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ORIGINAL PAPER

Modelling habitat use suggests static spatial exclusion zones are a non-optimal management tool for a highly mobile marine mammal

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Abstract

Understanding how animals use the space in which they are distributed is important for guiding management decisions in conservation, especially where human disturbance can be spatially managed. Here we applied distribution modelling to examine common dolphin (*Delphinus* sp.) habitat use in the Hauraki Gulf (36°S, 175°E), New Zealand. Given the known importance of the area for foraging and nursing, we assessed which variables affect *Delphinus* occurrence based on generalised additive models (GAMs), and modelled probability of encounter. Behavioural information was included to assess habitat use by feeding and nursing groups and determine whether persistent hotspots for such activities could be identified and meaningfully used as a spatial management tool. Using data collected from dedicated boat surveys during 2010–2012, depth and sea surface temperature (SST) were frequently identified as important variables. Overall, seasonal predictive occurrence maps for the larger population resembled predictive maps of feeding groups more than nursery groups, suggesting prey availability has important implications for the distribution of *Delphinus* in this region. In this case, static spatial exclusions would not be the best management option as the core areas of use identified for these activities were large and shifted temporally. It appears that at the scale examined, most of the Hauraki Gulf is important for feeding and nursing rather than specific smaller regions being used for these functions. In cases where static management is not the optimal tool, as suggested here for a highly mobile species, a dynamic approach requires more than a boundary line on a map.

Keywords Common dolphin · *Delphinus* · Predictive mapping · Species distribution modelling · Spatial management

Introduction

Understanding how animals use the space in which they are distributed is important for guiding management decisions (Guisan et al. 2013). Most studies of cetacean habitat use investigate the relationship between occurrence and environmental predictors over that of direct prey due to data availability (e.g., Panigada et al. 2008; Marubini et al. 2009; Garaffo et al. 2010; Santora 2011). For instance, cetacean associations with environmental factors such as sea surface temperature (SST) or chlorophyll concentration are often classified as an indirect relationship, usually used as a proxy for prey distribution and concentration (Heithaus and Dill 2002; Bräger et al. 2003; Cañadas and Hammond 2008; Azzellino et al. 2008; Dawson et al. 2013; Eierman and Connor 2014). Biological factors, such as group composition, are also known to affect habitat use (Cañadas and Hammond 2008; Guidino et al. 2014; Hartel et al. 2014; Melly et al. 2017). Habitat use models help determine which environmental and/or biological variables may be more important

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to explain species' distributions (Ferguson et al. 2006) and serve as a predictive tool to aid conservation and management strategies (Cañadas et al. 2005; Silva et al. 2012; Redfern et al. 2013).

Habitat heterogeneity and the biological requirements of a species interact to produce patterns in distribution and habitat use (Ballance 1992). Therefore, linking behaviour to distribution enables a better understanding of the function behind any habitat use patterns (Norris and Dohl 1980; Hastie et al. 2004; Parra et al. 2006; Ribeiro et al. 2007). This is important when attempting to manage populations exposed to human activities (Soldevilla et al. 2017; Tyne et al. 2017) and can be critical for the establishment of conservation areas and management strategies (Cañadas et al. 2005; Ashe et al. 2010). While static ocean management can be considered less challenging than dynamic protection (Maxwell et al. 2015; Pérez-Jorge et al. 2015), protected areas need to be representative of species key biological functions (e.g., feeding and breeding habitats; Reeves 2000) but also follow shifts in the marine environment. Static management will be ineffective if habitat use changes over time (Hartel et al. 2014).

Common dolphins (*Delphinus* spp.) are highly mobile and have a widespread global distribution, which is known to be affected by several environmental parameters such as depth, slope, and chlorophyll concentrations, that may directly and/or indirectly affect prey distribution and concentration (Hui 1979; Au and Perryman 1985). For example, common dolphins occur in a range of water depths, using shallow (< 100 m) waters in some locations such as the eastern Ionian Sea in the Mediterranean (Bearzi et al. 2005) and the Gulf St. Vincent, Australia (Filby et al. 2010). In other areas, including the western Ligurian Sea in the Mediterranean (Azzellino et al. 2008) and around the Azores in the mid-Atlantic Ocean (Silva et al. 2014), they use deeper pelagic waters (> 1000 m).

In New Zealand, common dolphins have been recorded around much of the coastline, with year-round presence in some regions and only seasonal occurrence in others (Stockin and Orams 2009). However, both sighting and stranding data suggest this species is the most concentrated off the northeastern coast of the North Island (Stockin and Orams 2009). The Hauraki Gulf region has been identified as an important area for common dolphins (Stockin et al. 2008a; Dwyer et al. 2016), specifically for feeding (Stockin et al. 2009) and nursing (Stockin et al. 2008a). Stockin et al. (2008a) reported a high proportion of groups containing calves compared with other populations, and behavioural analyses showed that common dolphins use the Hauraki Gulf extensively for foraging (46.8% of the activity budget)—considerably more so than in other regions of New Zealand such as the Bay of Plenty (17% of the activity budget) or overseas (Stockin et al. 2009).

Common dolphins are subject to significant levels of tourism pressure in New Zealand, especially in the North Island where multiple operators with several vessels interact with the species in different core areas throughout the known range of the species (Neumann and Orams 2006; Stockin et al. 2008b; Meissner et al. 2015). In the Hauraki Gulf, foraging has been shown to be significantly disrupted by the presence of tour boats, resulting in shorter foraging bouts, less time spent foraging overall, and more time required for foraging dolphins to return to their initial behavioural state (Stockin et al. 2008b). For Hauraki Gulf common dolphins, any adverse effects of local tourism might be compounded for those individual dolphins that move between core areas (Meissner et al. 2015; Hupman 2016) by increasing their overall exposure to tourism. For this reason, protective measures have become necessary within the Gulf to mitigate the risks of reduced feeding and nursing due to ongoing tourism interactions.

The Department of Conservation is the regulatory body responsible for the management of marine mammal species in New Zealand waters. Given the need for managers to understand the local Hauraki Gulf area in terms of managing the effects of tourism on common dolphins, but in the absence of spatially explicit habitat data for *Delphinus*, this study examined common dolphin habitat use in the Hauraki Gulf. We used distribution modelling based on generalised additive models (GAMs) to identify important variables affecting the occurrence of common dolphins in the inner Hauraki Gulf (IHG) and in waters off the west coast of Great Barrier Island (GBI; i.e., outer Hauraki Gulf). Predictive distribution models were then applied to make predictions regarding the probability of encountering *Delphinus* in the IHG or off GBI, with the inclusion of behavioural information for feeding and nursery groups to further elucidate habitat use patterns. Given the known importance of the Hauraki Gulf for feeding and nursing common dolphins (Stockin et al. 2008a; Dwyer et al. 2016) and that common dolphin presence in the Gulf is significantly affected by latitude and water depth (Stockin et al. 2008a), we hypothesised that persistent hotspots for these activities could be spatially identified and meaningfully used as part of managed exclusion zones for tourism operations.

Materials and methods

Study area

The Hauraki Gulf (Fig. 1) is a relatively shallow, semi-enclosed body of water on the northeast coast of the North Island, New Zealand (Manighetti and Carter 1999; Black et al. 2000). Circulation in the Hauraki Gulf is strongly influenced by surface winds and their interaction with tidal

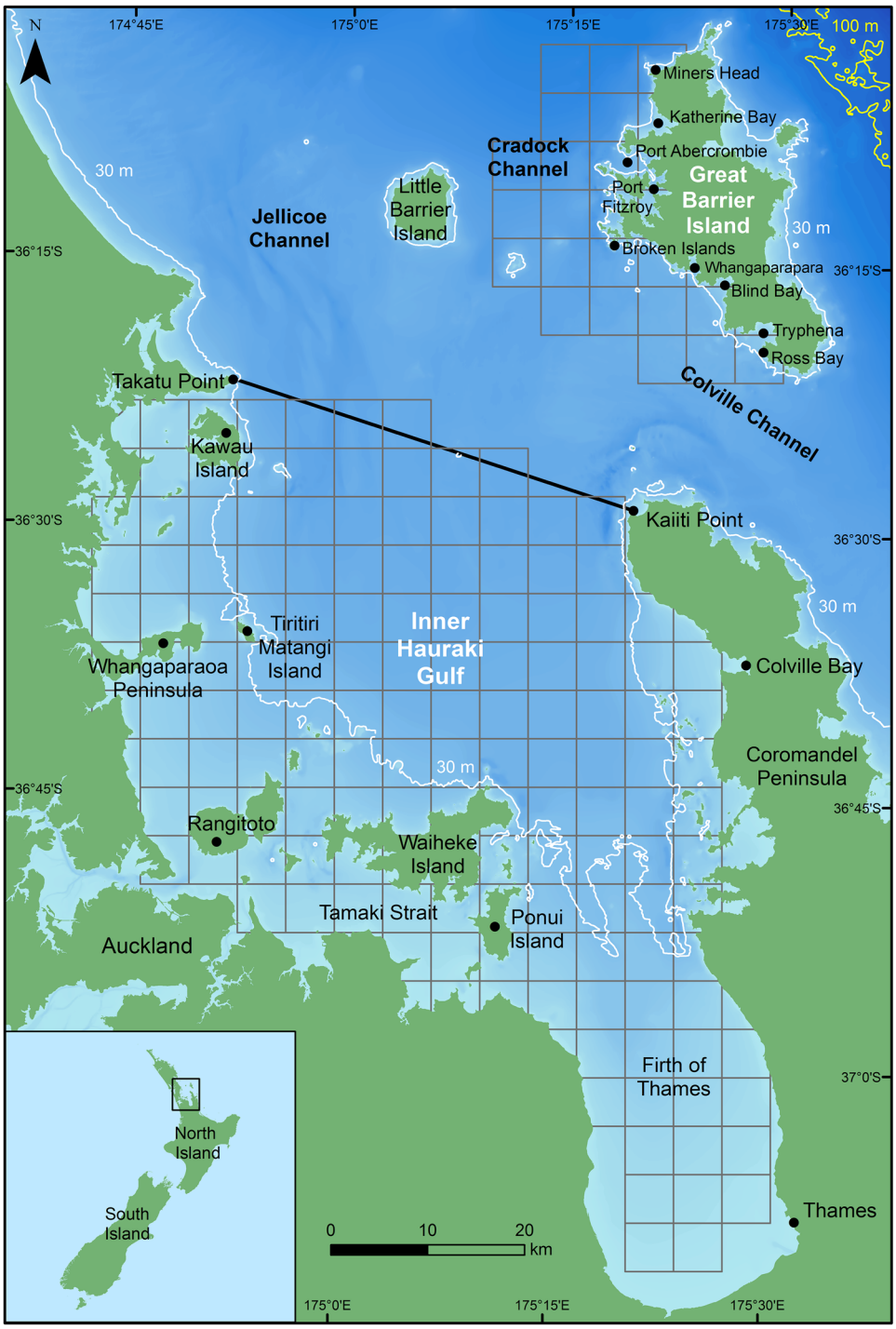

Fig. 1 The Hauraki Gulf, New Zealand. The solid black line (from Takatu Point to Kaiiti Point) indicates the boundary between the inner Hauraki Gulf (IHG) and outer Hauraki Gulf that includes Great Barrier Island (GBI), the white lines show the 30-m isobath and the yellow lines the 100-m isobath. Bathymetry is depicted with darker shades of blue representing deeper waters; data courtesy of NIWA (Mackay et al. 2012). The 5 × 5-km grid is shown in grey. Inset: Location of the Hauraki Gulf, North Island, New Zealand

currents, in addition to physical barriers such as headlands and islands that enhance local upwellings (Black et al. 2000). Warm waters from the East Auckland Current (EAUC) flow into the northerly entrance of the Hauraki Gulf during summer and autumn when easterly winds and downwellings are more prevalent (Zeldis et al. 2004). Westerly winds that are favourable for upwellings prevail in late winter and spring (e.g., Chang et al. 2003; Zeldis et al. 2004).

Two regions of the Hauraki Gulf were sampled in this study, the IHG and GBI (Fig. 1). The dividing line between inner and outer Hauraki Gulf waters was between Takatu Point and Kaiiti Point (Fig. 1). The IHG sampling area included all waters south of the delineating line and covered 3480 km^2. The 542 km^2 GBI study site in the outer Gulf mainly incorporated the coastal waters off the western side of the island, i.e., all waters between Miners Head in the

north and Ross Bay in the south, up to a distance of 10 km offshore (Fig. 1).

Data collection

Sighting data were collected during dedicated monthly boat surveys between January 2010 and November 2012 in the IHG and between January 2011 and November 2012 off GBI. Surveys were conducted from a 5.5 m boat powered by a 100 hp four-stroke engine when weather and sea conditions permitted. Survey design is described in detail in Dwyer et al. (2016). In brief, time spent travelling along survey tracks actively searching for marine mammals was classified as *on effort*. When the vessel left the survey track to approach dolphins, the survey mode switched to *off effort* until returning to the track to resume searching. *Off effort* mode also included all other occasions when the vessel was away from the survey track (e.g., returning to harbour because of deteriorating sea conditions or collecting data on a sighting group). Surveys were conducted in conditions of Beaufort sea state 3 or less and vessel speed was maintained at ~ 10 knots.

When a common dolphin group was detected, the vessel left the survey track (i.e., *off effort*), approached to within 50 m of the group/individual, and commenced data collection. Water depth (± 0.1 m) was measured using an on-board depth sounder at the location of the group when first sighted. All observational and environmental data were collected using an XDA Orbit II Windows Mobile device. CyberTracker version 3 software (Steventon et al. 2002) was programmed for logging observational data (e.g., behavioural state) and to record the GPS position of the vessel every 60 s throughout the survey day. Beaufort sea state was logged at 15 min intervals. After observational data were recorded, the vessel returned to the survey route and resumed *on effort* to continue searching for further individuals/groups.

Group composition (i.e., age class of individuals) and the initial behavioural state were visually assessed and recorded for each encounter. A group of dolphins was defined as any number of individuals observed in apparent association, moving in the same general direction and often, but not always, engaged in the same activity (Shane 1990). Age class and behaviour definitions follow those previously described for common dolphins using Hauraki Gulf waters (Stockin et al. 2008a, 2009, respectively). The initial behavioural state of the group was assessed before the vessel reached within 50 m. When determining the behavioural state, groups were scanned from left-to-right to ensure inclusion of all individuals in the group and avoid potential biases caused by specific individuals or behaviours (Mann 1999). The behavioural state was determined as the category in which > 50% of individuals were involved in, with all represented behaviours logged when an equal proportion of the group was engaged in different behaviours (Stockin et al. 2009). Feeding groups were classified as all groups for which the initial behavioural state 'forage' was recorded. Nursery groups were defined by the presence of at least one neonate. This conservative definition was selected rather than 'groups that contained at least one neonate and/or calf', because calves are present in the Gulf year-round and are found in a high proportion of groups (Stockin et al. 2008a).

Data analysis

Sampling data

Grids of 5 × 5-km cells were created for the IHG and GBI study areas using ArcGIS version 10.0 (ESRI, Redlands, California, USA; Fig. 1). All spatial data were processed using ArcGIS and Geospatial Modelling Environment (GME) version 0.7.2.0 (Beyer 2012), as per Dwyer et al. (2016).

Search effort was expressed as the number of kilometres of effort travelled through a grid cell per survey day. Beaufort sea state values were assigned to each 5 × 5-km grid cell for each sampling occasion (i.e., each time the vessel track passed through a cell on a survey day). The value corresponded with the sea state recorded at the mid-point of the vessel track within each grid cell.

Only *on effort* sighting data were included in analyses. Any dolphin sighting(s) in a grid cell were denoted by a '1' and an absence of sightings was denoted by a '0'. As such, a grid cell received a '1' regardless of the number of sightings (i.e., presence, maximum one per day). For the habitat use models driven by behavioural traits, feeding and nursery groups were assigned a '1' and groups initially observed in other behavioural states or that did not include neonates were assigned a '0'.

Environmental data

The following environmental variables were considered to influence the distribution of common dolphins: depth, slope, tidal current, SST, and net primary productivity (NPP). These variables were selected because of their known effect on common dolphin occurrence in the Hauraki Gulf (Stockin et al. 2008a) and other waters worldwide (e.g., Cañadas et al. 2005; Cañadas and Hammond 2008; Moura et al. 2012). All were averaged at the 5 × 5-km grid level as follows: The mean depth (m) and slope (°) of grid cells were calculated in ArcMap using the NIWA Hauraki Gulf bathymetric dataset (Mackay et al. 2012). Depth data for cells where dolphins were recorded (i.e., presence) were collected using the on-board depth sounder and within 100 m of the position of the group when it was first sighted. For cells where dolphins were not encountered (i.e., absence), depth was retrieved

at the midpoint of the track segment in each cell surveyed using the NIWA Hauraki Gulf bathymetric dataset (Mackay et al. 2012). The mean maximum tidal current (ms^{-1}) for each grid cell was extracted from the existing New Zealand Marine Environment Classification raster 'tidal_curr' (https://www.niwa.co.nz/coasts-and-oceans/our-services/marine-environment-classification), which was derived from a hydrodynamic model that simulated tidal current and output the depth-averaged maximum tidal current (Snelder et al. 2005). Daily SST data (°C) were obtained for the period of the study (i.e., from January 2010 to November 2012) from the Physical Oceanography Distributed Active Archive Centre (PO.DAAC, NASA Jet Propulsion Laboratory, Pasadena, California, USA; https://earthdata.nasa.gov/about/daacs/daac-podaac) at a 1 km spatial scale and subsequently averaged for each 5 × 5-km grid cell. The daily SST data were used in the models and to calculate the monthly mean SST values for each region to examine SST patterns. The SST within-month standard deviation was calculated for each grid cell as a measure of variability that is expected to be largest where strong oceanographic activity occurs in regions of strong spatial gradients or in regions of variable freshwater influence (Hadfield et al. 2002). NPP data (mg C m^{-2} day^{-1}) were remotely collected (www.science.oregonstate.edu/ocean.productivity) and based on the Vertically Generalised Production Model (VGPM; Behrenfeld and Falkowski 1997). The VGPM is a model that estimates net primary production from chlorophyll using a temperature-dependent description of chlorophyll-specific photosynthetic efficiency. NPP values were extracted as 8-day averages for each grid cell and NPP within-month standard deviation was also calculated. However, the NPP covariates were not included in the models because NPP values could not be obtained for all grid cells (mainly due to cloud cover, see Dwyer 2014) and there were concerns about reliable interpretation of the ocean colour data as chlorophyll algorithms do not perform accurately in waters where multiple co-existing, but not necessarily co-varying, dissolved and particulate marine and terrigenous substances affect ocean colour (Morel and Prieur 1977; Magnuson et al. 2004; Tzortziou et al. 2007; Zheng and DiGiacomo 2017). This is typically associated with inshore coastal regions like the Hauraki Gulf that is surrounded by New Zealand's largest city, Auckland, and features several estuaries and extensive coastal areas that are threatened by increased sediment runoff from the land (Seers and Shears 2015).

The spatial variables considered for the models were easting, northing, and distance to shore. Distance to shore (km) was calculated using the ArcGIS *near* tool to measure the distance between the centroid of each grid cell and the nearest point of land. If a cell centroid was located on land, the distance to shore was classified as zero.

Models and predictions

Binomial GAMs (with logit link function) were used to model the probability of encounter, where the response variable was a binary variable indicating sighting presence/absence within a grid cell. Models were chosen based on sensitivity and specificity calculated using Leave-One-Out cross-validation (LOOCV; details are described in steps 5 and 6 below). Separate datasets and models were used for each of the following: (1) groups of common dolphins in the Hauraki Gulf (IHG and off GBI), (2) feeding groups of common dolphins in the IHG, and (3) nursery groups of common dolphins in the IHG. The basic analytical workflow is shown in Fig. 2 and described in detail below. All analyses were carried out using R version 3.5.3 (R Core Team 2014).

Step 1 Sub-sampling the data.

All data were highly unbalanced (with many more non-occurrences ('zeroes') found than occurrences). Consequently, the dataset was reduced so it contained all occurrences, but only an equivalent number of randomly selected zeroes. In total, ten randomly sampled replicates of zeroes were used (in steps 1–5) for each dataset. This reduction in zeroes served two purposes:

1. It sped-up model fitting, and
2. It greatly improved final model sensitivity (i.e., probability of correctly detecting an occurrence), albeit at the cost of lower specificity (correctly identifying those

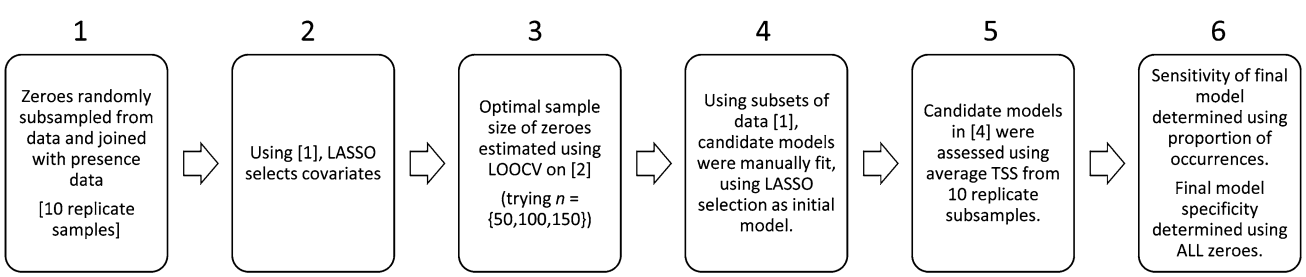

Fig. 2 Workflow showing key steps used in each stage of analysis for any dataset

units without an occurrence). The number of zeroes was considered a hyper-parameter and tuned in step 3.

Step 2 Develop an initial parsimonious model.

The following were fit as covariates in the initial model: year, season, northing, easting, depth, slope, distance to shore, tidal current, SST, SST within-month standard deviation, Beaufort sea state, and all meaningful interactions among the variables. These variables were selected based on their hypothesised biological importance and the feasibility of obtaining reliable measurements, with northing and easting included as proxies for unknown variables. The common dolphin habitat model jointly modelled the occurrence of dolphins using data from both areas (IHG and GBI), but area was examined as a possible covariate. Austral seasons were defined as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November) to allow comparisons with previous studies conducted on common dolphins in the Hauraki Gulf (Stockin et al. 2008a). The discrete nature of subset selection methods (e.g., stepwise selection—where predictor variables are retained or dropped) is known to give biased standard errors, p values and regression coefficients and exacerbated collinearity problems as well as highly variable models, i.e., small changes in the data may give very different models (Derksen and Keselman 1992; Breiman 1996; Tibshirani 1996; Harrell 2001, Zou and Hastie 2005; Morozova et al. 2015). Consequently, we opted to use the LASSO (Least Absolute Shrinkage and Selection Operator), a widely-used model selection method (Heinze et al. 2018). The general idea of the LASSO is to reduce the residual sum of squares by adding a penalty term in the least squares objective function that shrinks the coefficients towards zero. The penalty term of the LASSO effectively adds a penalty term bias in an attempt to select a midpoint between high bias (overly simplistic) models and high variance (overfitting to the training data; Hastie et al. 2009). When the LASSO parameter, λ, is small, the resultant coefficients are similar to ordinary least squares estimates. However, as λ increases, shrinkage occurs so that variables that are at zero are discarded. Consequently, a major advantage of LASSO is that it is a combination of model regularization (i.e., reducing the likelihood of overfitting) and a parsimonious selection of covariates. We implemented LASSO model selection using the R package 'glmnet' (Friedman et al. 2010). The LASSO parameter, which weights the penalty term and regularizes the model, was determined by choosing the value that minimizes the prediction error rate using tenfold cross-validation (using the default values in the function 'glmnet::cv.glmnet()'.

Step 3 Find the optimal sample size.

A GAM using binomial distribution and logit link function was used to model occurrence. Non-linear components of the GAMs used thin-plate splines fit via restricted maximum likelihood (REML) within the R package 'mgcv' (Wood 2017). Non-linearity was examined using component plots, and, if the default smoothness appeared to overfit the data, then flexibility was constrained by manually selecting the number of knots. The GAM model fit covariates selected by the LASSO in step 2—this model was used to determine the sample size of zeroes that maximized the True Skill Statistic (TSS; Allouche et al. 2006), i.e., the sum of model sensitivity (how well the model predicted occurrences) and specificity (how well it predicted zeroes) using LOOCV. For each model [i.e. (1) all, (2) feeding and (3) nursery group models], the number of zeroes randomly sampled was increased (from its initial value equal to the number of occurrences) by 50 to determine if this improved the TSS. For each sample size, the TSS was calculated by building the model with all occurrences and each of the ten random samples of zeroes. The sample size with the highest average TSS (from the ten replicates) was determined to be the optimal sample size (see step 5 for a description of how TSS was calculated). Invariably, we found that increasing the number of subsampled zeroes in the model decreased sensitivity by more than the concurrent gain in specificity. So, in all models, the sample size of (randomly sampled) zeroes was the same as the number of occurrences—full results are shown in Supplementary Table 1.

Step 4 Fitting GAMs.

Variables were manually added (or removed) in an attempt to improve the out-of-sample TSS values of the GAMs. Non-linearity was examined using component plots, and, if the default smoothness appeared to overfit the data, then flexibility was constrained by manually selecting the number of knots.

Beaufort sea state was retained in all models because of its known effect on detecting cetaceans during field studies (e.g., Barlow et al. 1988; Gannier 2005) and by including it as an explanatory variable, models could consider at least some detection effects (Forney 2000). Similarly, effort was used as an offset in all models to account for the fact that more search effort is expected to yield more sightings.

Steps 5 and 6 Fitting and assessing candidate models.

Each candidate model was fit using the same ten replicate sub-sampled datasets (consisting of all presence data and the ten replicate samples of zeroes). All candidate models are shown in Supplementary Table 2. Maximizing the average TSS was used as the basis for choosing the 'best model'. TSS scores of each candidate model were based on out-of-sample model predictions determined using two components:

1. Presence/absence of values within the sub-sampled data was predicted using LOOCV.

2. Absences that were not included in the sub-sampled data were predicted using a parameter set derived from fitting the entire sub-sampled data. Model parameter values using the entire sub-sampled dataset were used in all tables presented in the results.

In this manner, each candidate model had ten sets of predictions that were used to calculate ten values of TSS.

Non-linear effects of covariates were graphically displayed showing how the probability of encounter varied when holding all other covariates constant at their mean level (Beaufort level was held at zero, and, if the model also included a seasonal covariate, the effect assumed the season was 'summer'). Confidence intervals (at the 50% and 95% levels) were calculated assuming asymptotic normality and are also shown on these plots.

Probability values for each grid cell were calculated at the seasonal level (using seasonal averages for non-static variables such as SST). The inverse link transformation was used to obtain probability values on the scale of the original response variable since the results of the calculations were based on the scale of the linear predictor (Guisan and Zimmermann 2000). For binomial GAMs, the inverse logistic transformation is

$$p\,(y) = \frac{\exp\,(\mathrm{LP})}{1 + \exp\,(\mathrm{LP})},$$

where LP is the linear predictor fitted by logistic regression. This transformation provided probability values for each grid cell that were used to create predictive maps using ArcGIS. Predictive values were not calculated for a small number of grid cells as they were not sampled in all seasons (IHG: $n = 5$; GBI: $n = 3$). These cells were not colour-coded and remained white on the predictive maps.

Results

Sampling data

Survey effort totalled 279 d between January 2010 and November 2012. A total of 887.6 h were spent *on effort*, totalling 16,786 km of *on effort* tracks within the IHG grid cells. Between January 2011 and October 2012, 243.9 h were spent *on effort* in the GBI study area, with track effort totalling 4017 km. Effort data are detailed further in fig. 2 and table 2 in Dwyer et al. (2016) and a map showing GPS tracklines is presented in Supplementary Fig. 1. Although attempts were made to cover all areas homogeneously, effort was not uniform across either study site (i.e., the 5 × 5-km cells did not receive equal amounts of survey effort). For the IHG, 386 *on effort* dolphin sightings included 59 feeding and 39 nursery groups; corresponding to 274 total, 52 feeding and 37 nursery group 'grid cell sightings' (i.e., presence per grid cell per survey day). For GBI, 76 *on effort* dolphin sightings included 12 feeding groups and 3 nursery groups; corresponding to 44 total, 6 feeding and 3 nursery group 'grid cell sightings'.

Table 1 Parameter estimates of significant variables selected in the final common dolphin models for the inner Hauraki Gulf (IHG) and Great Barrier Island (GBI; GAM with binomial distribution and logit link function)

Term	Estimate	SE	*Z* value	*p* value
Intercept	2.101	0.888	2.366	0.02*
Slope	3.014	1.761	1.711	0.09
SST	−0.876	0.184	−4.765	< 0.001***
Depth-SST	0.017	0.004	3.968	< 0.001***
Slope-SST	−0.242	0.114	−2.120	0.03*
Beaufort (1)	−0.502	0.365	−1.375	0.17
Beaufort (2)	−0.639	0.335	−1.905	0.06
Beaufort (3)	−0.769	0.391	−1.969	0.05*
	edf		χ^2 statistic	*p* value
Current-Season (summer)	1.000		13.585	< 0.001***
Current-Season (autumn)	1.000		0.932	0.33
Current-Season (winter)	1.006		0.697	0.40
Current-Season (spring)	2.351		7.692	0.04*
Depth-Area (IHG)	2.894		25.590	< 0.001***
Depth-Area (GBI)	2.395		15.463	0.001**
% of deviance explained: 21.0				

Interaction terms are denoted by (-); significance codes are ***0.001, **0.01, *0.05

edf estimated degrees of freedom

Environmental data

For the IHG, grid cells with deeper waters were located centrally and further north, while areas with increased slope were observed close to shore (although not in southerly regions, e.g., Firth of Thames; Fig. 1). Regions with strong tidal currents were apparent in the Firth of Thames, close to the Colville Channel and in the channels between islands. At GBI, water depths were greater for northern grid cells, regions of increased slope mostly occurred in grid cells closer to shore, and the greatest tidal currents were adjacent to the Colville Channel and between Little Barrier and Great Barrier Islands. These patterns are presented in Supplementary Fig. 2.

Mean monthly SSTs revealed that the coolest and warmest water temperatures were experienced in August (IHG 13.2 ± 0.2 °C; GBI 14.3 ± 0.3 °C) and February 2011 (IHG 22.0 ± 0.1 °C; GBI 21.6 ± 0.1 °C), respectively. The

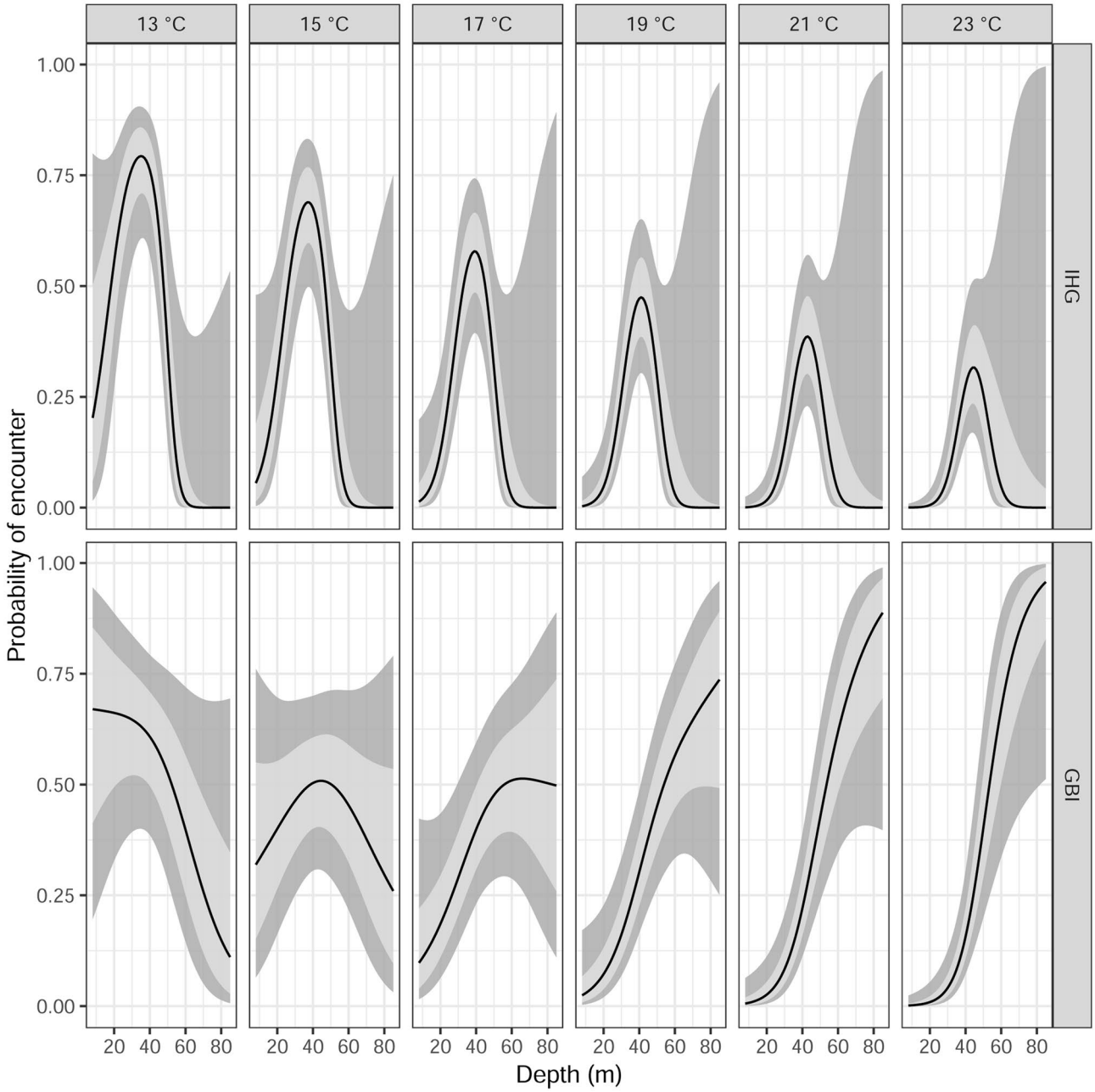

Fig. 3 Interaction between depth and sea surface temperature (SST) on the probability of encountering common dolphins in the inner Hauraki Gulf (IHG) and off Great Barrier Island (GBI), New Zealand. The black line is the average probability; shaded areas show one- and two-standard error intervals

temperature range was smaller at GBI than in the IHG, where both the highest and lowest temperatures were recorded. Waters also remained comparatively warmer at GBI for longer in autumn and winter. During summer, GBI inshore waters were cooler than IHG waters, especially compared with western and southern regions of the IHG where average temperatures were the highest. In winter, GBI waters were warmer than IHG waters, with average temperatures decreasing with increasing latitude.

Habitat models

Environmental variables that were frequently important in the top habitat models were depth, slope, current, season and SST. The chosen and candidate models are presented in Supplementary Table 2.

Dolphin habitat use

The final IHG and GBI common dolphin occurrence model explained 21.0% of the deviance (Table 1). The model suggested that overall probability of encounter was greater in cooler water temperatures, in areas of low to moderate tidal current, increased slope, and generally in deeper waters (i.e., 30–50 m for the IHG and 50–80 m for GBI; Table 1, Figs. 3 and 4). The exception was for GBI, where the probability of encounter was predicted to be greatest in shallower waters (< 20 m) with SSTs lower than 13 °C (Fig. 3). Probability of encounter in areas with low currents was highly significant in summer (Fig. 4). Overall, the most significant variables were SST, the depth-SST interaction, the effect of depth in the IHG, and the effect of current during summer (Table 1). Additionally, Beaufort sea state was a significant factor (Table 1), suggesting that the chances of encountering common dolphins increased with calmer sea states.

Predictive maps indicated central northern regions of the IHG had the greatest probabilities of encountering dolphins during all seasons, with higher probabilities in areas close to the 30-m depth contour in winter (Fig. 5). The overall probability of encountering dolphins increased within the IHG over winter and spring when water temperatures were cooler (Fig. 5; Supplementary Fig. 3). Cells closer to shore also had increased probability values when SSTs were lower (Fig. 5; Supplementary Fig. 3). Use of the IHG remained relatively

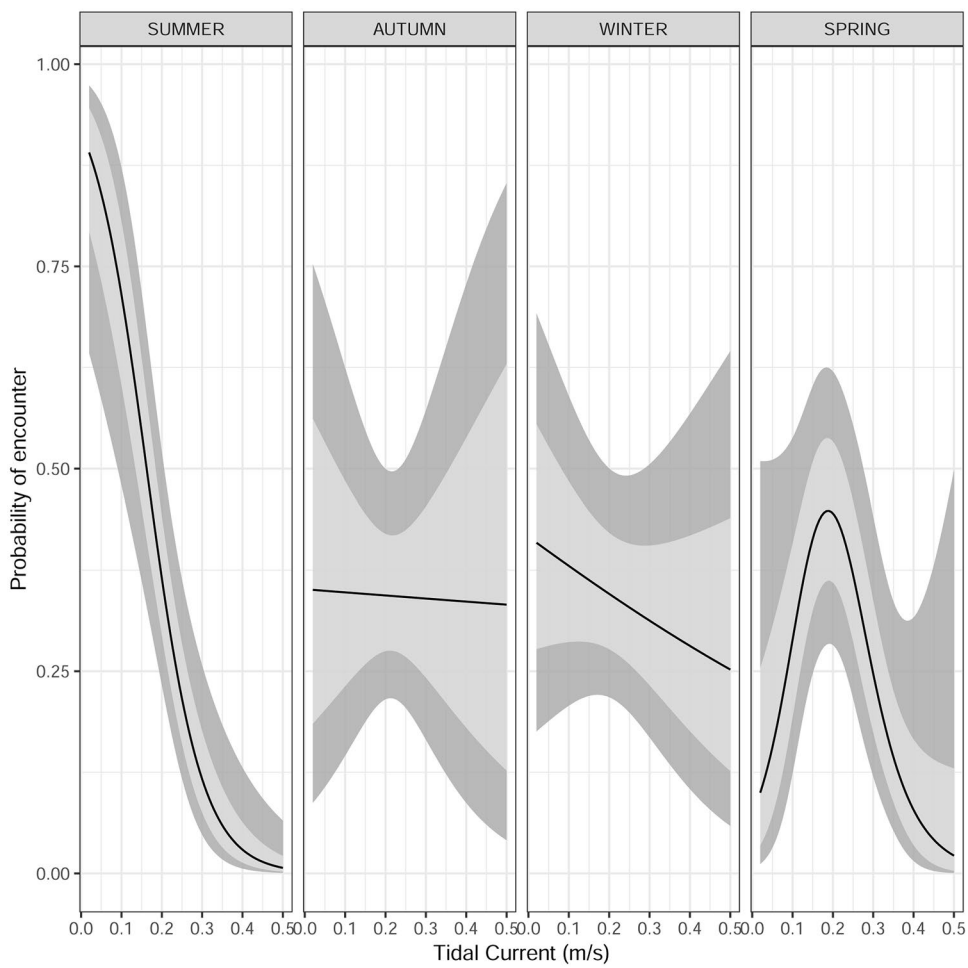

Fig. 4 Interaction between tidal current and season on the probability of encountering common dolphins in the inner Hauraki Gulf (IHG) and off Great Barrier Island (GBI), New Zealand. The black line is the average probability; shaded areas show one- and two-standard error intervals

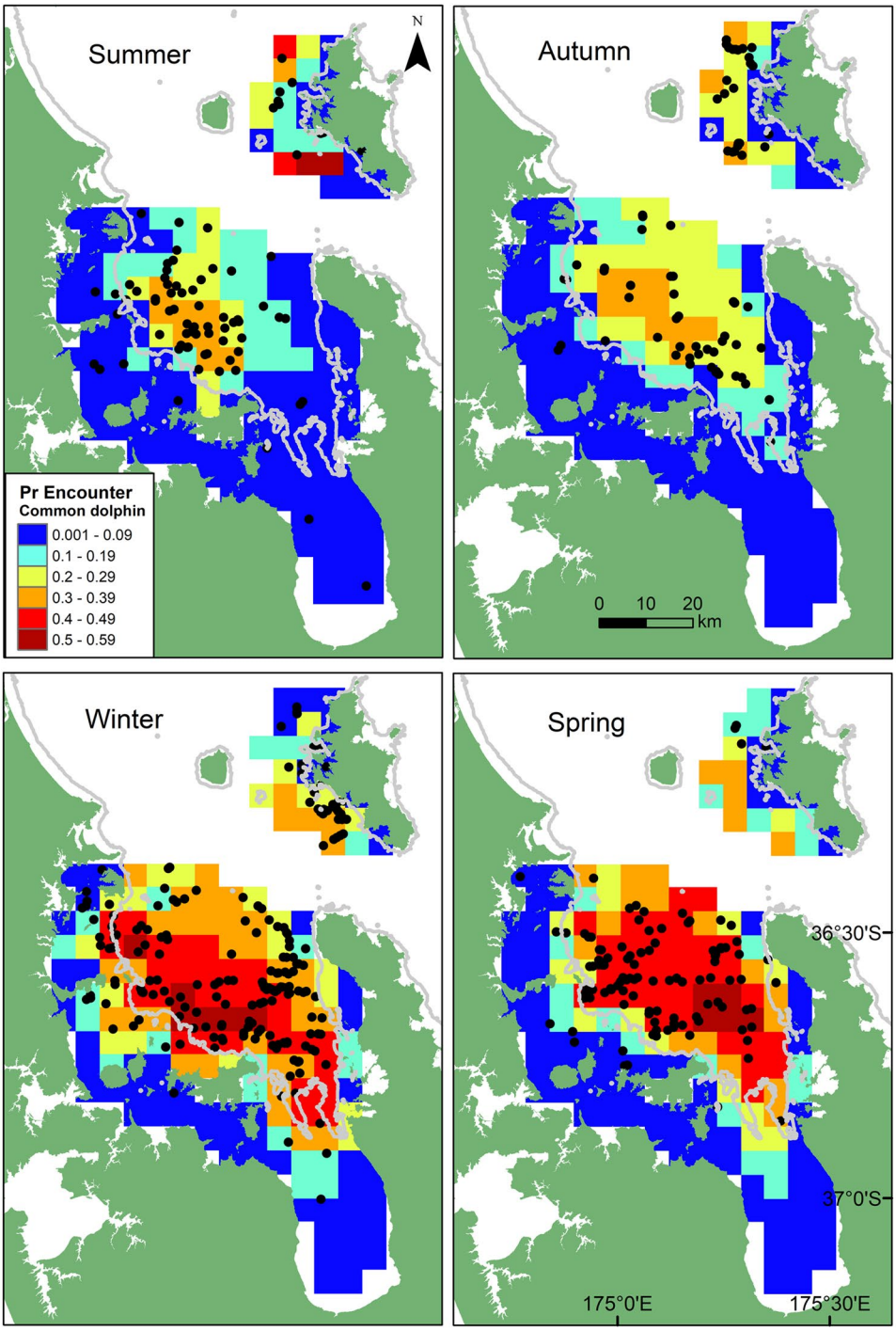

Fig. 5 Predicted seasonal probabilities of encounter for common dolphins in the Hauraki Gulf, New Zealand. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show real sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012 and Great Barrier Island (GBI) surveys in 2011–2012. The 30-m isobath is shown as a grey line

Table 2 Parameter estimates of significant variables selected in the final common dolphin model (GAM with binomial distribution and logit link function) for feeding groups in the inner Hauraki Gulf (IHG)

Term	Estimate	SE	*Z* value	*p* value
Intercept	0.904	1.617	0.559	0.58
SST	−0.169	0.097	−1.745	0.08
Beaufort (2)	0.521	0.538	0.969	0.33
Beaufort (3)	0.637	0.721	0.883	0.38
	edf		χ^2 statistic	*p* value
Depth-Season (summer)	1.839		5.905	0.08
Depth-Season (autumn)	1.000		3.450	0.06
Depth-Season (winter)	1.000		2.793	0.95
Depth-Season (spring)	1.000		6.014	0.01*
% of deviance explained: 18.1				

Interaction terms are denoted by (-); significance codes are ***0.001, **0.01, *0.05

edf estimated degrees of freedom

low in autumn. At GBI, probability of encounter in northern and deeper regions was predicted greater in summer and autumn, and greater in southern and shallower regions over winter (Fig. 5; Supplementary Fig. 2).

Habitat use by feeding groups

Very few sightings were made relative to the amount of effort for feeding or nursery groups in the GBI region; therefore, models were only fit for feeding and nursery groups in IHG waters. The final model for feeding groups explained 18.1% of the deviance (Table 2). The predictive maps (Fig. 6) showed similar patterns to the overall dolphin occurrence maps (Fig. 5), with a greater chance of encountering feeding groups in northern and central regions and increased probabilities in winter and spring compared with summer and autumn when considering the full range of depth categories. The overall probability of encountering feeding groups was predicted greatest in cooler waters, although this result was not significant ($p = 0.08$; Table 2). Figure 6 showed that in general, winter and spring showed the highest probabilities of encounter in shallow water (note the evidence of this relationship was only strong for spring), with increased probability of encounter during summer at depths of approximately 40–50 m (Fig. 7). High probability cells were more concentrated on the eastern side of the IHG in winter compared with spring and summer (Fig. 6).

Habitat use by nursery groups

The final nursery group model explained 43.0% of the deviance (Table 3). Probability of encountering nursery groups declined significantly in autumn and increased in deeper waters and in areas of decreased slope (Table 3). The predictive maps suggested that the probability of encountering nursery groups was greater within more central and northerly regions of the Gulf in spring and summer (Fig. 8). Beaufort sea state was also a significant factor suggesting the chances of detecting a nursery group increased in calmer sea states.

Hotspots for feeding and nursery groups

Based on the predictive mapping, common dolphin use of the Hauraki Gulf was relatively widespread for both feeding and nursery groups. Both activities were predicted to occur more commonly across central and northerly areas of the Hauraki Gulf, with the same general areas used for both feeding (Fig. 6) and nursing (Fig. 8) functions. Therefore, the core areas of use that could be spatially identified for these activities occurred over large spatial scales and shifted temporally (i.e., winter and spring for feeding groups, and summer for nursery groups). Spatially, it appears that most of the Gulf area is used for these functions rather than any distinctive smaller regions within the Gulf being important for feeding and nursery groups.

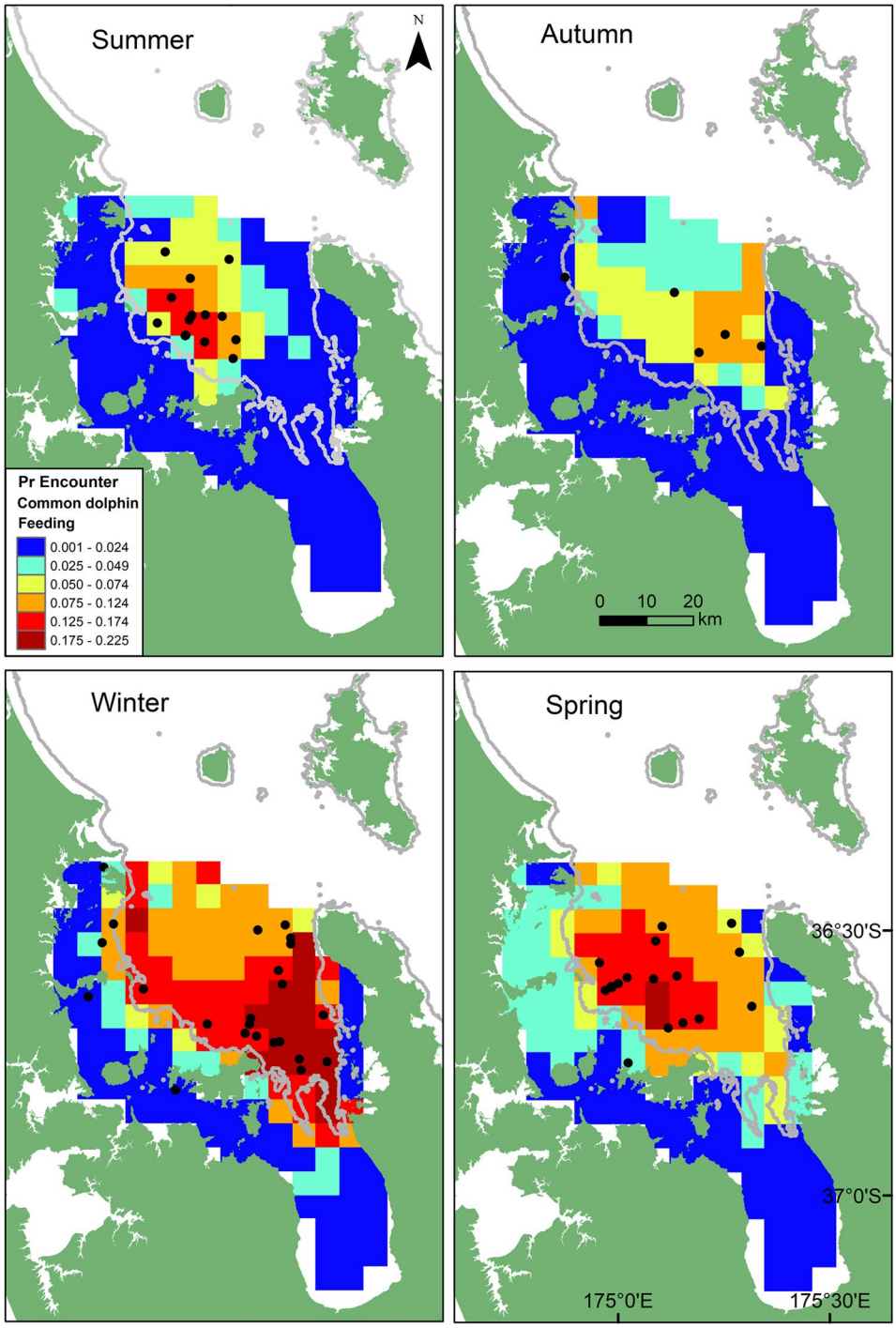

Fig. 6 Predicted seasonal probabilities of encounter for feeding groups of common dolphins in the Hauraki Gulf, New Zealand. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show real sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012. The 30-m isobath is shown as a grey line

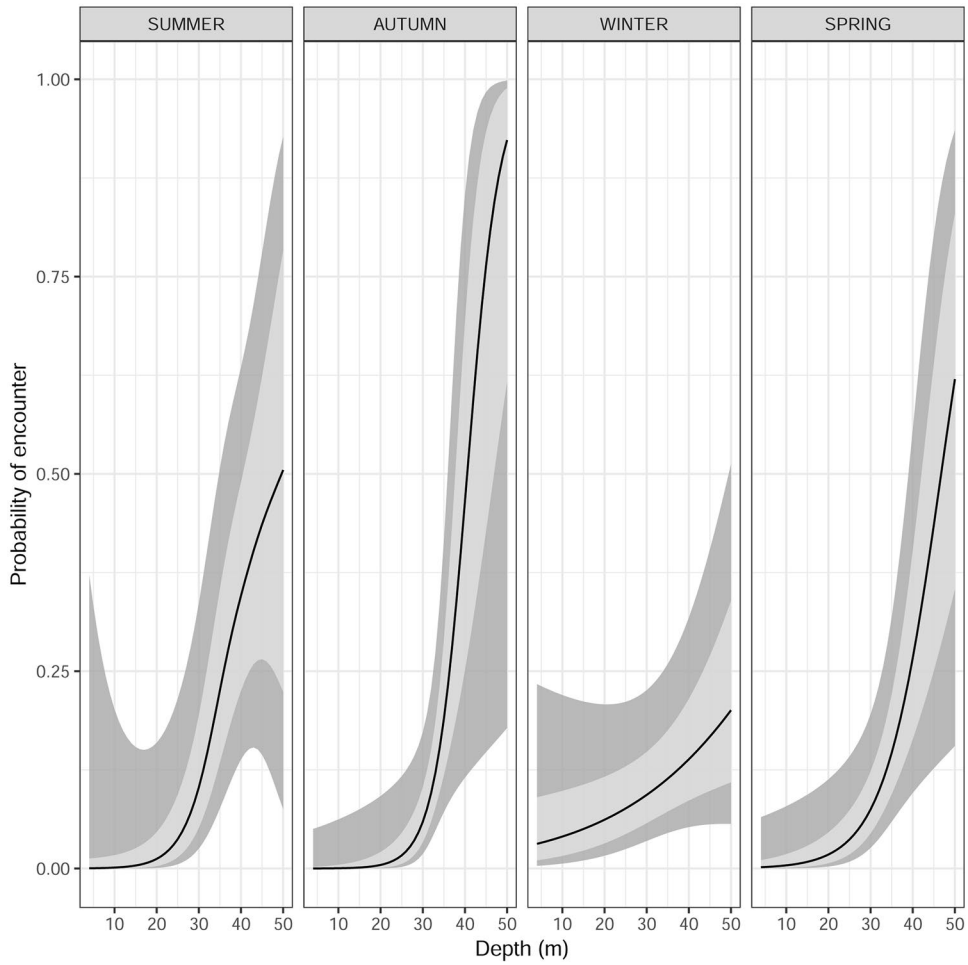

Fig. 7 Interaction between depth and season on the probability of encountering feeding groups of common dolphins in the inner Hauraki Gulf (IHG), New Zealand. The black line is the average probability; shaded areas show one- and two-standard error intervals

Table 3 Parameter estimates of significant variables selected in the final common dolphin model (GAM with binomial distribution and logit link function) for nursery groups in the inner Hauraki Gulf (IHG)

Term	Estimate	SE	*Z* value	*p* value
Intercept	2.333	1.917	1.212	0.23
Depth	0.047	0.030	1.562	0.12
Slope	−8.210	2.666	−3.079	0.002**
Season (autumn)	−3.032	1.129	−2.687	0.007**
Season (winter)	−0.975	1.292	−0.755	0.45
Season (spring)	−0.052	0.799	−0.065	0.95
Beaufort (1)	−3.772	1.553	−2.428	0.02*
Beaufort (2)	−3.387	1.385	−2.446	0.01*
Beaufort (3)	−4.976	1.635	−3.043	0.002**
% of deviance explained: 43.0				

Significance codes are ***0.001, **0.01, *0.05

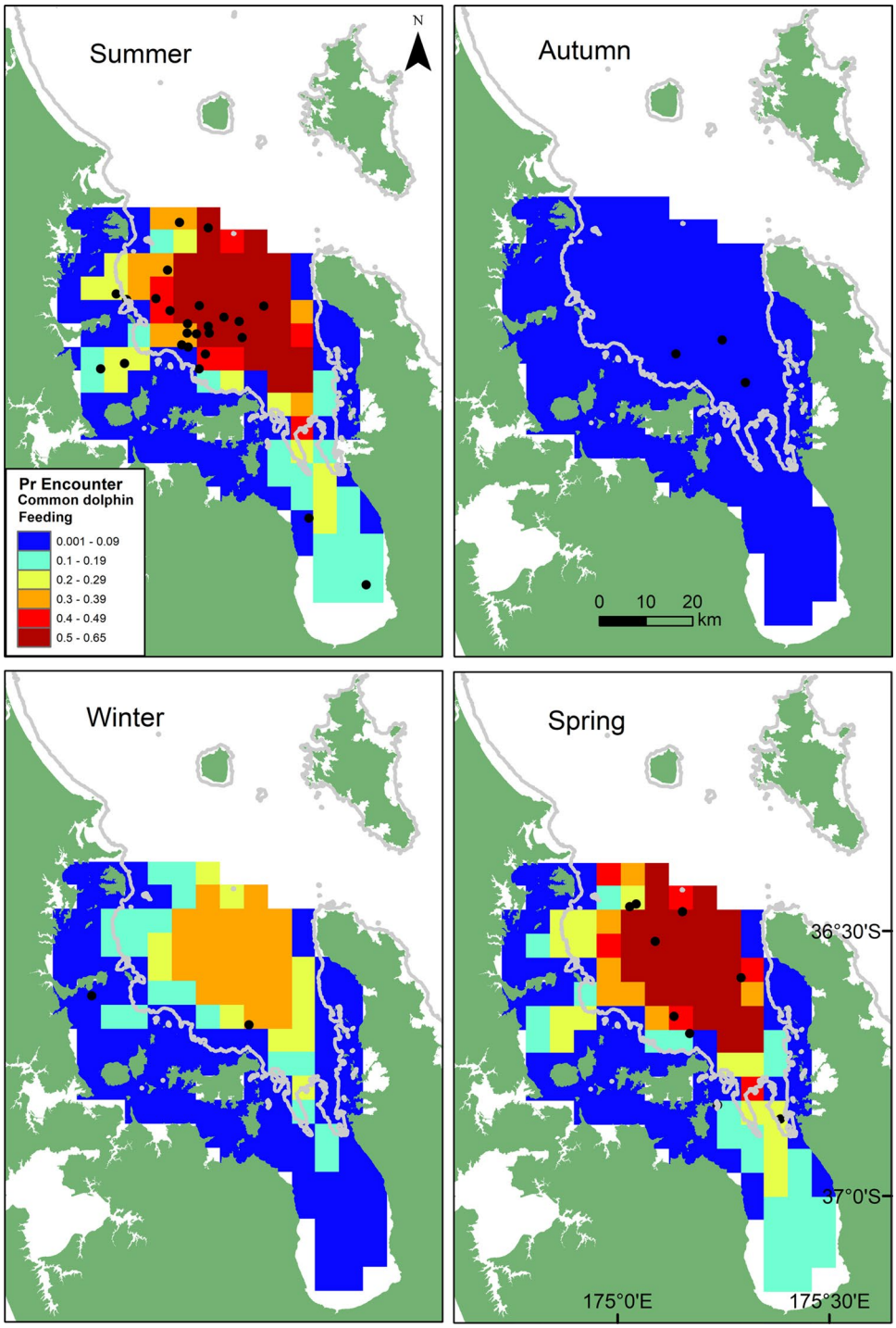

Fig. 8 Predicted seasonal probabilities of encounter for nursery groups of common dolphins in the Hauraki Gulf, New Zealand. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show real sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012. The 30-m isobath is shown as a grey line

Discussion

Disturbance to marine mammals from vessel interactions and the associated effects (e.g., increased energetic demands, acoustic disturbance, and reduced juvenile survival) are well documented (Buckstaff 2004; Bejder 2005; Karpovich et al. 2015; Machernis et al. 2018). Spatial management, such as restricting access to a habitat, is one tool often recommended to reduce exposure to human activity (e.g., Tyne et al. 2015). However, our analyses indicate that static spatial management of common dolphins in the Hauraki Gulf would not be the optimal management tool to mitigate the known risks of reduced feeding associated with ongoing tourism vessel interactions. This was evident by the absence of persistent hotspots for feeding or nursery groups that could be meaningfully used as part of managed exclusion zones.

Our predictive mapping improves the current understanding of the spatial and temporal habitat use of the Hauraki Gulf by common dolphins and creates a baseline for spatial planning and decision making. However, our results come with some limitations. Modelling the occurrence of mobile species inhabiting a highly dynamic environment is challenging given the degree of random variability and the large number of possible explanatory variables used to try to capture the heterogeneity in environmental conditions. While some variables were highly significant for certain regions in this study, the explained deviances for two of the models (the IHG/GBI and the feeding group models) were relatively low. Such results are often typical for this type of data (e.g., Ferguson et al. 2006; Cañadas and Hammond 2008; Embling et al. 2010) and have been attributed to factors such as the spatial scale of the study area (Cañadas and Hammond 2008) or a mismatch in predictor variables used as proxies for prey distribution or abundance (Ferguson et al. 2006). For example, our analyses may have been limited by not including a measurement for productivity in our models. As a result, spatial management tools such as spatial exclusion zones for tourism operations can be affected by low levels of certainty associated with predictive models.

The environmental variables that were most frequently significant in the habitat models presented here were depth and SST. Depth was also identified as one of the most important factors driving the spatial distribution of cetaceans in the Hauraki Gulf in a recent aerial survey study (Kozmian-Ledward 2014). Model results indicated that the greatest probability of encountering common dolphins within the IHG was during the colder months of winter and spring (when SSTs were lowest) and within deeper waters (30–50 m), the latter consistent with a previous study of common dolphin occurrence (Stockin et al. 2008a). The highest chances of encountering common dolphins off GBI was also in deeper waters (50–80 m) during warm SSTs; but in shallow waters (< 20 m) during very low SSTs of 13 °C. There did not appear to be any well-defined spatial trends in SST that could explain these patterns (see Supplementary Fig. 3). It seems more likely that encounter probabilities may be related to prey movements, i.e., that depth is a proxy for prey distribution and/or location in the water column. For example, pilchard (*Sardinops neopilchardus*) are known to be more abundant in bays and harbours in New Zealand when water temperatures are cooler (Ministry for Primary Industries 2013) and are also known to form compact schools particularly during the summer (Fisheries New Zealand 2018). Both of these factors may help explain the increased probability of encountering *Delphinus* in the IHG during the colder months but off GBI during the warmer months.

Northern and central regions of the IHG were used year-round by common dolphins, while for shallow inshore waters, the probability of encounter increased during winter and spring. Short-beaked common dolphins (*D. delphis ponticus*) in the Black Sea are known to move from offshore waters to shallow coastal waters to feed on Black Sea anchovy (*Engraulis encrasicolus ponticus*) and Black Sea sprat (*Sprattus sprattus*) in the winter and summer, respectively (Reeves and Notarbartolo di Sciara 2006). A change in prey availability and/or their seasonal distribution within Gulf waters may have also affected the change in common dolphin habitat use.

Although the occurrence of clupeid fish such as pilchards and sprats (*Harengula antipoda*) has been documented as erratic and their migrations difficult to predict (Young and Thomson 1926), they have been described as locally abundant in some regions of New Zealand such as Wellington harbour in winter and spring (Young and Thomson 1926; Ministry for Primary Industries 2013). Changes in seasonal abundance or movements of pilchards in the Hauraki Gulf have not been assessed, as with other important species in the diet of common dolphins, such as jack mackerel (*Trachurus* spp.). However, limited fisheries catch data obtained from the Ministry for Primary Industries for the period of this study show some alignment with the findings presented here, with a significant proportion of the annual pilchard catch taken during the winter month of August (Dwyer 2014). Baker (1972) suggested that minimum water temperatures of approximately 14 °C may be warm enough to support year-round spawning of pilchards off northeastern New Zealand. Such a consistent source of prey could explain the year-round use of the Hauraki Gulf by common dolphins, as suggested by Stockin et al. (2008a).

The inclusion of functional data into the models provided further information about habitat use of common dolphins in the Hauraki Gulf, as previously demonstrated by Cañadas and Hammond (2008) for short-beaked common dolphins in the southwestern Mediterranean. Feeding groups were predicted to occur more commonly in northern-central regions of the IHG during winter and spring. These data correspond well with the results of an earlier (2002–2005) behavioural study that found most foraging common dolphins were found in the deepest waters of the IHG, and primarily during winter and spring (Stockin et al. 2009). While feeding groups were generally observed in deeper waters in this study, it was still possible to encounter a feeding group in shallow regions, but only when SSTs were at their lowest. Overall, the seasonal predictive occurrence maps for the larger population resembled seasonal predictive maps of feeding groups more than nursery groups, suggesting prey availability likely has important implications for the general distribution and habitat use patterns of common dolphins in the IHG.

Nursery groups in the IHG were most prevalent during summer, in line with other North Island studies (Stockin et al. 2008a; Meissner et al. 2014) and common dolphin

research conducted overseas (Cañadas and Hammond 2008). The prediction for increased use of areas with similar water depths (~40 m) by nursery groups (Fig. 8) and the general population (Fig. 5) is consistent with Meissner et al. (2015) who also reported groups in similar water depths regardless of group composition in the Bay of Plenty. However, these results differ to those reported by Stockin et al. (2008a) who found that groups including neonates were typically observed in shallow waters of less than 20 m depth. It is not clear whether the different observations represent a change in habitat use over the period of the two studies or differences in survey methodologies. The latter seems less likely given that most of the data analysed in Stockin et al. (2008a) were collected from a tour vessel that spent more time in deeper waters searching for whales, and thus presumably would have had more opportunities to encounter neonates in deeper waters. Unfortunately, small sample sizes precluded the fitting of functional models for GBI to help elucidate these patterns further.

The predictive maps revealed relatively widespread use of the central Hauraki Gulf for both feeding and nursery groups, albeit with temporal differences in use (feeding groups most prevalent in winter and spring, and nursery groups most prevalent in summer). Spatial exclusion zones for tourism operations would, therefore, be difficult to implement for these activities given the areas that were identified as important were large, covering most of the areas used by common dolphins and consequently the tour vessels. As such, placing a large static spatial exclusion boundary the size of the area used by feeding and nursery groups would not be the best management tool in terms of stakeholder support or practicalities such as the ease of enforcement (Wilhelm et al. 2014).

Our study used one spatial scale (i.e., 5 × 5 km grid cells within a combined 4022 km^2 area of the Hauraki Gulf) to assess habitat use. Previous studies have examined the effects of different spatial scales on cetacean distribution and habitat use with mixed results; for example Redfern et al. (2008) did not identify significant differences in selected variables, their functional forms, or high and low-density regions of predictive maps when assessing different spatial resolutions for dolphin habitat use in the eastern tropical Pacific. González García et al. (2018) examined high and coarse spatial resolutions when investigating habitat preferences of Azorean blue whales (*Balaenoptera musculus*), reporting that both scales were valid and beneficial for capturing larger oceanographic features (coarse resolution) and more localised short-term events (high resolution). Conversely, Scales et al. (2017) assert that the use of coarse-scale data risks significant predictive inaccuracy in habitat models. It cannot be ruled out that using a finer resolution in our study may have identified several smaller distinctive core areas of use given that species distribution patterns may be governed by processes at multiple scales (Dormann 2007). However, it seems unlikely that any potential identification of smaller hotspots would result in a recommendation for the use of spatial exclusion zones in this case given the temporal shifts in intense use of the central and northern regions of the Gulf. Moreover, any smaller hotspots would still be expected to be widely distributed across large areas of the Gulf. Additionally, selecting a wider spatial extent [e.g., northeastern North Island waters—for which movements of common dolphins outside of the Hauraki Gulf are known (Hupman 2016)] may have identified the entire Hauraki Gulf as the preferential area for the population, as previously suggested (Dwyer et al. 2016). However, the aim of this study was to investigate habitat use within the Gulf, given the extent and known effects of tourism within the region. Following the results presented here, it would be prudent to examine habitat use at such a wider scale to determine the relative importance of Hauraki Gulf waters for common dolphins and indeed other cetaceans.

Visual surveys for cetaceans are known to be affected by imperfect detection; i.e., detection of groups/individuals is rarely perfect (Bailey and Adams 2005). This is due to factors such as sighting methods, sighting cues, search conditions, and group size (Barlow et al. 2001). While survey protocols in the present study were kept consistent during the entire sampling period to try to minimise factors affecting detection, and variables (Beaufort sea state and effort) that were deemed to have significant effects on the detection of cetaceans during boat surveys were incorporated into the models, these variables did not account for detection probability explicitly or spatially. As such, the results we present will underrepresent true levels of habitat use since imperfect detection will result in negatively biased results (MacKenzie et al. 2002). Nevertheless, the identification of high and low use areas in this study is expected to be consistent whether detection probability was accounted for or not, as demonstrated in Dwyer (2014) when assessing predictions of common dolphin habitat use in the Hauraki Gulf based on both generalised linear models and occupancy models.

In cases where the use of static management areas is not the preferred tool, particularly for highly mobile species, other management priorities should be considered. Management options other than static spatial exclusion include but are not limited to increased enforcement of regulations, reassessment of permissible viewing distances and vessel speeds, and temporal closures (Machernis et al. 2018). Dynamic ocean management (i.e., management that rapidly changes in space and time in response to changes in the ocean and its users) has also been proposed as a promising tool that allows for near-real-time adjustments to conservation strategies (Maxwell et al. 2015; Abrahms et al. 2019). Hazen et al. (2018) demonstrate that dynamic closures of the California drift gillnet fishery could be up to ten times

smaller than existing static closures while simultaneously supporting fishing opportunities and maintaining adequate protection of endangered nontarget species. Examples of existing dynamic protection mainly relate to specific industries such as fisheries, for example, the temporary restriction of certain types of commercial fishing in areas of the Atlantic where unexpected aggregations of the critically endangered North Atlantic right whale (*Eubalaena glacialis*) are observed (Asaro 2012). Dynamic management tools that use real-time predictions of species distributions to minimise fisheries impacts have also been successfully applied to loggerhead sea turtle (*Caretta caretta*) in the Pacific Ocean (Howell et al. 2015) and southern bluefin tuna (*Thunnus maccoyii*) off south-eastern Australia (Hobday and Hartmann 2006; Hobday et al. 2011). Furthermore, the concept of mobile marine protected areas (that are not industry-specific and could focus on protecting habitats or species and thereby offer a more ecosystem-based approach) and its application to protect highly mobile species of concern is a promising development for the future (Maxwell et al. 2015).

For common dolphins in the Hauraki Gulf, the suitability of alternative management options such as time-out periods or avoidance of feeding and nursery groups should be investigated. Additionally, the importance of the Hauraki Gulf region for feeding groups of common dolphins highlights the need to protect their food source. However, stock assessments for the main prey species of common dolphins are lacking and they continue to be commercially fished at levels that may or may not be sustainable (Dwyer 2014). The use of dynamic management tools such as mobile marine protected areas (an ideal approach for mitigating the effects of tourism interactions on common dolphins in the Hauraki Gulf) will become possible as temporal and spatial predictions of species distributions improve with enhanced data availability through improved technology.

The option of temporal exclusion based on the results presented here is not feasible given the relatively coarse temporal resolution (season) of this study. Fernandez et al. (2017) suggested that exploring temporal resolutions of 7–8 days is most appropriate for highly dynamic ecosystems and highly mobile species. However, more fine-scale temporal analyses were not possible in this study as it was difficult to collect enough sighting data for analyses at the weekly/monthly scale. Future studies should collect sightings data over a longer monitoring period to ensure a larger sample size for defining long-term hotspots.

Conclusion

Depth and SST were identified as the most important predictors of common dolphin occurrence in the Hauraki Gulf in this study. The core areas of use for nursery and feeding groups that could be identified from the predictive mapping were large and shifted temporally. Therefore, we suggest that spatial exclusion zones would not be the best management tool from a stakeholder or practical enforcement perspective for mitigating any adverse impacts on these functions in this region. In cases where static management is not the optimal tool, as suggested here for a highly mobile species, a strategic approach requires more than a boundary line on a map. For the Hauraki Gulf, we recommend the consideration of alternative management strategies, including monitoring and if need be, conserving critical prey resources within the region. Finally, our distribution modelling and predictive mapping are available to support management decisions, particularly those relating to marine spatial planning and effects of tourism.

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Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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