filby et al. 2014), interactions with fishing boats and gear (Byard et al. 2013), entanglements with marine debris (Kemper et al. 2005), habitat loss and degradation (Edyvane 1999), pollution (Lavery et al. 2008, Monk et al. 2014) and intentional killings from shooting and stabbing (Kemper et al. 2005). The cumulative impact of anthropogenic threats over time can lead to the displacement of dolphins from an area and/or population decline (e.g. Lusseau 2005, Watson-Capps & Mann 2005, Bejder et al. 2006). This highlights the need to identify bottlenose dolphin preferred habitat along the southern Australian coast, particularly in areas where threats concentrate, such as South Australia's capital city, Adelaide.

Information on habitat preferences for southern Australian bottlenose dolphins is lacking, with previous studies limited to estuarine and tidal inlets of the Port River estuary and Barker Inlet in Adelaide (Cribb et al. 2008, 2013). This semi-enclosed, sheltered area is characterized mostly by shallow water (0.5 to 6 m, but can reach up to 17 m in the dredged shipping channel) and likely provides a nursery area for a small number of about 70 southern Australian bottlenose dolphins (Kemper et al. 2008, Steiner & Bossley 2008). Dolphins within this area have a year-round preference for bare sand habitat; however, seagrass preference increases during summer and autumn, and could be indicative of a seasonal pattern in habitat preference (Cribb et al. 2013). Water properties (e.g. temperature and depth) have no significant influence on dolphin presence within this area; instead, it is suggested that prey movement may influence dolphin presence (Cribb et al. 2008). Currently, the habitat preferences of bottlenose dolphins inhabiting coastal areas adjacent to the Port River and Barker Inlet are unknown. In contrast to the Port River, adjacent areas are characterised by an open coastal habitat in the large Gulf St Vincent (GSV), consisting of deeper water (up to 40 m in depth) and additional habitat types (e.g. temperate reefs). Given the differences in habitat characteristics, dolphins along Adelaide's metropolitan coast may use these areas in a different manner. A relatively high number of dolphins (244 individuals) were identified within Adelaide's metropolitan coast, and the presence of year-round and seasonal residents within this area suggests that at least some areas are important for this species and likely provide preferred habitat (Zanardo et al. 2016).

The aims of this study were to (1) quantitatively assess the relationships between southern Australian bottlenose dolphin occurrence and ecogeographical variables along Adelaide's metropolitan coast, (2) identify any preferred habitat, and (3) investigate potential behavioural processes that may influence species distributions. Here, we identify preferred habitat as areas of high probability of dolphin occurrence, which reflects their distribution across space and time (Hastie et al. 2004). We used ensemble modelling to identify areas of high probability of dolphin occurrence through a consensus-modelling framework, and investigated whether this distribution changes across the austral seasons. To investigate the importance and potential ecological function of these preferred habitats, we calculated the percentage of core and representative behavioural ranges that overlap with areas of high dolphin probability of occurrence.

MATERIALS AND METHODS

Study site and data collection

The study site was located within GSV, a relatively shallow and large inverse estuary in the central region of southern Australia's temperate coastline (Fig. 1). The study area covered approximately 195 km^2 of the metropolitan coastal waters of Adelaide, including 40 km of the coast, extending up to 7 km offshore and reaching maximum depths of 25 m. Benthic habitat types within the study area include seagrass beds, temperate reefs and bare sand (Bryars 2003). Tidal regimes within this region are variable, but mostly semi-diurnal, and can reach up to about 3 m (Harvey et al. 1999).

Boat-based surveys were conducted between December 2012 and August 2014 in Beaufort sea state <3 m and swell <1 m. No surveys were carried out in spring (September to November) due to generally poor weather conditions during this time of year. Surveys followed a predetermined zig-zag line transect layout (ca. 100 km) at speeds of approximately 13 to 17 km h^{-1}. Observations of dolphins were made by 3 to 5 observers by naked eye and with the aid of 7 × 50 Fujinon binoculars. Dolphins were defined as part of the same group if they were within a 100 m radius of each other and heading in the same direction if travelling (Irvine et al. 1981). Once a dolphin group was sighted, survey effort was ceased and the dolphins were approached to a distance of approximately 30 m to record data on location (using a hand-held GPS), time, group size, age composition (following Zanardo et al. 2016) and predominant behavioural activity (i.e. the behavioural state of ≥50 % of the individuals as observed at the surface). Predominant behaviour was recorded as travelling, feeding, socialising, milling or resting (modified from Shane et al. 1986; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m569p253_supp.pdf for definitions). These data were recorded every 5 min thereafter or when there was a change in group behaviour, size and/or composition.

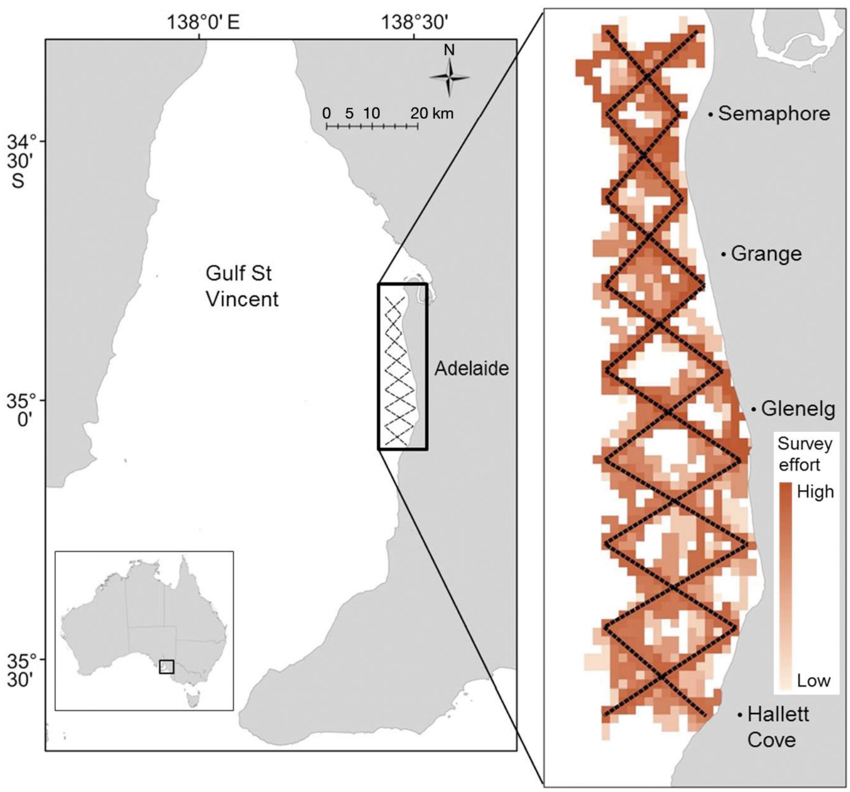

Fig. 1. Study area in coastal metropolitan Adelaide, South Australia. Boat survey transects are located along the dashed line and survey effort is represented by the coloured shading, as detailed in the key

Ecogeographical predictor variables

Ecogeographical variables used to model dolphin distribution included all benthic habitat types that have been mapped within the study area (seagrass beds, temperate reefs and bare sand), water depth and bathymetric slope. Previous studies show that habitat type and water depth influence the distribution and availability of fish species in GSV (McGlennon & Kinloch 1997, Bryars 2003, Fowler & Jones 2008), which may influence bottlenose dolphin distribution (see Ingram & Rogan 2002). Sea surface temperature and salinity were not included in the analysis as predictor variables due to low spatial variation and resolution across the study site. Benthic habitat type and water depth data were obtained from the Nature Maps database of the South Australian Government (Department of Environment, Water and Natural Resources; https://data.environment.sa.gov.au/NatureMaps/Pages/default.aspx). At present, there are no benthic habitat data available for 9% of the study area, therefore these areas (and dolphin sightings within) were excluded from analysis and masked out from presence–absence maps. We used ArcMap 10.2.2 (ESRI) to calculate bathymetric slope from bathymetric grids using the Spatial Analyst extension.

All ecogeographical variables were sampled at a 500 × 500 m resolution within ArcMap to ensure adequate detail of ecogeographical variables across the study area and to remain consistent with the sampled scale of presence–absence data (see below). Collinearity (correlation between ecogeographical variables) was investigated using Pearson's correlation coefficient (r) for all combinations of variables in R v3.1.1 (R Core Team 2014). Variables were considered correlated if $r > 0.5$.

Presence–absence response variables

The response variable used for species distribution modelling was the presence–absence of dolphins (groups or single animals). The locations of dolphins obtained while on transect were imported into ArcMap and binary presence–absence maps were prepared for each austral season (summer, autumn and winter), taking into account survey coverage. Survey coverage was quantified by mapping the total number of on-effort survey tracks and adding a 250 m buffer (average distance to which dolphins could be reliably observed from the boat) on either side of the tracks. Each 500 × 500 m grid within the area of survey coverage was classified as either 1 (dolphin presence) or 0 (dolphin absence). Grids were also characterised by the mean of each ecogeographical predictor variable, and land adjacent to the survey area was masked from presence–absence maps.

Dolphin presence was defined by any group or individual animal sighted while on survey effort. Data on species true absence, however, are difficult to obtain, particularly for mobile and wide-ranging species (Mackenzie & Royle 2005). False absences occur when a species is considered absent from a particular area, when it may in fact occur in that area. Occurrences of false absences may be due to sampling design, observer effort, group size (i.e. smaller groups are more likely to go undetected) and/or species detection probability (i.e. dolphins may be underwater and unavailable for detection) (Gu & Swihart 2004, Barbet-Massin et al. 2010). Failure to detect a species can lead to biased models and thus do not provide a true estimate of species distributions (Gu & Swihart 2004). To reduce false absences, we selected absence cells based on areas of the highest survey effort (Phillips et al. 2009). Survey effort within the area of survey coverage was quantified for each austral season sampled by calculating the length of on-effort survey tracks within each 500 × 500 m grid cell (MacLeod 2013) and ordered from highest to lowest effort. Cells with the highest survey effort and no dolphin presence for each season were selected as absence cells and were thus areas most likely to represent true absences. The number of absence cells selected for each season was the same as the number of presence cells.

Ensemble species distribution modelling

To investigate the distribution and preferred habitat, we used 6 different and contrasting modelling algorithms implemented within the Biomod2 package in R v.3.1.1 (Thuiller et al. 2009). These modelling algorithms included 2 regression methods, generalised additive models (GAMs, Guisan et al. 2002) and generalised boosted models (GBMs, Friedman et al. 2000), 2 classification methods, classification tree analysis (CTA, De'ath & Fabricius 2000) and flexible discriminant analysis (FDA, Hastie et al. 1994), and 2 machine learning methods, random forest (RF, Breiman 2001) and maximum entropy (MaxEnt, Phillips et al. 2006). These modelling algorithms perform well as SDMs (Guisan et al. 2002, Phillips et al. 2006, Franklin 2010) and provide a comparison between 3 different modelling approaches.

SDMs were constructed separately for summer, autumn and winter seasons using a binomial error distribution and the logit link function. We implemented a 10-fold cross-validation method and a data split of 75/25% for respective model calibration and testing

(Thuiller et al. 2009). The importance of the ecogeographical variables was calculated using a randomisation procedure in Biomod2 based on 10 permutation runs (Thuiller et al. 2009). This method is independent of the modelling technique and thus provides a direct comparison between models. The procedure calculates the correlation between the standard predictions (i.e. fitted values) and predictions where 1 variable has been randomly permutated. High correlation (little difference between 2 predictions) indicates that the variable is not important in the model, and conversely, a low correlation indicates that the variable is important. Variables are ranked from 0 to 1 according to the mean correlation coefficient; the variable with the highest ranking has the most influence on the model, while a value of 0 assumes no influence of that variable (Thuiller et al. 2009).

SDMs based on presence–absence data may lead to commission and omission errors (Guisan & Thuiller 2005, Franklin 2010). Commission errors arise when models predict species occurrence in areas where the species does not occur (false positives), while omission errors fail to predict species occurrence in areas where the species does occur (false negatives) (Guisan & Thuiller 2005). Such errors may be costly, particularly when trying to delineate critical species habitat; for example, it could be expensive to protect habitat that is not important (Franklin 2010). To evaluate SDM performance and prediction accuracy, and compare modelling methods, we used the area under the curve (AUC) metric of the receiver operating characteristics plot calculated in Biomod2. AUC is a threshold-independent measure of the ratio between the observed presence–absence values and model predictions (Fielding & Bell 1997). Values of AUC range from 0 to 1; values above 0.5 indicate that the model predictions perform better than random, whereas values below 0.5 indicate that the model predictions are no better than what would be expected by chance.

We then combined all 6 modelling algorithms to generate an ensemble prediction of dolphin presence across the study area for each season (Thuiller et al. 2009). Single SDMs were weighted based on their predictive accuracy (the higher the evaluation score, the more weight given to the model) (Marmion et al. 2009); only models with AUC values above 0.5 were used to create the ensemble models. Ensemble models were then used to provide a visual output of probability of species occurrence, where values range from 0 to 1, indicating lowest to highest probability of occurrence, respectively. To include spatial context in the ensemble models, we employed a post hoc method that recalculates the model output for each location based on the surrounding geographical area (Ashcroft et al. 2012). This method considers the amount and quality of habitat in neighbouring areas, and is suitable for modelling processes that do not currently have an inbuilt mechanism that considers spatial context (e.g. Biomod2) (Ashcroft et al. 2012). Finally, we used AUC values to test whether the final ensemble models performed better than their corresponding single models (Marmion et al. 2009).

Behavioural use of preferred habitats

We investigated the importance and potential ecological function of areas of high dolphin presence using dolphin location and behavioural data. We used chi-squared tests to assess if behaviour varied across seasons and used kernel density estimates (Worton 1989) to identify core areas (i.e. areas of intensive use) within the representative range of animals according to behaviour and season. To ensure a reliable representation of kernel density estimates, we restricted analysis to behaviours recorded on ≥25% of all sightings; this excluded socialising and resting behaviours. Milling was also excluded because our observations indicated that it is most likely a transitional behavioural state (e.g. Constantine et al. 2004) whose function is poorly understood. Kernel density estimates were calculated using the 'kernel interpolation with barriers tool' available within the geostatistical analyst toolbox in ArcMap (following methods described in McLeod 2013). We then extracted kernel ranges of 50 and 95% probability of occurrence (following McLeod 2013) for feeding and travelling behaviours for each season. Kernel ranges of 50% were considered areas of intense use for feeding (i.e. core feeding areas) or travelling (i.e. core travelling areas) and 95% kernel ranges were considered the representative feeding and travelling ranges of bottlenose dolphins within our study area. Finally, to assess if a particular behavioural process might be driving the distribution patterns described by the ensemble models of dolphin presence, we calculated the percentages of the core areas and representative ranges that overlapped with areas >0.5 probability of occurrence (extracted from the ensemble model) for each season. It is important to note that the estimation and inferences we make on core (intensive use) areas in this study are at the population level (i.e. dolphin groups recorded in the study area). In addition, the observed locations used for our kernel density estimates reflect diurnal behavioural activity over the length of the study period (2 yr). Therefore, the core feeding and travelling areas identified here may differ from individual patterns of space use and may also differ from areas used by dolphins during the night and/or over the long term.

RESULTS

A total of 83 survey days were completed (approximately 545 h of survey effort, covering a distance of approximately 8134 km) between December 2012 and August 2014. Survey effort varied between seasons due to restrictions by weather conditions (Table 1). Over the survey period we encountered a total of 345 dolphin groups (Table 1).

Presence–absence of dolphins across seasons

We found no collinearity between ecogeographical variables (r < 0.5 for all combinations of variables), therefore SDMs were run with all variables. The AUC for single SDMs indicated that most models performed better than random with variation between seasons: AUC for summer SDMs ranged from 0.39 to 0.85 (median = 0.63); AUC for autumn SDMs ranged from 0.49 to 0.74 (median = 0.62); and AUC for winter SDMs ranged from 0.41 to 0.82 (median = 0.62) (Fig. 2). Ensemble models all performed better than the single SDMs (Fig. 2).

Table 1. Seasonal number of survey days, dolphin groups encountered and dolphin presences used to model dolphin distribution along the Adelaide metropolitan coast between December 2012 and August 2014

	Summer	Autumn	Winter
Surveys	28	36	19
Dolphin groups	101	162	82
Dolphin presences	85	145	75

During summer, the most influential variable for the GAM, RF and MaxEnt was benthic habitat type (Table 2). The response curve from the GAM indicated that low profile reef was the most important habitat, followed by macroalgae and bare sand (Fig. S1a in the Supplement at www.int-res.com/articles/suppl/m569p253_supp.pdf). However, response curves from RF and MaxEnt indicated that temperate reefs (low profile reef, macroalgae) and bare sand were important for predicting dolphin presence. The most influential variable for both CTA and FDA was slope (Table 2), indicating a preference for steeper slopes (from 0.2 to 0.8 m; Fig. S1a). The most influential variable for the GBM was water depth (Table 2) and indicated a preference for shallow water depths (<8 m; Fig. S1a). Using these data, the summer ensemble model predicted dolphin presence to occur predominantly over temperate reef habitat types and in shallow water depths, with a high probability of dolphin presence within the southern metropolitan waters (Fig. 3).

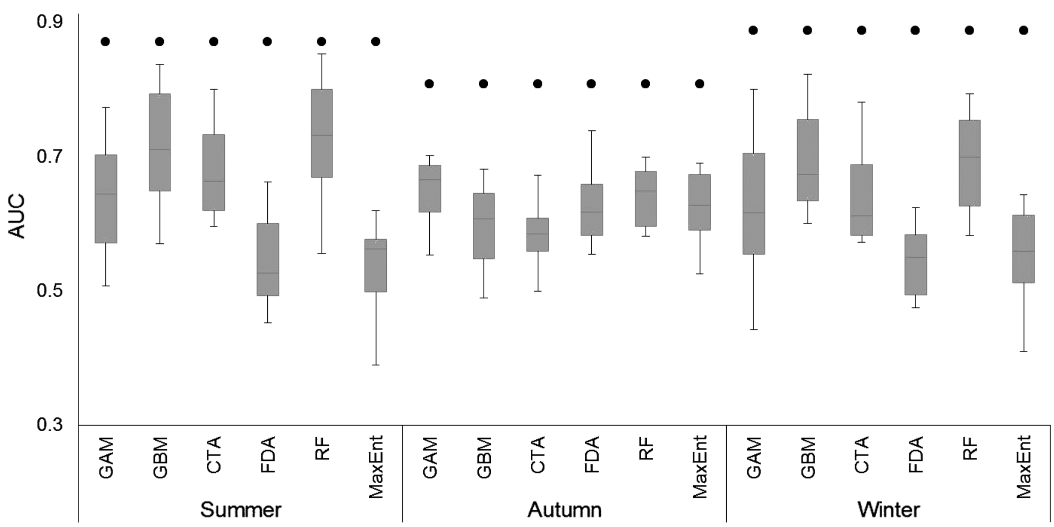

Fig. 2. Differences in model accuracy (AUC of the receiver operating characteristics plot) between the 10 cross-validation runs of each single species distribution model (box–whisker plot) and ensemble models (●) across seasons (summer, autumn and winter). GAM, generalised additive model; GBM, generalised boosted model; CTA, classification tree analysis; FDA, flexible discriminant analysis; RF, random forest; MaxEnt, maximum entropy. AUC values above 0.5 indicate that the model predictions perform better than random. Whiskers indicate highest and lowest AUC values

Table 2. Importance of ecogeographical variables for bottlenose dolphins in Adelaide's metropolitan waters over summer, autumn and winter, using 6 modelling algorithms: generalised additive model (GAM), generalised boosted model (GBM), classification tree analysis (CTA), flexible discriminant analysis (FDA), random forest (RF) and maximum entropy (MaxEnt). **Bold**: ecogeographical variables of greatest influence

	Summer						Autumn						Winter					
	GAM	GBM	CTA	FDA	RF	MaxEnt	GAM	GBM	CTA	FDA	RF	MaxEnt	GAM	GBM	CTA	FDA	RF	MaxEnt
Water depth	0.368	**0.402**	0.444	0.000	0.341	0.360	**0.758**	**0.707**	**0.896**	**0.971**	**0.539**	**0.638**	0.182	**0.393**	**0.593**	**0.977**	0.417	**0.618**
Benthic habitat	**0.499**	0.350	0.437	0.343	**0.485**	**0.740**	0.251	0.096	0.000	0.000	0.278	0.027	0.051	0.014	0.000	0.000	0.077	0.262
Slope	0.218	0.367	**0.472**	**0.597**	0.333	0.314	0.101	0.183	0.545	0.000	0.226	0.259	**0.775**	0.720	0.528	0.000	**0.551**	0.349

During autumn, water depth was the most influential variable for all 6 single SDMs (Table 2). Models generally predicted a higher probability of occurrence in shallow waters (<5 m; Fig. S1b). In agreement with these single SDMs, the autumn ensemble model predicted a high probability of dolphin presence in shallow waters (Fig. 3).

During winter, the most influential variable for the GBM, CTA, FDA and MaxEnt was water depth (Table 2). The response curves between these models varied; however, there appeared to be some preference for deeper water depths (>15 m; Fig. S1c). The most influential variable for the GAM and RF was slope (Table 2), in which models also indicated a preference for a range of slopes (Fig. S1c). Using these data, the winter ensemble model predicted a higher probability of dolphin presence in deeper offshore waters (Fig. 3).

Behavioural use of preferred habitats across seasons

The most frequently observed behaviours were feeding, milling and travelling (respectively comprising 108, 98 and 91 groups; Fig. 4). Socialising was observed only 26 times, while resting was observed only once. Analysis of pairwise comparisons indicated that group size did not differ significantly between travelling and foraging behaviours (Kruskal-Wallis = 23.77, p = 0.072), therefore groups exhibiting these behaviours should have similar detection probabilities. Dolphin feeding and travelling behaviours varied significantly between seasons (feeding χ^2 = 13.23, df = 2, p = 0.001; travelling χ^2 = 12.11, df = 2, p = 0.002). Feeding groups were most predominant throughout summer and autumn, while travelling groups were most predominant throughout winter (Fig. 4). Milling and socialising behaviour did not vary significantly between seasons (milling χ^2 = 3.88, df = 2, p = 0.14; socialising χ^2 = 2.64, df = 2, p = 0.27).

The percentages of feeding and travelling core areas (50% kernel range) and representative ranges (95% kernel range) that overlapped with areas of high probability of occurrence are summarised in Table 3 and Fig. 3. During summer and autumn, a larger percentage of core feeding areas overlapped with areas of high dolphin probability of occurrence (60 and 86%, respectively) in comparison to core travelling areas (56 and 50%, respectively; Table 3). During winter, the percentage of core and representative feeding areas that overlapped with areas of high dolphin probability of occurrence (43 and 49%, respectively) were comparable to the core and representative travelling areas (44 and 46%, respectively; Table 3, Fig. 3). These results suggest that areas of high probability of dolphin occurrence are predominantly used for feeding.

DISCUSSION

Modelling species–environment relationships can provide important insights into the ecological processes determining species distribution, with significant implications for conservation and management. Here, we show that the Adelaide metropolitan coast provides important habitat for southern Australian bottlenose dolphins, with animals using particular areas preferentially on a seasonal basis. Our ensemble model results indicated that water depth was the most important predictor of dolphin distribution; however, the relative influence of this variable changed across seasons. Overlap of core feeding areas with areas of high dolphin probability of occurrence suggests that foraging behaviour, and therefore prey distribution and availability, are likely key drivers of dolphin presence along Adelaide's metropolitan coast. Further, our results demonstrate the effectiveness of ensemble modelling approaches in reducing the predictive uncertainty of single-model techniques.

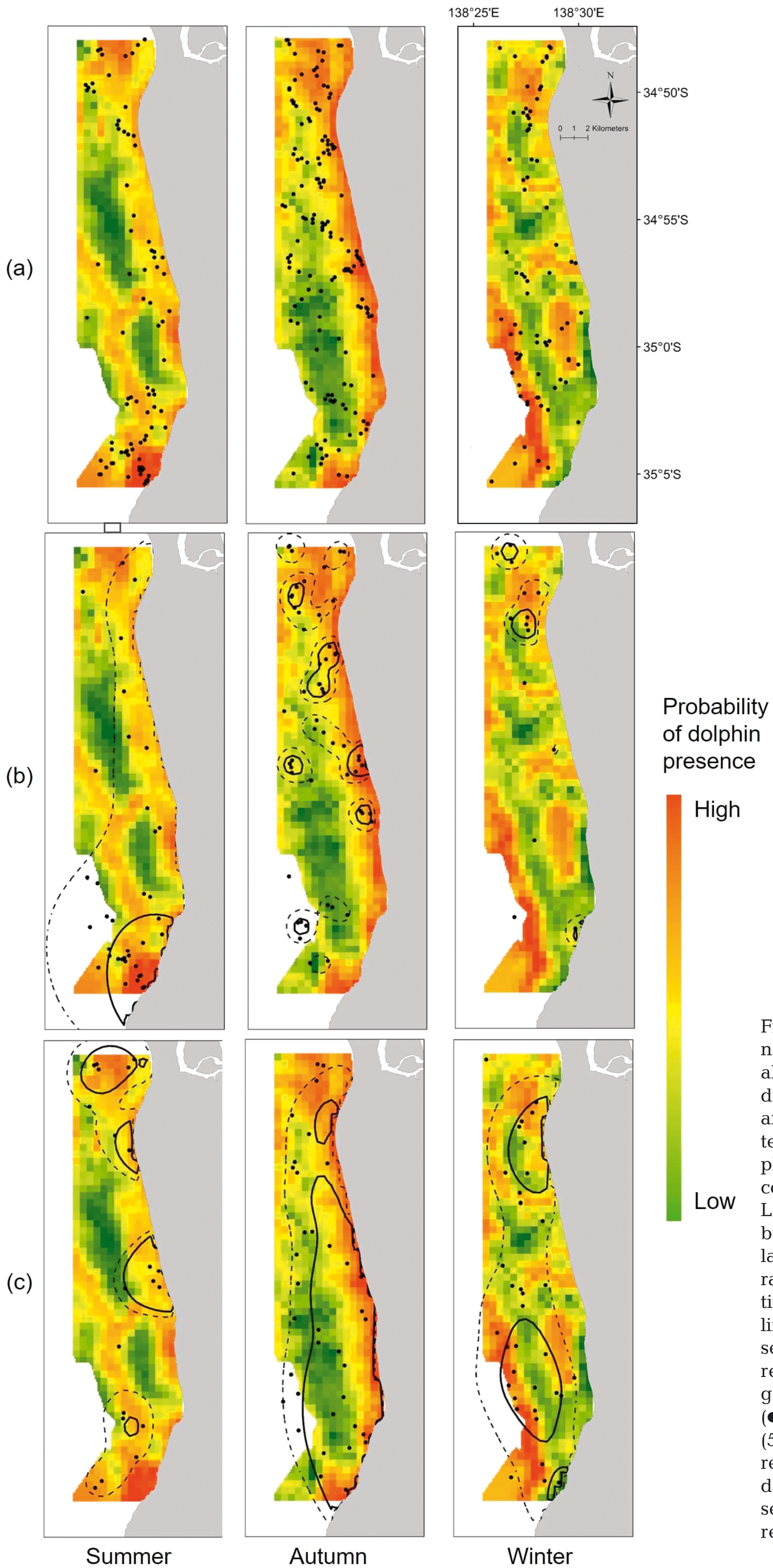

Fig. 3. (a) Ensemble models of bottlenose dolphin probability of occurrence along Adelaide's metropolitan coast during summer (December to February), autumn (March to May) and winter (June to August). Probability of dolphin occurrence is represented by the coloured shading, as detailed in the key. Location of dolphin sightings used to build the models is shown (●). (b) Overlap of core areas of use (50% kernel range, solid black line) and representative range (95% kernel range, dashed line) of dolphin feeding groups with the seasonal probability of dolphin occurrence. Locations of dolphin groups engaged in feeding behaviour are shown (●). (c) Overlap of core areas of use (50% kernel range, solid black line) and representative range (95% kernel range, dashed line) of travelling groups with the seasonal probability of dolphin occurrence. Locations of dolphins engaged in travelling behaviour are shown (●)

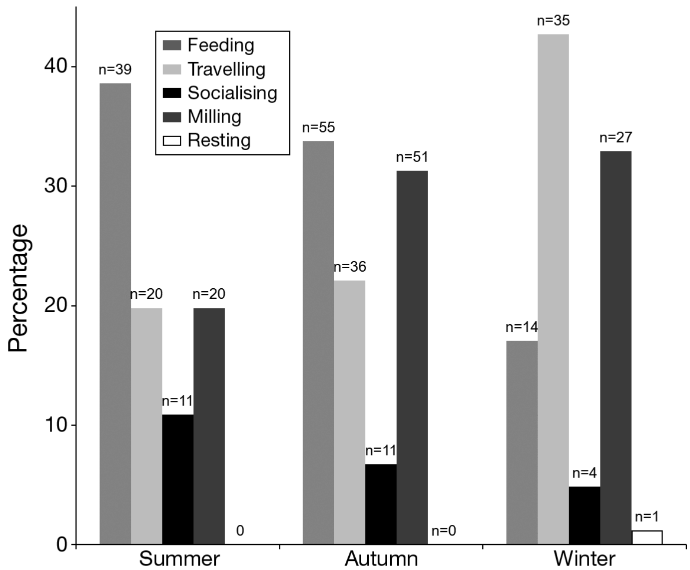

Fig. 4. Percentage of groups according to season and predominant behavioural activity of southern Australian bottlenose dolphins along Adelaide's metropolitan coast between December 2012 and August 2014. n-values are presented above bars

Table 3. Percentages of core (50% kernel range, Kde50) and representative (95% kernel range, Kde90) behavioural ranges that overlapped with areas of high probability of occurrence across seasons

	Feeding		Travelling	
	Kde50	Kde95	Kde50	Kde95
Summer	60	32	56	44
Autumn	86	64	50	49
Winter	43	49	44	46

Ecogeographical predictors of dolphin distribution

Dolphins along the Adelaide metropolitan coast appear to favour shallower, nearshore areas in both summer and autumn, and prefer somewhat deeper areas further offshore in winter. Similar seasonal variations in dolphin distribution and habitat preferences are reported for Indo-Pacific bottlenose dolphins *Tursiops aduncus* in Bunbury, Western Australia, and Hector's dolphins *Cephalorhynchus hectori* in New Zealand, and are suggested to be associated with changes in prey availability (Rayment et al. 2010, Sprogis 2015).

Previous studies on bottlenose dolphins in South Australia suggest that the distribution patterns of dolphins in the Port River estuary and Barker Inlet in GSV are a response to prey movements (Cribb et al. 2013). Temporal and spatial variation in prey availability can influence marine predators' distributions and movements (Lima 2002, Beauchamp et al. 2007, Torres et al. 2008). For example, baleen whales migrate hundreds to thousands of kilometres to particular prey hotspots and feeding grounds throughout the globe (Kenney et al. 2001), the seasonal distribution of Pacific northwest killer whales *Orcinus orca* correlates with prey movements (Felleman et al. 1991); and Hawaiian spinner dolphins *Stenella longirostris longirostris* follow the smaller diel migration patterns of their prey (Benoit-Bird & Au 2003). In this study, core feeding areas overlapped significantly with predicted areas of high dolphin presence, suggesting that prey movements may have an impact on dolphin distribution, particularly during summer and autumn. Southern calamari squid *Sepioteuthis australis* is a predominant prey item of bottlenose dolphins in South Australia, followed by various species of both demersal and pelagic fish (Gibbs et al. 2011). Throughout summer, numbers of squid and small fish (e.g. whiting *Sillaginodes punctatus*, western Australian salmon *Arripis truttaceus*, trevally *Pseudocaranx* spp., garfish *Hyporhamphus melanochir* and yellow-eyed mullet *Aldrichetta forsteri*) peak within the temperate reef habitats of the southern metropolitan coast and Fleurieu Peninsula (McGlennon & Kinloch 1997, Triantafillos 2002, Bryars 2003, Steer et al. 2007). The large congregation of prey items in reef habitats is concurrent with the core summer feeding area and suggests the importance of this benthic habitat type for Adelaide's bottlenose dolphins during summer.

During autumn, the summer congregations of squid and fish species tend to disseminate. Spawning squid aggregations travel northwards to the upper regions of the gulf (Triantafillos 2002), while garfish and yellow-eyed mullet are generally found within the shallow metropolitan waters, and salmon move sporadically throughout the metropolitan coast (McGlennon & Kinloch 1997, Jones et al. 2002). The diffusion of prey species along the coast during autumn may explain the more widespread distribution and habitat preference of dolphins during this season, and the occurrence of more than one core feeding area.

In winter, the higher probability of dolphin presence in areas farther from the coast, together with the significant decrease in feeding behaviour, is likely the result of prey dispersal outside of the metropolitan coastal area. During this time, nearshore waters become colder and exposed to increased water turbidity from stormwater (Kaempf 2006, Environment Protection Authority 2013). Consequently, fewer numbers of squid are present along the metropolitan coast (Triantafillos 2002, Steer et al. 2007), and a number of fish species disperse to deeper waters and/or move to areas in southern GSV (e.g. garfish and King George whiting) (McGlennon & Kinloch 1997, Jones et al. 2002, Fowler & Jones 2008). Smaller numbers of dolphins along the metropolitan coast during winter (Zanardo et al. 2016), and the higher number of observed travelling behaviours support potential movements of individuals to deeper offshore areas. Overall, we hypothesize that prey availability is a key driver of dolphin distribution along the Adelaide metropolitan coastline. We recommend that futures studies investigate diet and feeding ecology of southern Australian bottlenose dolphins within GSV, to better elucidate the influence of prey on dolphin distribution, behaviour and preferred habitat.

Prey availability may also interact with other synergistic factors, including predation risk (Heithaus & Dill 2002, Hastie et al. 2004) and water temperature (Bräger et al. 2003), which may also influence seasonal variations in dolphin distribution and preferred habitat. White sharks *Carcharodon carcharias* are a known predator of dolphins in South Australia (Bruce 1992). Sightings of white sharks occur more frequently over spring and summer, with greater numbers observed in northern GSV and fewer along the metropolitan coast (Huveneers & Drew 2014, Huveneers et al. 2014). Typically, dolphins avoid predatory sharks (Heithaus 2001); for example *T. aduncus* in Shark Bay, Western Australia, avoid foraging in shallow waters when predation risk is high and only return to these areas when shark numbers are very low (Heithaus & Dill 2002). Thus, in summer, southern Australian bottlenose dolphins may move to shallower waters closer to shore to lower predation risk. Conversely, in winter, when shark observations are not as frequent in GSV (Huveneers et al. 2014), dolphins may be able to use areas further offshore due to a lower risk of white shark predation.

Sea surface temperature is also shown to correlate with the distribution of a number of cetacean species (see Bräger et al. 2003). Observations of dolphin populations across seasons document fewer sightings, or a change in distribution and habitat use during colder winter months (Barco et al. 1999, Maze & Würsig 1999, Chilvers et al. 2003). Colder water temperatures may influence individuals directly through thermoregulation and energetic demands; for example, when temperatures move below 20°C, dolphins require a higher energetic intake to build blubber stores (Ross & Cockcroft 1990). Alternatively, indirect influences of cold temperatures may result from effects of temperatures on the distribution of prey and predators (discussed above) (Scott et al. 1990, Barco et al. 1999). Within GSV, highest temperatures (~25°C) occur towards the end of summer, and lowest temperatures (~12°C) occur towards the end of winter (Kaempf 2006). During these winter months, sea surface temperatures are colder along nearshore shallow areas than within the middle of the gulf (Kaempf 2006). Therefore, the higher probability of dolphin presence in waters farther from the coastline during winter may reflect a combination of factors, including prey availability and dolphin metabolic and energetic demands.

Effectiveness of ensemble modelling approaches

The results from this study support the effectiveness of ensemble modelling approaches in reducing the predictive uncertainty of single models. We found some discrepancies in the importance of ecogeographical variables between single SDMs, and we were able to overcome these issues using ensemble modelling. We encourage the use of ensemble modelling for future studies assessing cetacean distribution and habitat use, as this method can be used to provide a more robust representation of preferred habitats, which is essential to implement strategies for species conservation and management.

Implications for conservation management

Coastal dolphins living in close proximity to urbanised cities are at risk from anthropogenic threats from increasing activities and developments (Jefferson et al. 2009). Such anthropogenic pressures are known to affect dolphin behaviour and distribution (Heithaus & Dill 2002, Lusseau 2005, Bejder et al. 2006). In the Adelaide metropolitan coast and adjacent areas, anthropogenic activities intensify throughout summer, with increased numbers of recreational fishing, boating, water activities (i.e. kayaking, jet skiing) and increased dolphin swim-with tourism. This peak in anthropogenic activities coincides with the largest estimates of dolphin abundance along the metropolitan coast (Zanardo et al. 2016). The combination of increased anthropogenic activities and larger dolphin numbers puts individuals at increased risk from these threats. Of particular concern during summer is the southern metropolitan area, where anthropogenic activities are likely to overlap with this seasonal 'hotspot' of dolphin occurrence and potentially cause disturbances. For example, tourism boats that use the area alter the short-term behaviour of dolphins and lead them to spend more time milling and less time feeding, travelling and socialising (Peters et al. 2012).

Our study indicates that the southern metropolitan waters are a predominant feeding area in summer. Furthermore, most socialising behaviours, mating and newborn calves, were observed throughout summer (Fig. 4), and most occurred within the southern metropolitan area (data not shown). Therefore, the increased occurrence of tourism and recreational boats within the southern metropolitan area over summer may have a negative impact on dolphin feeding and socialising behaviour. Disturbances to foraging behaviour may result in the inability to meet nutritional requirements, while disturbances to mating and mothers with newborn calves may affect the reproductive rate of a dolphin population (Lusseau 2004). In the long term, this has been shown to lead to population declines and/or displacement of dolphins from important habitat areas (Lusseau 2005, Watson-Capps & Mann 2005, Bejder et al. 2006). To mitigate these anthropogenic disturbances, protection measures may include limiting access to areas where biologically significant behaviours occur (e.g. Lusseau & Higham 2004, Notarbartolo-di-Sciara et al. 2009), or where these overlap with fishing pressures (e.g. Slooten et al 2006).

Currently, the management of anthropogenic activities on coastal dolphins in South Australia is limited to restrictions on vessel and swimmer approach distances. Additional management strategies include the establishment of the Adelaide Dolphin Sanctuary (ADS) within the Port River estuary and Barker Inlet (Department of Environment, Water and Natural Resources 2005). Management strategies within the ADS include the monitoring of dolphins through land and water surveys, vessel speed restrictions, and engagement with the community to reduce marine debris and inhibit dolphin provisioning. Unfortunately, these management strategies do not extend to other areas of the South Australian coast, leaving the vast majority of the urban coast under-regulated. Threats to southern Australian bottlenose dolphins are likely to increase in the future, with proposed coastal developments (Department of Planning, Transport and Infrastructure 2010) and plans to establish additional boat-based marine and dolphin tourism experiences in South Australia (National Parks South Australia 2016). This highlights the need to implement additional management strategies for dolphins along the South Australian coast.

The results from this study provide management agencies with information to consider for the implementation of seasonal management strategies to mitigate the potential detrimental effects of human activity on bottlenose dolphins within Adelaide's coastal water. Access and speed restrictions of recreational and tourism boats to important dolphin feeding habitats should be implemented, particularly during summer and autumn, to decrease dolphin–boat interactions and limit behavioural disruptions. Fishing limitations within such areas could also enhance fish assemblages in important habitats and thus continue to provide an adequate food source for metropolitan dolphins over the long term. Further, coastal boat ramp signs and surface markers indicating the location of important dolphin habitats, would help enhance public awareness and protection of these areas. The implementation of these management strategies should go hand in hand with continued monitoring of the local dolphin population and the evaluation of anthropogenic pressures on southern Australian bottlenose dolphins.

Overall, understanding species–environment relationships is crucial for future conservation of marine mammals. Apart from identifying preferred habitat, understanding the behaviourally (foraging adaptations, reproduction, intra-interspecific interactions) and environmentally mediated processes (prey production and concentration, prey behaviour and life history) that influence marine mammal distributions will further our understanding of their ecology and improve our ability to inform their conservation management (Palacios et al. 2013). The ensemble modelling and kernel density analysis used in this study can be applied to location and behavioural data of other marine species, and used to identify important habitats and the potential ecological function they provide to marine species.

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