Long-term trends in habitat use and site fidelity by Australian humpback dolphins *Sousa sahulensis* in a near-urban embayment

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ABSTRACT: Habitat use and site fidelity in coastal dolphins can vary in space and time, and are important components in conservation planning and predicting the impacts of environmental change. Little is known of long-term patterns of habitat use and site fidelity in threatened tropical delphinids. Here, we investigate trends in habitat use and site fidelity of Australian humpback dolphins *Sousa sahulensis* in Moreton Bay, a near-urban embayment in Queensland, Australia, using spatially referenced sightings from systematic surveys and government datasets. Data from 1992 to 2016 were assigned to 3 time periods with similar spatial coverage and compared using ecological niche and kernel models. We also used behavioural data collected from 2014 to 2016 to investigate the potential ecological function underpinning recent habitat preferences. A long-term fidelity and consistency in habitat use was evident at an industrialised port at the mouth of the Brisbane River, but patterns of habitat use were more dynamic elsewhere. Models of spatial patterns of behaviour suggested that areas used consistently were mostly foraging habitats. A marked shift in habitat use away from the northwestern side of Moreton Bay was evident after 1999, which we suggest was due to a decline in habitat integrity exacerbated by periodic floods. Our results imply that the optimal conservation strategy for the species would be to focus on areas that are long-term core habitats, whilst safeguarding against environmental change by maintaining habitat integrity across the broader area delineated by their ecological niche.

KEY WORDS: Habitat use · Ecological niche modelling · Site fidelity · Coastal dolphin · Humpback dolphin

INTRODUCTION

Knowledge of the distribution and habitat requirements of wildlife is vital for conservation planning, identifying threats and predicting the consequences of environmental change (e.g. Roger et al. 2007, Grech & Marsh 2008). However, ecological monitoring is typically short term whereas distributional shifts in response to environmental or biological change may manifest over much longer timescales (Sundby & Nakken 2008, Poloczanska et al. 2009). Movement and habitat-use patterns can also vary substantially within and between species, and over space and time (McHugh et al. 2011, Phillips et al. 2017, Meager et al. 2018).

This variability is exemplified by the delphinids, which includes species that range over a variety of habitats and large areas, such as killer whales *Orci-*

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nus orca (Baird & Whitehead 2000, Olsen et al. 2018), and species that can exhibit strong site fidelity (i.e. the tendency to return to a previously occupied location, Switzer 1993), such as coastal dolphins (reviewed by Gowans et al. 2007). Habitat use and site fidelity also vary within delphinid species. For example, common bottlenose dolphins *Tursiops truncatus* form resident communities with strong multigenerational site fidelity to areas where prey is abundant (Urian et al. 2009, Wells 2009), but often have low site fidelity and wide-ranging behaviour offshore (Wells et al. 1999) or in coastal habitats with variable food resources (Ballance 1992, Defran & Weller 1999, Defran et al. 1999).

It is therefore thought that site fidelity and movement patterns in delphinids are linked to the predictability and distribution of resources, as well as predation risk (Ballance 1992, Gowans et al. 2007). Fidelity to previously beneficial and familiar sites can be a low risk strategy compared with searching for new sites (Krebs & Inman 1992), whereas flexible habitat use or wide-ranging movement patterns allow species to respond opportunistically to prey patches (Heithaus et al. 2007, Sims et al. 2012).

Site fidelity can also arise from philopatry (Kokko & Lopez-Sepulcre 2006), social transmission (Valenzuela et al. 2009) or niche conservatism (i.e. the tendency of a species to retain aspects of their fundamental niche over time, Wiens & Graham 2005, Wiens et al. 2010). Socioecological function also plays a role in shaping spatiotemporal variation of site fidelity and habitat use in delphinids. What constitutes an ideal resting or socialising habitat may be a poor habitat for foraging and vice versa (Keith et al. 2013). For example, spinner dolphins *Stenella longirostris* use inshore habitats of large islands in Hawaii to rest and socialise during the day, and forage in pelagic waters at night (Norris & Dohl 1980, Benoit-Bird & Au 2009).

Among the delphinids, humpback dolphins *Sousa* spp. are known for their restricted inshore distribution and narrow habitat selectivity (Koper et al. 2016, Parra & Cagnazzi 2016, Karczmarski et al. 2017a), which can expose them to a variety of threats including pollution and fisheries bycatch (Ross et al. 2010, Cagnazzi et al. 2013, Gui et al. 2017). The similarity of habitat-use patterns between *Sousa* species suggests niche conservatism, which implies that their response to environmental change or anthropogenic impacts may be limited by the spatial extent of suitable habitat (MacLeod 2009). As a consequence, local populations in highly developed areas may be susceptible to habitat loss (Lin et al. 2016, Karczmarski et al. 2017a).

The Australian humpback dolphin *Sousa sahulensis* (hereafter humpback dolphin) is a threatened tropical dolphin with a limited range and low densities in surveyed areas (Parra & Cagnazzi 2016), listed as a Vulnerable species in the Australian state of Queensland and by the International Union for Conservation of Nature (IUCN, Parra et al. 2017). In Queensland and the Northern Territory, they are mostly found in shallow inshore waters less than 15–20 m deep and within 20 km of the nearest river mouth (Parra et al. 2004, Palmer et al. 2014b, Parra & Cagnazzi 2016). Research to date suggests that they exhibit short-term and periodic fidelity at the fine scale (Parra et al. 2006a, Palmer et al. 2014a, Hunt et al. 2017) and longer-term residency to embayments or coastlines at the broader scale (i.e. >1000 km^2, Cagnazzi 2011, 2013, Cagnazzi et al. 2011). Published studies on habitat use and site fidelity of humpback dolphins have been limited to 5 yr or less; long-term patterns of habitat use and residency over decadal timescales remain unknown.

Towards the southeastern limits of the species range in Moreton Bay, Queensland, Australia, a population of humpback dolphins resides in an embayment ~1523 km^2 in area (Corkeron et al. 1997), separated from the nearest resident population to the north by ~150 km of ocean-exposed coastline. Here, we compiled 25 yr of spatially referenced data from both systematic surveys and opportunistic sightings to examine long-term trends in habitat usage and ecological niches of humpback dolphins in Moreton Bay. We also used a contemporary behavioural dataset to examine the potential ecological function(s) driving habitat use by humpback dolphins. We hypothesise that niche conservatism in humpback dolphin results in long-term site fidelity to nearshore areas of Moreton Bay, but that this fidelity is shaped by the socioecological function of the habitat. More specifically, we predict that several key biophysical features, namely distance to land, distance to river mouth and water depth (Parra et al. 2006b), have acted to delineate the ecological niche of humpback dolphins in Moreton Bay over the time period, and that this niche has been consistent over time. Our alternative hypothesis is that habitat usage, site fidelity and ecological niches have changed over time in response to the long-term decline of habitat integrity on the western side of Moreton Bay (Kirkman 1978, Pressland et al. 1998, Coates-Marnane et al. 2016) and/or periodic environmental perturbations (Stephenson et al. 1977, Meager & Limpus 2014).
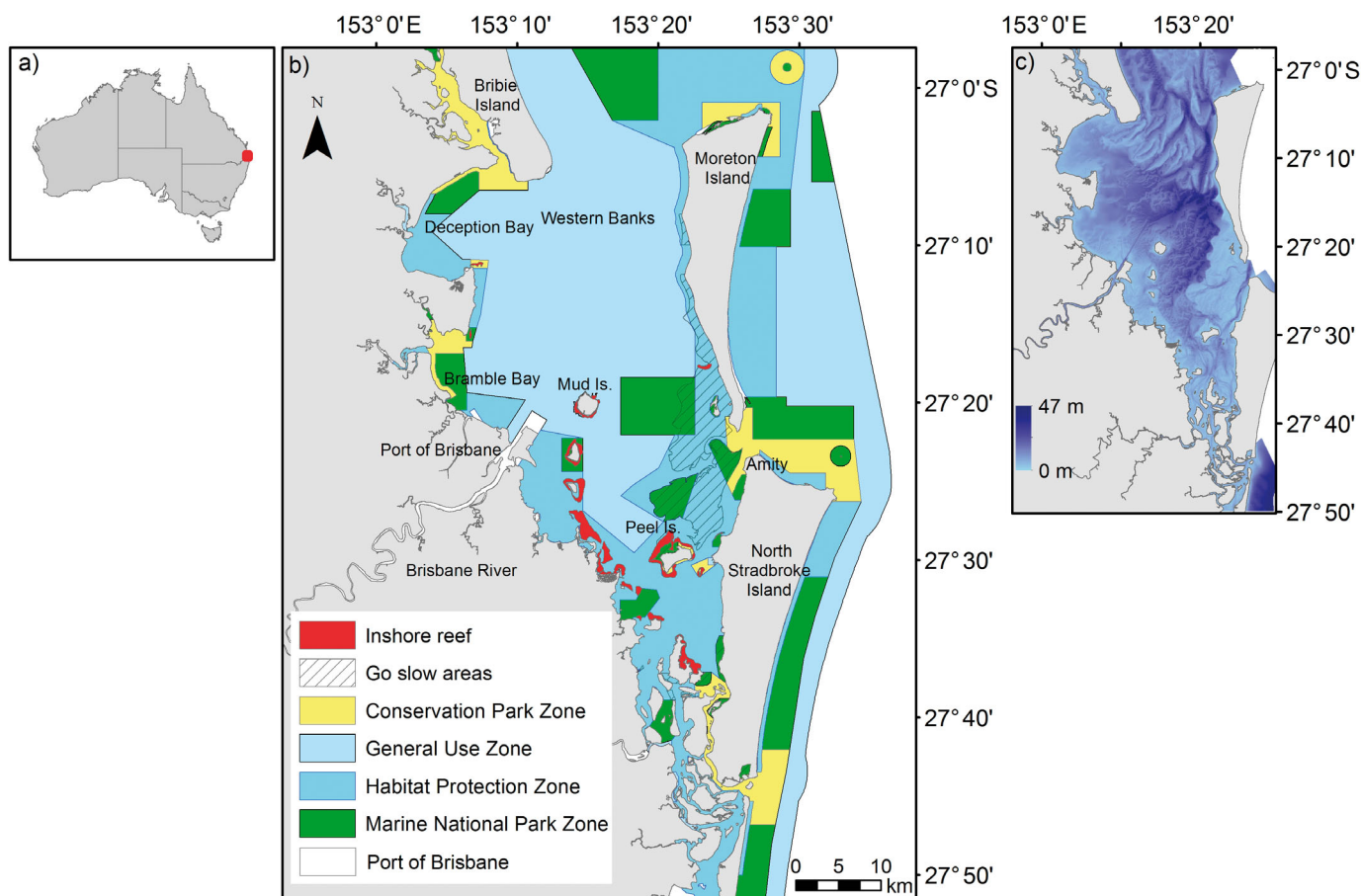
Fig. 1. (a) Moreton Bay in Australia and (b) the current marine park (reserve) zoning and the location of inshore reefs. All fishing is prohibited in the Marine National Park Zone and is limited in the Conservation Park Zone. Trawling is only permitted in the General Use Zone and outside of the marine park (https://qld.gov.au/environment/costs-waterways/marine-parks/zoning). Vessel speed restriction areas ('Go Slow areas') are indicated by cross hatching. (c) Bathymetric relief of the study site (no data are available for the white areas)

MATERIALS AND METHODS

Study site

Moreton Bay is a large, shallow subtropical embayment in Queensland, eastern Australia (Fig. 1, approximately 1523 km^2 in area and <40 m depth, Dennison & Abal 1999). Significant changes in Moreton Bay over the past 40 yr have included development and major capital works in the western Bay, severe flooding events and a large reduction in otter trawling associated with marine park rezoning and fisheries legislation (Table 1). Most urbanisation has occurred on the western side of Moreton Bay, where dolphins may be exposed to risks such as persistent bioaccumulative contaminants (Hermanussen et al. 2004, Shaw et al. 2004, Hermanussen 2009) and a

high volume of vessel traffic (Queensland Transport and Main Roads 2012). A long-term decline in habitat integrity and water quality on the western side of Moreton Bay has also been well documented (Kirkman 1978, Pressland et al. 1998, Coates-Marnane et al. 2016 and other references herein) and these conditions are exacerbated by periodic flooding (Stephenson et al. 1977, Meager & Limpus 2014). On the northeastern side of Moreton Bay, water quality is high and protection is afforded by marine reserves and vessel-speed reduction zones (Fig. 1). The marine park (reserve) now encompasses much of the area, with the exception of the Port of Brisbane (Fig. 1).

The humpback dolphin adult population size in Moreton Bay was estimated to be between 119 and 163 in the period from 1984 to 1987 (95% CI: 81–251,

Table 1. Sources of georeferenced sightings data and significant events that occurred in the time period. Information on the timing and severity of floods was based on a timeline from the Australian Bureau of Meteorology (http://bom.gov.au/qld/flood/fld_history/brisbane_history.shtml). DES: Queensland Department of Environment and Science; WildNet: the Queensland Government wildlife database

Period	Years	Number of positions	Approx. number of individuals	Survey methods	Significant events within study period	Sources
1	1992–1999	147	167	Vessel and aerial surveys, opportunistic sightings	• Major floods in December 1991–March 1992, May 1996 • Marine Park zoning plan 1997 • Major *Lyngbya majuscula* bloom late 1999–2000 • Progressive upgrades to waste-water treatment plants in catchment • Cessation of coral dredging at Mud and St Helena Islands in 1995	WildNet, Lanyon & Morrice 1997, Hale et al. 1998, McPhee 2017
2	2003–2011	114	668	Vessel surveys, opportunistic sightings	• Upgrades to waste water treatment programmes • Large reduction of otter trawling effort from 1999 to 2008 (fisheries legislation and marine park rezoning) • Marine Parks (Moreton Bay) Zoning Plan 2008, enacted 2009 • Construction of new bridges across Bramble Bay (2008–2010) and the Brisbane River (2007–2011) • Expansion of the Port of Brisbane (2008–2011) • Severe flooding in January 2011	WildNet, Ansman 2011 surveys
3	2012–2016	234	740	Vessel surveys, opportunistic sightings	• Major flood in January 2013 (short-lived, pulse event) • Extension of Brisbane Airport, sand extraction from Middle Banks 2013–2014	Surveys described herein, DES surveys and patrols, WildNet

Corkeron et al. 1997) and more recently between 128 and 139 from 2014 to 2016 (95% CI: 67–274, J. J. Meager & E. R. Hawkins, unpubl. data).

Vessel surveys were conducted across 6 different sectors in Moreton Bay from 2014 to 2016 (Supplement 1 at www.int-res.com/articles/suppl/m603p227_supp.pdf), with each sector taking 1 d to complete with a vessel speed of 10–16 km h^{-1}. Surveys were only undertaken when sea surface conditions were suitable for sighting dolphins (Beaufort sea state of ≤3) during intensive sampling blocks that coincided with the austral summer (2014) and winter–spring (2014–2016), and involved 54 d of survey effort in 2014 (30 d in winter and 24 d in summer), 46 d of effort in winter–spring 2015 and 34 d of effort in winter–spring 2016. For each individual or group encountered, the initial geographic location was recorded using a GPS and the behavioural state (travelling, socialising, resting or foraging; Table S2 in Supplement 3 at www.int-res.com/articles/suppl/m603p227_supp.pdf)

was determined while we subsequently followed the individual or group. Behavioural state represented the predominant behavioural pattern of the group (i.e. >50% of the dolphins exhibited the behaviour), which was defined as more than one dolphin within an approximate 100 m radius that were mostly engaged in the same behavioural state (Irvine et al. 1981). Groups were followed for up to 60 min but only the initial location and behavioural state are analysed here.

Collation and spatial-temporal stratification of sightings data

Spatially referenced sightings of humpback dolphins were sourced from scientific publications, reports, PhD theses and Queensland Government datasets (Table 1, Supplement 1). There are 2 potential sources of bias in comparing the spatial distribu-

tion of sightings between different studies and time periods: (1) the spatial-temporal distribution of sampling effort and (2) relative sampling intensity. Here, we use the strategy of assigning data into time periods to obtain a trade-off of sampling intensity and comparable spatial-temporal coverage, with each stratum featuring a combination of systematic vessel surveys and opportunistic sightings (Table 1). The general rationale of this approach was to use the systematic surveys to balance spatial effort across time periods, and opportunistic sightings to balance sampling intensity across time periods. This resulted in 3 time periods that were considered to have comparable spatial-temporal coverage: Period 1 (1992−1999, total number of sightings, n = 167), Period 2 (2003−2011, n = 114) and Period 3 (2012−2016, n = 234). Details on how the sightings data were collated and a comparison of the spatial coverage of each time period are provided in Supplement 1. Because group numbers were not provided for every sighting, each sighting was given an equal weight in the analyses.

Comparisons of utilisation distributions between time periods

We examined whether the occurrence of humpback dolphins was consistent or variable over time using population-level kernel density estimators. Kernel density estimators have long been used to delineate the home ranges of animals (Anderson 1982, Worton 1989), but have more recently been used to characterise the distribution of species, including delphinids across space (Martins et al. 2013, Denoël & Ficetola 2015, Zanardo et al. 2017). We use the term 'utilisation distribution' (UD) as it applies to the latter case, which represents the probability density function that takes the whole population into consideration. The area enclosed by the 95% isoline was selected to represent population habitat use, and the 50% isoline was selected to represent the core areas of habitat use (Worton 1989, Parra 2006).

A number of measures were undertaken to reduce bias from relative sampling intensity because in theory UD estimates reach an asymptote with sample size (Börger et al. 2006), which means that smaller UDs would be expected when there are fewer sightings of dolphins. First, the bandwidth of the smoothing parameter for the kernel density estimator was set to be equal for all time periods (Kelsall & Diggle 1995). Global bandwidth (h) was estimated in the 'adehabitatHR' package (Calenge 2011) of R (R Development Core Team 2017) using a fixed normal

kernel ($h = \sigma n^{-1/6}$), where the estimated variance in the x and y coordinates was given by $\sigma^2 = 0.5[\mathrm{var}(x) + \mathrm{var}(y)]$ and n was the number of locations. A rule-based approach was then used to estimate $h_{\mathrm{ad\ hoc}}$ (Kie 2013), which reduced under-smoothing by incrementally reducing h until the 95% isoline fractured into 2 or more polygons.

Second, locations were spatially thinned (rarefied) to take into account differences in sample sizes between study periods (Aiello Lammens et al. 2015). The UD for the period with the fewest locations (Period 2, n = 114) was compared with what would have been the case had sampling effort been the same in each period. We used a custom R script (R Development Core Team 2017) to (1) subsample 114 random locations from Periods 1 and 3, (2) estimate the new UDs and (3) generate comparative metrics. Steps (1) to (3) were repeated for 500 bootstrap samples, and global and local comparative metrics were then averaged over the samples. Global similarity was calculated by spatial correlation tests based on 1000 pixels selected at random; and by the *I* metric, which ranges from 0 where there is no overlap between distributions to 1 when distributions are identical (Warren & Seifert 2011). Local dissimilarity was analysed using the SigDiff function in the R package 'SDMTools' (VanDerWal et al. 2014), which computes the significance of local pairwise differences relative to the mean and variance of all differences (Januchowski et al. 2010, Bateman et al. 2012). Spatial surfaces were then reclassified following Bateman et al. (2012) to indicate (1) areas where the first UD predicted higher densities of humpback dolphins (SigDiff ≥ 0.975) and (2) areas where the second UD predicted significantly higher densities of humpback dolphins (SigDiff ≤ 0.025).

Ecological niche modelling

We also compared the distribution of humpback dolphins between periods using maximum entropy modelling (MaxEnt, v. 3.3.3, Phillips et al. 2006) to build ecological niche models (ENMs, sensu Warren 2012). MaxEnt uses species occurrence data in conjunction with environmental data to estimate the distribution of a species by finding the distribution that has the maximum entropy (Elith et al. 2006, Phillips et al. 2006), and is therefore based on the assumption that there is a causal link between the distribution of the species and the environment.

MaxEnt is robust above a threshold sample size of ~50; thus, no adjustments were made for sample

size across time periods for this analysis (Wisz et al. 2008, Virgili et al. 2018). Sightings within each period were treated as presence-only data. The background extent for pseudo-absences included marine and estuarine areas of Moreton Bay that were surveyed, and 10 000 background locations were selected at random (Supplement 1). The R package 'ENMeval' (Muscarella et al. 2014) was used to tune the models, based on minimising Akaike's Information criterion (with small sample correction, AIC_c, Burnham & Anderson 2002) over a candidate model set that included linear, quadratic, hinge, product and threshold features, and regularisation coefficients from 0.5 to 4.0 (in increments of 0.5). Information theoretic approaches were used where there was no convincing evidence that a single model was the best among the candidate set (i.e. Akaike weight of evidence, w_i < 0.95) (following Burnham & Anderson 2002). Model fit was assessed by *k*-folds cross-validation whereby for each of the 5 iterations the data were randomly assigned into a training dataset containing 80% of the sightings and a test dataset including 20% of the sightings (Merow et al. 2013). Goodness of fit criteria included mean AUC (area under the receiver operating characteristics curve, Merow et al. 2013) and by visual assessment of observed sightings against the grid of predicted distributions (in the default MaxEnt logistic format) (Supplement 2 at www.int-res.com/articles/suppl/m603p227_supp.pdf). The relative contribution of each predictor variable to final models was evaluated by a permutation importance test, which is based on the drop in AUC when values for that variable are randomly permutated (converted to normalised percentage, Phillips 2006). A bootstrap procedure (100 samples) was then used to calculate the mean and variance of the contribution of each variable. To compare the area of suitable habitat between periods, we then reclassified the grids to calculate the total area where predicted probabilities were ≥0.3. This threshold was based on maximising the sum of sensitivity and specificity (Liu et al. 2013) using the bootstrapped averages (range: 0.34 in Period 3 to 0.38 in Period 1).

Environmental predictors of habitat use

Seven biophysical predictor variables were selected because they were thought to influence the distribution of humpback dolphins (Parra et al. 2006b, Parra & Cagnazzi 2016), and were screened for collinearity (pairwise Pearson correlation coeffi-

cients < |0.5|). The focus was on selecting predictors that were comparable across the study period, rather than dynamic habitat attributes such as sediments and seagrass distribution. Included variables were depth, distance from the 10 m depth contour, seafloor slope, distance from shore, distance from inshore reef, distance from mangroves and distance from river mouths. Depth was derived from high-resolution soundings from Maritime Safety Queensland using the 'ANUDEM' algorithm of ArcGIS (v 10.4, Esri), and was used to calculate seafloor slope and distance from the 10 m contour. The water depth at which humpback dolphins were sighted was also estimated from the bathymetric map. Depths shallower than 1 m were not included in the analysis as they were considered too inaccurate because of a tidal range of around 2 m. The distance from mangroves and distance from inshore reefs (i.e. inshore rocky and fringing subtropical coral reefs) was derived from the 'Moreton Bay broad-scale habitats 2008' layer under a Creative Commons license from the Queensland Government. All distances were Euclidean.

Behavioural drivers of habitat use

Generalised additive models (GAMs) were used to model spatial patterns in behaviour (Hastie & Tibshirani 1986, Wood 2006), using only the Period 3 survey data because comparable data were not available for the earlier periods. Four behavioural states were considered for the analyses: 'foraging', 'socialising', 'travelling' and 'resting', and were tested separately as binomial responses (e.g. foraging = 1 and not foraging = 0) (see Table S2 in Supplement 3 for definitions of behavioural states). The location at the commencement of the follow of the focal group/individual and the corresponding behavioural state observed at this time were used for this analysis. GAMS were implemented in the 'mgcv' package of R (Wood 2018) using a 2D tensor product spline to model spatial effects (Wood 2006). The significance of a model term was evaluated by bootstrapped log-likelihood ratio tests against the null model (1000 runs). The final model was then checked for overdispersion. Models were predicted over the area defined by the minimum convex polygon of the spatially referenced behavioural data, and then interpolated using the natural neighbours tool in ArcGIS. Behaviour-specific UDs were estimated following the same $h_{ad\ hoc}$ method used to estimate UDs for each time period.
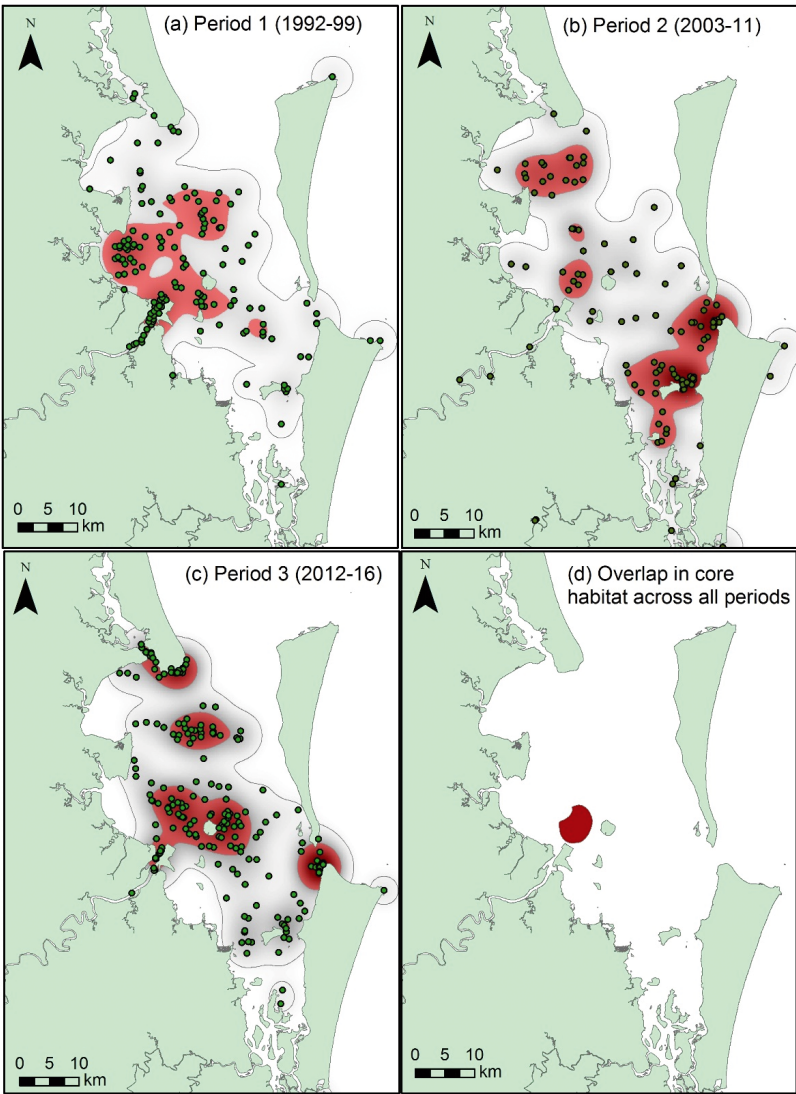
Fig. 2. Utilisation distributions for each period: (a) Period 1 (1992–1999); (b) Period 2 (2003–2011); (c) Period 3 (2012–2016). The red shaded areas represent the core habitat area (enclosed by the 50% isoline), the grey polygons represent the 95% isoline and the green points are the sightings. (d) Overlap between 50% core habitat areas (Periods 1, 2 and 3)

to 0.81), whereas the correlation coefficient indicated that Period 2 and 3 UDs were the most similar ($r = 0.58$) and Period 1 and 3 UDs were the most different ($r = 0.30$) (Table 2). At the local scale, significant differences were evident between the time periods with a shift away from Bramble Bay and the Brisbane River estuary from Period 1 to 2 (Fig. 3a, refer to Fig. 1 for place names). This corresponded to an increase in humpback dolphin density in the southeastern areas of Moreton Bay, and to a lesser extent, increased densities of humpback dolphins in the Western Banks area.

Significant distributional shifts were also evident away from Deception Bay and areas of southeastern Moreton Bay from Period 2 to 3, corresponding to an increased density at Bribie Island and in central Moreton Bay (Fig. 3b). The distributional shift away from Bramble Bay and the Brisbane River estuary persisted into Period 3 (Fig. 3c). Core habitat overlap across all 3 periods was restricted to an area adjacent to the Port of Brisbane (a total area of 25.5 km^2; Fig. 2d).

Ecological niche modelling

The total area of suitable habitat delineated by the ENMs (p > 0.5) was 670.4 km^2 in Period 1, 625.2 km^2 in Period 2 and 496.2 km^2 in Period 3. The ENM prediction grids indicated that a marked shift away from the

RESULTS

Utilisation distribution: comparison between periods

Two core habitat areas (50% UD 'nuclei') were evident in Period 1, compared with 4 in Periods 2 and 3 (Fig. 2). Core habitat areas were only present in the central western area of Moreton Bay in Period 1, but were also present in the northern and southern areas in Periods 2 and 3. The global I metric indicated an overall similarity between time periods (I from 0.74

Table 2. Coefficients of similarity (bootstrap mean with confidence intervals) between utilisation distributions (UDs) for each period, where 0 is no overlap and 1 is complete overlap (refer to Table 1 for details of each period). *r*: Pearson's correlation coefficient; *I*: metric of similarity

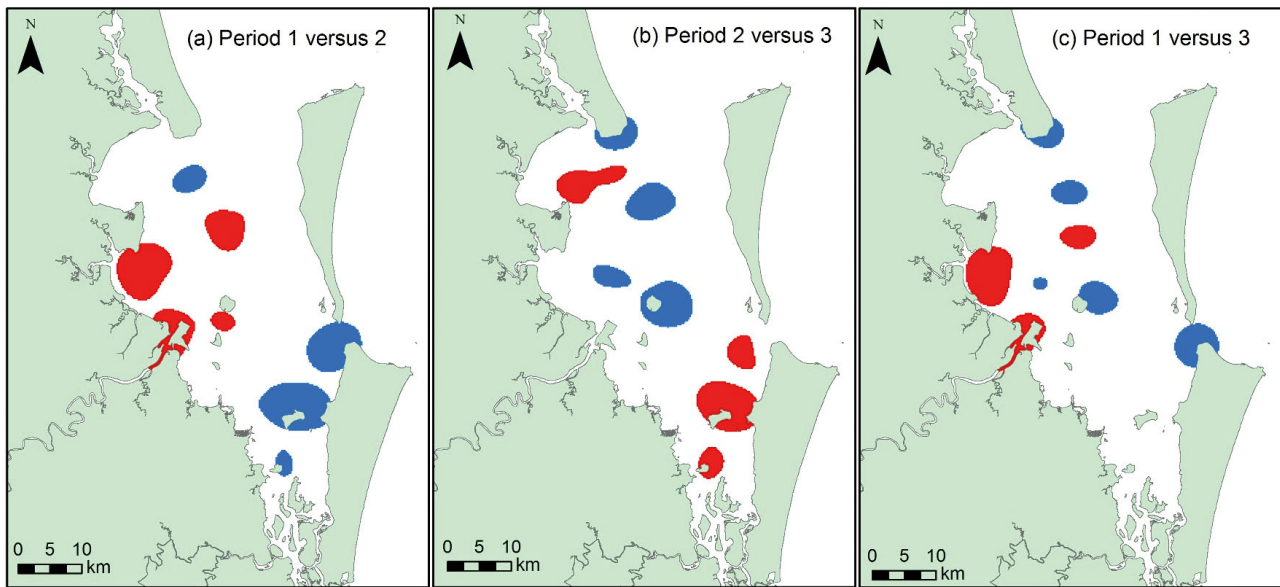|		Period 1	Period 2	Period 3
Period 1	*r*	1	0.30 (0.25–0.35)	0.50 (0.41–0.58)
	I	1	0.74 (0.71–0.76)	0.81 (0.78–0.85)
Period 2	*r*		1	0.58 (0.49–0.64)
	I		1	0.82 (0.79–0.84)

Fig. 3. Comparisons of utilisation distributions between periods. The red shading indicates areas where Australian humpback dolphins are significantly more likely to occur in the first time period, and the blue shading where humpback dolphins are significantly more likely to occur in the second period: (a) Period 1 (1992–1999) versus Period 2 (2003–2011); (b) Period 2 (2003–2011) versus Period 3 (2012–2016), and (c) Period 1 (1992–1999) versus Period 3 (2012–2016)

landward margins of northwestern Moreton Bay (i.e. away from Bramble and Deception Bay) towards the south and central areas of Moreton Bay (near Mud Island) occurred from Period 1 to Period 2, and continued into Period 3 (Fig. 4). Habitat suitability was more variable between time periods in the Western Banks area of Moreton Bay (Fig. 4). In Period 3, habitat suitability also increased on the southern shores of Bribie Island.

Distance from rivers was the most important determinant of habitat suitability in Period 1, whereas distance from inshore reef was the primary driver of habitat suitability in Periods 2 and 3 (Table 3, Fig. 5). Depth or measures associated with depth, such as the
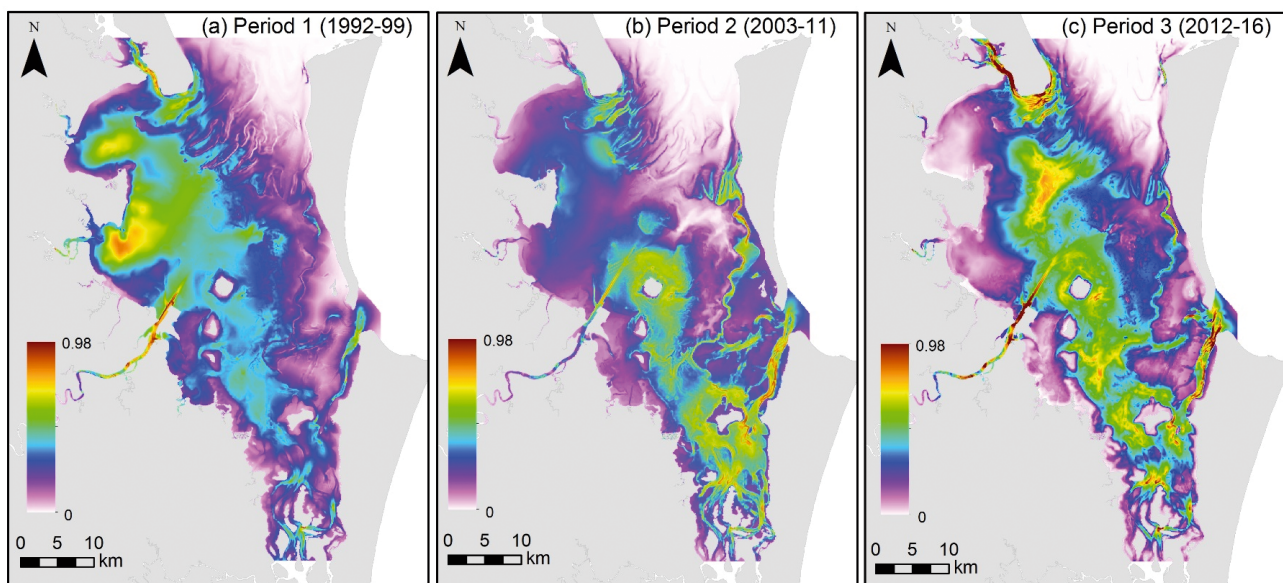

Fig. 4. Ecological niche models representing the areas in geographic space with high habitat suitability for Australian humpback dolphins: (a) Period 1 (1992–1999), (b) Period 2 (2003–2011) and (c) Period 3 (2012–2016). Warmer colours denote the most suitable habitats and can also be interpreted as a higher probability of Australian humpback dolphin presence. Prediction surfaces are averaged over 100 bootstrap samples

Table 3. Coefficients and goodness of fit for MaxEnt models. The value given for each predictor variable is the mean permutation importance (as a regularised percentage) over the 100 bootstrap samples, with bold text highlighting the most important variable. AUC: area under curve. L: linear; Q: quadratic; P: product; H: hinge

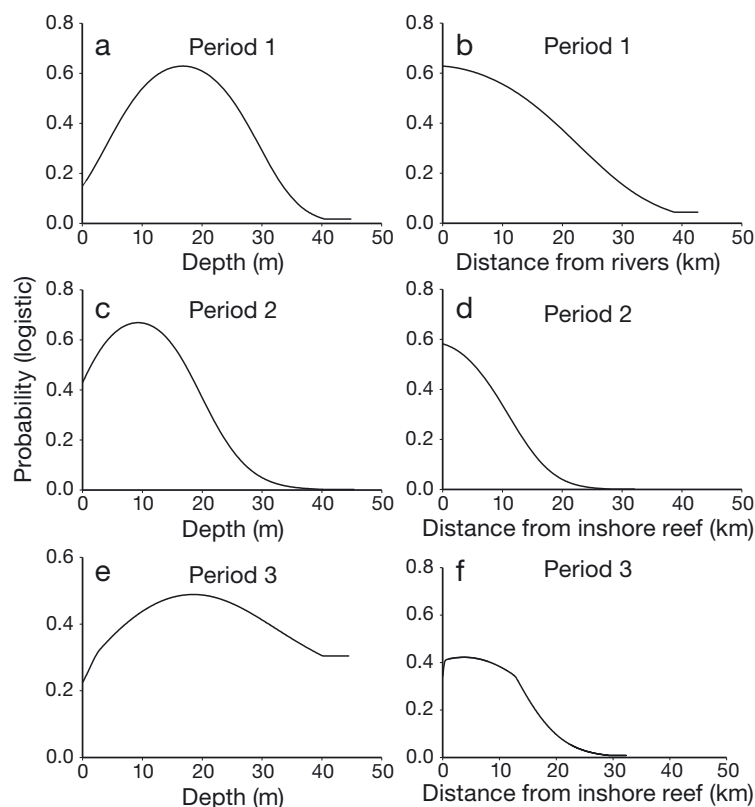| Model fit and predictor variables	Period 1	Period 2	Period 3
Model mean AUC	0.774	0.803	0.797
Regularisation parameter	3	1.6	3.5
Features	LQHP	LQ	LQHP
Distance from rivers	**23**	3.6	9
Depth	21.3	16.5	15.4
Distance from inshore reef	15.5	**41.6**	**19.6**
Distance from 10 m depth contour	13.3	15.3	18.5
Bathymetric slope	5.1	9.8	7.7
Distance from shore	9	17.3	16.1
Distance from mangroves	12.8	4.7	13.8

Fig. 5. Influence of environmental variables on predicted habitat suitability (*y*-axis, probability of presence), calculated from models that included only the given variable. (a,c,e) Influence of depth (bathymetry) for each period. (b,d,f) Most important environmental variable for each period (Table 3)

distance to the 10 m depth contour, were important in all periods. The dome-shaped influence of depth on habitat suitability was markedly similar across periods (Fig. 5a,c,e). The depth-only MaxEnt model predicted highest habitat suitability at 8.9, 8.4 and 10.5 m for Periods 1, 2 and 3, respectively. Humpback

dolphins were observed in areas from 1 to 32 m (n = 488) deep with a mean depth of 8.7 m (±SE = 5.2 m). Habitat suitability also declined with distance away from inshore reefs and with distance from the shore in all periods, although the relative predictive importance of the variables differed between periods (Table 3).

Behavioural drivers of habitat use

Overall, there were 213 spatially referenced observations of group behavioural state between 2014 and 2016 (Fig. 6a). There was a strong effect of location on the probability of humpback dolphins foraging (deviance = 50.28, p < 0.001; smooth terms: X^2 = 34.9, p < 0.001, n = 213), with high probabilities of foraging near Bribie Island, the Brisbane River estuary–Port of Brisbane, Western Banks and Amity on North Stradbroke Island (Fig. 6b). The probability of a humpback dolphin travelling also depended on location (deviance = 45.42, p = 0.018; smooth terms: X^2 = 30.19, p < 0.01, n = 213), with higher probabilities of travelling in the northwestern and central eastern sides of Moreton Bay (Fig. 6c). In general, areas with a higher predicted probability of travelling tended to occur between core habitats (Fig. 2c), whereas areas with a higher predicted probability of foraging tended to overlap with core habitats. There was no significant spatial effect on socialising (deviance = 0.54 p = 0.21, n = 213) or resting (deviance = 6.150, p = 0.173, n = 213).

DISCUSSION

The core habitat of humpback dolphins around the mouth of the Brisbane River and in the Port of Brisbane was markedly consistent over the 25 yr time period, whereas habitat use in peripheral areas towards the northern and southern limits of the study area was more dynamic. On the Western Banks and in southern areas of Moreton Bay, the location of core habitat varied considerably between periods. Models of spatial patterns of behaviour indicated that the area from the Brisbane River estuary to the Port of Brisbane (and adjacent) was a key foraging site, whereas travelling was more prevalent between core habitats.
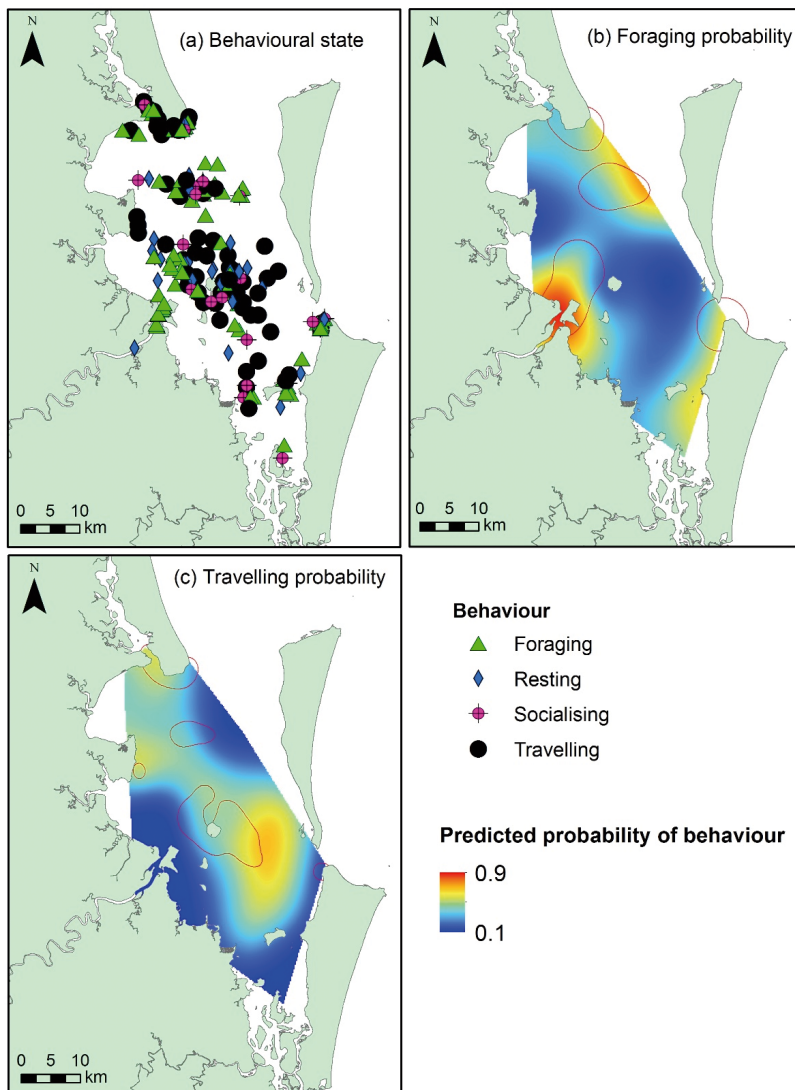
Fig. 6. (a) Behaviour of Australian humpback dolphins sighted in the surveys during Period 3 (2014–2016). (b) Modelled probability of foraging. (c) Modelled probability of travelling. In (b) and (c), the red lines denote the 50% isolines of the utilisation distribution of each behavioural state

Both ENMs and UDs indicated a pronounced shift away from the landward margins of Bramble Bay between Period 1 (1992–1999) and Period 2 (2003–2011), which was maintained throughout Period 3 (2012–2016). Both the ENMs and UDs also indicated a shift away from Deception Bay from Period 2 to Period 3. The most plausible explanation for these results was a localised decline in the availability of food resources for humpback dolphins (predominantly fish, Parra & Jedensjö 2014) associated with habitat degradation, high nutrient loads and sedimentation that have been well documented in Bramble Bay and Deception Bay (Kirkman 1978, Abal et

al. 1998, Pressland et al. 1998, O'Brien et al. 2012, Adams et al. 2016). Long-water residence times coupled with historical degradation of the catchments to Bramble and Deception Bay (Pine and Caboolture Rivers) manifests in pronounced and long-lasting effects of periodic floods on the northwestern side of Moreton Bay (Stephenson et al. 1977, O'Brien et al. 2012, Coates-Marnane et al. 2016). Environmental monitoring data are not available for Period 1, but from 2000 to 2014, an Ecosystem Health Monitoring Program (www.ehmp.org/) ranked Bramble Bay as having severe to medium impacts, and Deception Bay as poor to showing signs of recovery in 2014 (Table S3 in Supplement 4 at www.int-res.com/articles/suppl/m603p227_supp.pdf). Similarly, a recent study has described a major expansion of muddy sediments in the areas adjacent to the Caboolture River (Deception Bay) and Pine River (Bramble Bay) relative to an earlier survey in 1970 (Lockington et al. 2017). No long-term fish monitoring data in the area are available, but the results of a recent survey indicated that fish communities were less abundant and less diverse on the northwestern side of the Bay compared with the central and eastern sides of the Bay (Gilby et al. 2016).

Humpback dolphins are known to associate with trawlers in Moreton Bay to feed on trawler discards (Corkeron 1990), but in spite of a major reduction in overall trawling effort from 1999 to 2008 (Courtney et al. 2012) trawling remains widespread over the area (e.g. Courtney et al. 2016). A change in the spatial distribution of trawling effort is therefore unlikely to have explained the shift in distribution of humpback dolphins. However, it is possible that provisioning in the form of illegal hand-feeding of humpback dolphins has influenced the fine-scale distribution of dolphins at Amity Point, where it has occurred intermittently since at least the early 2000s (McPhee 2017, P. Corkeron, pers. comm.).

While the models detected a contraction of core habitat out of the Brisbane River towards the Port of Brisbane after Period 1, the lower estuary continued

to be used throughout the study period. This was despite major flooding events in Periods 1 and 2, and poor water quality since monitoring commenced in 2000 (Table S3 in Supplement 4). The Brisbane River has the largest catchment in Moreton Bay and has historically supported diverse and abundant marine invertebrate and fish communities (Davie & Hooper 1998), in addition to local beam trawl and net fisheries. Thus, the continued use of the Port of Brisbane and lower Brisbane River estuary by humpback dolphins across the 25 yr period indicates that this area continues to produce predictable food resources in spite of habitat change. However, there has been no long-term monitoring of fish communities to assess whether food availability in the area has changed over the study period.

The extent to which long-term site fidelity to the Port of Brisbane site may also be influenced by philopatry or social dynamics is unclear, and would require multigenerational longitudinal studies. However, there are indications from several studies that Australian humpback dolphins exhibit strong site fidelity (Parra et al. 2006a, Cagnazzi et al. 2011, Hunt et al. 2017) and low migration rates (<10%, Brown et al. 2014). Furthermore recent genetic studies along the east coast of Queensland indicate that dispersal in both male and female humpback dolphins is limited, and that Moreton Bay represents a putative population with limited gene flow to the nearest population in the Great Sandy Strait (Parra et al. 2018).

Social structure may play a role in shaping habitat use in Moreton Bay, as has been found in Moreton Bay with Indo-Pacific bottlenose dolphins (Ansmann et al. 2015). Recent results from photoidentification surveys from 2014–2016 suggest 5 distinct social communities of humpback dolphins (E. R. Hawkins et al. unpubl. data). Two of these communities in particular had comparatively little spatial overlap with the others, the first occurring mainly in northern Moreton Bay near Bribie Island and the other near Amity at North Stradbroke Island. Interestingly, the analysis of UDs in our study area indicated an increased presence of dolphins at Amity in Periods 2 and 3, and at Bribie Island in Period 3 (Figs. 2 & 3). However, we suspect that was the result of the earlier surveys missing these dolphin groups, rather than dolphins not using these particular areas, because dolphins were known to use the Amity area regularly during Period 1 (Van Parijs et al. 2002) and more search effort occurred around Bribie Island in Period 3 than in the earlier periods (Figs. S3 to S5 in Supplement 1). Notably, this was not a shortcoming of the ENMs, which indicated both areas had suitable habitat in all periods (Fig. 4). This was perhaps unsurprising given that ENMs are known for their ability to predict cetacean habitat suitability in areas where there is limited survey coverage (Breen et al. 2017, Gomez et al. 2017).

Long-term changes in ecological niches?

In our study, the ecological niche modelling indicated that the depth of the mouth of the Brisbane River estuary was more suitable for humpback dolphins than the mouths of the other main estuaries in Moreton Bay. Dredging has maintained the shipping channel at the Port of Brisbane since 1862 (http://portbris.com.au, accessed 21 March 2017), and may have hence played a role in maintaining a habitat preferred by humpback dolphins. Water depth and the physical features associated with water depth (such as distance to channels) are important habitat attributes for Australian (Parra et al. 2006a), Indian Ocean (Karczmarski et al. 2000, Koper et al. 2016) and Indo-Pacific *Sousa chinensis* humpback dolphins (Hung 2008, Ross et al. 2010, Dares et al. 2017).

Even though depth played an important role in defining the ecological niche of dolphins across all periods in our study, there was a notable shift in the importance of predictor variables of dolphin distribution between Periods 1 and 2. Distance from rivers had a much stronger influence on the ecological niche in Period 1 than in the latter periods, corresponding to the shift of core habitat away from the northwestern side of the bay (where the major river catchments are) to the centre of the bay. Conversely, distance from reefs became comparatively more important in Periods 2 and 3, which was largely because the reefs around Mud Island and Peel Island (Fig. 1) were used consistently across the 3 periods. Mud Island, Peel Island and other inshore reefs in Moreton Bay support diverse fish communities (Olds et al. 2012) and represent a stable and predictable food resource. The shift in the importance in some predictor variables of ecological niches across time periods suggests niche conservatism may not be as strong in this population as we predicted. It also suggests a degree of habitat flexibility that is probably not surprising given that the species is known to respond opportunistically to food sources such as trawler discards (Corkeron 1990, Parra 2006, Cagnazzi 2011).

The focus of the ecological niche modelling in our study was on biophysical habitat features that were stable across the time period, but numerous other habitat and environmental attributes are likely to

play a role in defining the realised niche of humpback dolphins in Moreton Bay, such as water clarity, prey availability, predators, temperature and competition with Indo-Pacific bottlenose dolphins (Corkeron 1990). Future ENMs from humpback dolphin could be improved by accounting for dynamic habitat features and interspecific interactions.

Potential implications for long-term population persistence in Moreton Bay

The ENMs indicated a 23% decline in the area of suitable habitat over the study period (640.4 km^2 to 496.2 km^2). Despite this decline, there was no strong evidence to suggest a corresponding decrease in the population given the relatively large confidence intervals around each of the abundance estimates available (1984–1987: 119–163 adults, 95% CI: 81–251, Corkeron et al. 1997; 2014–2016: 128–139; 95% CI: 67–274, J. J. Meager & E. R. Hawkins, unpubl. data). Yet, the observed long-term site fidelity of humpback dolphins to the Port of Brisbane could have consequences for their health and survival in this area. The Brisbane River and the central western side of Moreton Bay is where the highest concentrations of persistent bioaccumulative contaminants occur, both in the environment (Hermanussen et al. 2004, Shaw et al. 2004, Hermanussen 2009) and in marine fauna (Kayal & Connell 1995, Shaw et al. 2004, Hermanussen et al. 2006, Matthews et al. 2008). Although levels of contaminants in free-ranging dolphins in the area remain unquantified, concentrations of PCBs and DDTs in blubber of humpback dolphins that stranded dead in the central western areas of Moreton Bay were at levels near or above toxicological thresholds associated with population declines in other cetaceans (Weijs et al. 2016). As a large urbanized port, interactions with vessels and exposure to pathogens may also pose risks in the area (Van Parijs & Corkeron 2001, Bowater et al. 2003, Parra & Cagnazzi 2016).

Long-term fidelity in an area with known risks could suggest the potential for an 'ecological trap' (sensu Kokko & Sutherland 2001, Battin 2004) whereby dolphins persist in using a site despite habitat degradation. This is consistent with several studies on a sibling species, the Indo-Pacific humpback dolphin, which continues to inhabit areas in spite of habitat degradation or disturbance (Würsig et al. 2016, Dares et al. 2017), and a contraction of the population in the Pearl River Delta was associated with habitat loss (Lin et al. 2016, Karczmarski et al. 2017b). How-

ever, we are not able to determine whether or not the Port of Brisbane is functioning as an ecological trap without further investigation, and in particular, longitudinal studies of the health, site fidelity and reproductive performance of individual dolphins.

CONCLUSIONS

Our results suggested that habitat use and site fidelity over a 25 yr time series varied with habitat function, and implied an interplay between site fidelity and flexible responses to local resource variability. From the perspective of ecological niches, the results also suggested a level of niche flexibility in humpback dolphins. Although aspects of bathymetry had markedly similar influences on ENMs across the study period, the role of other predictors such as distance from rivers or distance from inshore reefs was more variable between periods.

These results have consequences for conservation management of humpback dolphins and for prioritising resources. The presence of localised core habitat areas that are used consistently over long time periods suggests that they are obvious candidates for focused conservation management. However, protecting habitat integrity across the broader area delineated by the ecological niche of the species may be an effective way to safeguard against future environmental change. The optimal allocation of conservation resources to support the long-term persistence of humpback dolphin populations would therefore have elements of both strategies. More generally, our results illustrate how historical changes in dolphin distribution can inform contemporary conservation management and underscore the need for a long-term approach to dolphin research.

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