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Environmental correlates of nearshore habitat distribution by the Critically Endangered Māui dolphin

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ABSTRACT: Effective management of space-use conflicts with anthropogenic activities is contingent upon reliable knowledge of a species' ecology. The Māui dolphin *Cephalorhynchus hectori maui* is endemic to New Zealand and is listed as Critically Endangered, mainly as a result of fisheries bycatch. Despite conservation efforts, the population was estimated at 55 animals in 2011. Here we investigate environmental correlates of Māui dolphin nearshore distribution, using 119 encounters with Māui dolphin groups during boat-based, coastal surveys across 4 summers (2010, 2011, 2013, 2015). We describe the nearshore distribution using a kernel density analysis with differential smoothing on the *x*- and *y*-axes to account for the nearshore preference of the dolphins and the survey design. In all years, dolphins were encountered consistently in a restricted area (4 year area of overlap: 87.3 km^2). We modelled habitat preference with boosted regression trees, using presence/absence of dolphins relative to static and dynamic environmental predictors. An index of coastal turbidity was created based on a near-linear relationship between Secchi disk measurements and log-transformed remotely sensed chl *a* concentration. Sea surface temperature (SST; 22.6% contribution), turbidity (22.2%), distance to major watersheds (17%), depth (14.5%), distance to minor watersheds (13.3%) and distance to the coast (10.4%) partly explained Māui dolphin distribution. We detected a match between predicted areas of high nearshore habitat suitability around North Island and historical sightings (76.2% overlap), thus highlighting potential areas of Māui dolphin recovery. Our study presents methods broadly applicable to distribution analyses, and demonstrates an evidence-based application toward managing Māui dolphin habitat.

KEY WORDS: Habitat selection · Kernel density analysis · Boosted regression trees · Remote sensing · Turbidity · Māui dolphins

INTRODUCTION

Detailed knowledge of species spatial and temporal distribution patterns is crucial to conservation research (Ferrier 2002, Rushton et al. 2004). Species distribution models (SDMs) help us understand the ecological relationships between a species' occurrence patterns and its environment, leading to better knowledge of its habitat preferences and spatial distribution. These models have grown popular because they can be directly applied to spatial planning and management of protected species and areas around the globe (e.g. Leathwick et al. 2008). SDMs are a relatively recent tool in marine ecology (Robinson et al. 2011) but

they have proved successful at informing the conservation of marine megafauna (e.g. pinnipeds, Costa et al. 2010; porpoises, Gilles et al. 2009; leatherback turtles *Dermochelys coriacea*, Howell et al. 2015; sea birds, Lieske et al. 2014; southern right whales *Eubalaena australis*, Torres et al. 2013; polar bears *Ursus maritimus*, Wilson et al. 2014). Indeed, SDMs are a powerful, descriptive and predictive tool to study animals that are hard to observe in the wild because of their high mobility, low densities and logistically challenging survey environment. This modelling approach is even more valuable when studying endangered species with extremely small ranges and population sizes (Engler et al. 2004) because their extrapolation power enables suitable habitat to be inferred even from a small number of observations, as long as the predictions are within the range of observed environmental conditions (Mannocci et al. 2015).

The Māui dolphin *Cephalorhynchus hectori maui* is a critically endangered subspecies endemic to New Zealand; it is currently encountered primarily along a 139 km stretch of nearshore habitat along the west coast of North Island (Oremus et al. 2012), yet the extent and regularity of its offshore distribution patterns are frequently debated (Du Fresne 2010). It is considered a separate subspecies of the more widely distributed Hector's dolphin (*C. hectori hectori*) found mostly around South Island (Baker et al. 2002). The Māui dolphin population size was recently estimated at 55 individuals older than 1 year of age (Hamner et al. 2014a), and numerous studies suggest a population decline in the last 3 decades associated with a loss of genetic diversity in this subspecies (Martien et al. 1999, Pichler 2002, Baker et al. 2013, Hamner et al. 2014a). As a result, Māui dolphins are classified as Critically Endangered by the International Union for the Conservation of Nature and nationally critical under the New Zealand Threat Classification (Baker et al. 2010).

Entanglement in fishing gear is the main threat to the Māui dolphin population: set nets, trawls and drift nets are the most likely cause of entanglement (Currey et al. 2012). Spatial management to restrict fishing effort has been in place since 2002, and expanded in range in 2008, 2010, 2012 and 2013 to now include much of the Māui dolphin's known, current range in the nearshore region (New Zealand Department of Conservation 2013). Although life-history traits of Māui dolphins (low reproductive capacity) limit a rapid population recovery, so far there is no evidence of increased population size or distribution range since the implementation of these protective measures. No abundance estimates for the Māui dolphin prior to the 1970s exist, but historical data consisting of opportunistic sightings, stranding and survey data suggest a contraction in range from all around North Island to the current extent restricted to the central part of the west coast, between Kaipara Harbour and Kawhia Harbour (Fig. 1; Russell 1999, Ferreira & Roberts 2003, Slooten et al. 2006, Du Fresne 2010, Oremus et al. 2012). Currently, Māui dolphins are mainly observed within 4 nautical miles (nmi) of the coast (7.4 km) but are occasionally observed further offshore, up to 7 nmi (Ferreira & Roberts 2003, Slooten et al. 2006, Du Fresne 2010, Oremus et al. 2012). In the summer, they are usually found in small groups of less than 5 individuals from both sexes, and occasionally in larger aggregations (>8 individuals) with a higher proportion of calves (Oremus et al. 2012). The average along-shore range of Māui and Hector's dolphins is relatively small (<50 km in both subspecies; Rayment et al. 2009, Oremus et al. 2012) although larger movements have been reported (Hamner et al. 2014b).

The distribution of Hector's dolphins appears to be linked to distance to shore, depth, sea surface temperature (SST), salinity, water clarity and chl *a* concentration (Bräger et al. 2003, Rayment et al. 2010, Miller 2015). Most of these oceanographic variables have also been shown to drive the distribution of other species of the *Cephalorhynchus* genus: Chilean dolphin *C. eutropia* (Ribeiro et al. 2007, Viddi et al. 2015) and Commerson's dolphin *C. commersonii* (Garaffo et al. 2011). In comparison, little is known about Māui dolphin habitat preferences. Due to qualitative observations of Māui dolphins in nearshore waters and close to river mouths, it has been hypothesized that their spatial distribution is influenced by some of the same environmental drivers as the other *Cephalorhynchus* species: distance to the coast, depth (Ferreira & Roberts 2003, Slooten et al. 2005, Rayment & Du Fresne 2007, Childerhouse et al. 2008, Dawson 2009, Du Fresne 2010) and water turbidity associated with estuaries (Dawson 2009) or not (Ferreira & Roberts 2003). Yet, no quantitative study of these environmental correlations has been undertaken to date.

The distribution of many marine megafauna, like that of the Māui dolphin, is also influenced by prey and predator distribution. However, data on these 2 factors are frequently lacking. SDMs typically include static and dynamic oceanographic features as proxies of ecosystem productivity and prey abundance. While static features (e.g. depth, bottom slope, distance to shore) often integrate habitat use patterns and are significant predictors, the functional distribution of all 3 trophic levels — prey, predator
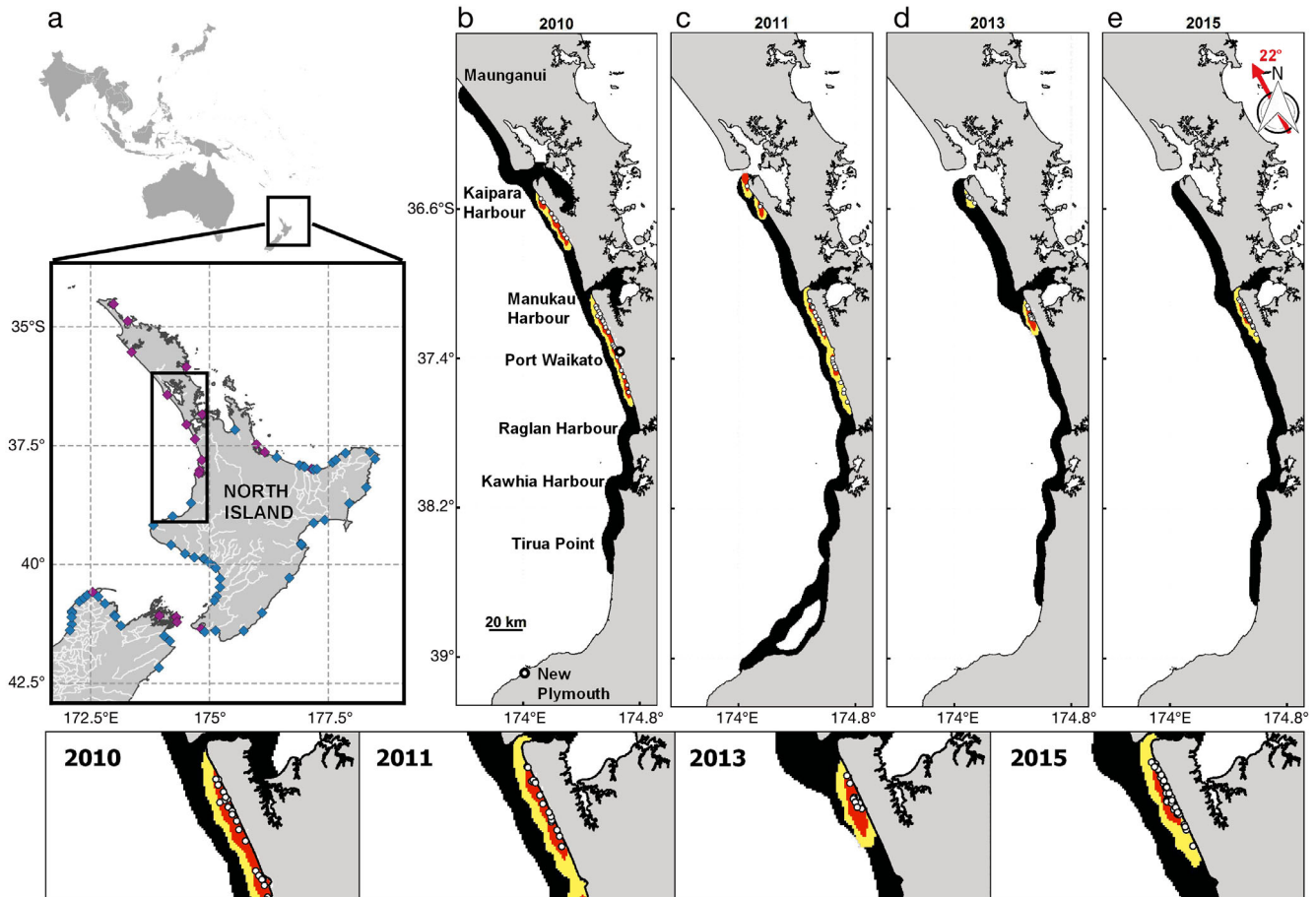
Fig. 1. Study area, kernel density estimates contours and Māui dolphin sightings during 4 years of summer surveys. (a) New Zealand North Island map with diamonds showing major watersheds: harbours (♦) and major rivers (♦). The primary study area on the west coast is demarcated by a black rectangle. (b–e) Māui dolphin areas of use are shown in colour: core areas of use in red (50% kernel contour) and broad distribution of encounters in yellow (95% kernel contour). Black areas correspond to 98% kernel contour areas of survey track lines effort for each year. Māui dolphin sightings for each year are shown (O). Kernel density estimates of Māui dolphin sightings were weighted by survey effort in each year. Lower panels enlarge the central area of the coast for each year where Māui dolphins were consistently encountered. The red arrow overlaid with the north arrow represents the angle at which the coordinate system was rotated to calculate kernel densities

and study species — responds at fine scales to their environment, requiring SDMs to incorporate more dynamic and representative variables to achieve increased model performance and predictability. When *in situ* data are not available, remotely sensed water characteristics (SST, chl *a*, salinity) provide readily accessible data at dynamic temporal and spatial scales (Redfern et al. 2006). Yet, not all potentially important environmental metrics are directly available via satellite-derived data. For instance, water turbidity is not always processed from satellite imagery in coastal areas, and alternative methods must be found to include these variables in marine SDMs.

In this study, we examined the nearshore summer distribution patterns of Māui dolphins at a population scale, as well as the ecological relationships between their occurrence and environmental variables. We

assessed the potential for remotely sensed chl *a* to be used as a turbidity measure to improve our SDM of Māui dolphins. For the first time, we described Māui dolphin nearshore habitat preferences and applied our model to predict habitat suitability both within their current range along west coast North Island and in other areas around North Island where no data had been collected.

MATERIALS AND METHODS

Survey protocol

Boat-based surveys were undertaken along the New Zealand North Island west coast from February to April over 4 years (2010, 2011, 2013, 2015; Table 1).

Table 1. Māui dolphin survey effort along the west coast North Island, New Zealand, and sample sizes by year. Presence: number of dolphin groups observed. Mean group size was calculated per year as well as over the 119 groups observed in total. Pres:dist covered = ratio between presence and distance covered

Year	Start–end dates	Survey effort (d)	Time on water (hh:mm)	Distance covered (km)	Presence	Mean group size (SD)	Pres:dist covered	Pseudo absence
2010	4 Feb–1 Mar	12	97:15	1143	35	5.4 (3.8)	0.031	494
2011	14 Feb–10 Mar	11	80:57	1022	28	3.9 (2.5)	0.027	524
2013	13 Mar–9 Apr	2	14:36	406	13	3.2 (2.0)	0.032	152
2015	12 Feb–1 Mar	12	103:13	1655	43	5.3 (2.7)	0.025	517
Total	–	37	296:01	4226	119	4.8 (3.0)	–	1687

The primary objective of these surveys was to locate dolphins for the purposes of photo-identification and the collection of genetic samples. Consequently, the surveys were generally conducted in nearshore water (distance to shore = 1.0 ± 1.5 km, mean ± SD; max = 15.6 km), where the dolphins are most often encountered (Ferreira & Roberts 2003, Slooten et al. 2006, Du Fresne 2010, Oremus et al. 2012). A total of 4 observers were posted in a 7 m rigid-hulled boat travelling at 15 to 20 knots and they visually scanned the surroundings at 360°, primarily in Beaufort sea states ≤2 (for more details see Oremus et al. 2012). During each dolphin group encounter, GPS position and time were recorded. Group size was calculated using the average between minimum and maximum estimates (Oremus et al. 2012). It is only possible to distinguish between Māui and Hector's dolphins from genetic analysis of biopsy samples, but the number of Hector's dolphins found in association with the Māui dolphins is small and unlikely to influence the habitat modelling (Hamner et al. 2014a). GPS points were also collected along the track lines for each survey day at an average frequency of <1 min. Every year, the west coast was surveyed from Kaipara Harbour (174.52° E, 37.06° S) to south of Tirua Point (174.62° E, 38.54° S), and occasionally up to Manganui and down to New Plymouth (Fig. 1). In 2015, water turbidity was measured using a Secchi disk (i.e. a disk attached to a rope and lowered into the water until it is no longer visible), at the beginning of every survey day, at every dolphin group location and on an hourly basis along the surveys.

Annual distribution patterns

To estimate areas of high Māui dolphin density, a bivariate fixed kernel method (Worton 1989) was used, adjusted for *a priori* knowledge of Māui dolphin distribution. Due to the extreme coastal distribution of Māui dolphins (Du Fresne 2010) and the design of the surveys, the coordinate system was rotated and the *x* and *y* smoothing parameters were modified to account for this known along-shore distributional bias. Dolphin locations were projected in the Universal Transverse Mercator coordinate system (UTM zone 60H) prior to calculations. The coordinate system was then rotated by 22° so the *y*-axis aligned with the dominant course of west coast North Island. This rotation allowed a realistic distortion of the 2-dimension kernel density estimate using a different smoothing parameter on the *y*-axis and the *x*-axis. This approach resulted in an asymmetric variation of the probability density function along the axis parallel to the coast, in contrast to the axis perpendicular to the coast. A Gaussian kernel function was used, set to a bandwidth of 3 km on the *y*-axis and 1 km on the *x*-axis. Probability of presence was estimated over a grid with cell size 500 × 500 m to allow for a relatively fine resolution of spatial structure at the scale of our study area.

The broad distribution of Māui dolphin encounters was defined as the 95% kernel contour, and the 50% kernel contour described the core area of use. All portions that overlapped with land were removed and the remaining kernel volumes were rescaled to 100 for each year. Finally, density estimates across all years were set to the same 0 to 100% scale, so that 100% relative probability of presence indicated cells with maximum probability of occurrence. A similar procedure was applied to calculate survey effort density from track line GPS positions each year using a smoothing parameter of 3 km on both axes. To calculate the annual weighted probability of Māui dolphin presence, rescaled annual maps of dolphin relative probability were divided by the matching annual map of survey effort density. The resulting annual weighted probability of presence grids was then set to the same scale, with 100% relative probability of presence being attributed to cells with maximum probability across all years.

Presence/absence dataset

In order to optimally model dolphin habitat selection, environmental conditions must be compared between locations where dolphins were observed (presence data) and where they were not (absence data) (Elith et al. 2006; our Table 1). In transect survey protocols, data are collected as 'presence points' and 'absence zones'. When building a binomial presence/absence distribution model, pseudo-absences are generally simulated within absence zones (Phillips et al. 2009). The method for selecting pseudo-absences must be thoroughly considered, as both the area over which the pseudo-absences are selected and their number can affect the model (Chefaoui & Lobo 2008, Phillips et al. 2009, VanDerWal et al. 2009). As we were interested in habitat selection at a relatively fine scale, we considered environmental variability with a 1 km spatial resolution and 1 d temporal resolution. Hence, for each survey day, pseudo-absence points were randomly distributed within the survey track strip-width (250 m minimum detection distance to each side), excluding areas within harbours containing ports (Kaipara, Manukau and Raglan Harbours), and within a 1 km radius exclusion area around each sighting to prevent overlap between pseudo-absence points and presence points (in accordance with our 1 km spatial resolution scale; Torres et al. 2008). As habitat at a given location was considered unchanged over the course of a day, exclusion areas around sightings were applied to both the outbound and inbound tracks, which often were in close proximity. To avoid serial correlation between pseudo-absences, daily groups of absence points were distributed with a minimum distance of 1 km from each other, and with a sample size proportional to the area surveyed.

Environmental data

Based on hypothesized Māui dolphin preferences (Ferreira & Roberts 2003, Slooten et al. 2005, Rayment & Du Fresne 2007, Dawson 2009, Du Fresne 2010), several environmental variables were collected for presence and pseudo-absence points to characterize habitat use (Table 2). A total of 4 static variables were collected: distance to the coast (DIST_COAST, km); distance to the closest minor watershed (DIST_MINWATERSHED, km); distance to the closest major watershed (DIST_MAJWATERSHED, km); and depth (DEPTH, m). In addition, 2 dynamic variables were included in the model: sea surface temperature (SST, °C) and a turbidity index (TURBIDITY). For more details about source and manipulation of environmental data, see Supplement 1 at www.int-res.com/articles/suppl/m551p261_supp.pdf.

Due to the hypothesized association between *Cephalorhynchus* dolphins and river mouths (Dawson 2009), we investigated the relationship between dolphin presence and watersheds (defined here as river mouths, or harbour entrances into which multiple rivers empty). Watersheds were classified into 2 categories: minor watersheds (minor river mouths) and major watersheds (major river mouths and harbour mouths). All distances were calculated as Euclidean distances after projecting in a UTM coordinate system (except for Ahipara Bay, where a local correction on distance was applied; see Supplement 1). Bathymetry was acquired at a 250 m resolution and corrected to compensate for values above mean lower low water (10 m was added over the whole depth grid). Bathymetry, coastline and river spatial data were provided by Land Information New Zealand (LINZ; https://data.linz.govt.nz/) and the National Institute of Water and Atmospheric Research (https://niwa.co.nz/).

Table 2. Environmental variables used to model Māui dolphin habitat and their contribution in boosted regression tree (BRT) models. Mean, SD and range are calculated over all positions in the training dataset (presence and pseudo-absences included, n = 1626). Model 1, containing all environmental variables, was selected as the best BRT model. Mean contribution of each predictor and the associated CV were calculated over 1000 runs on bootstrap samples of the training dataset. NASA: National Aeronautics and Space Administration; LINZ: Land Information New Zealand; NIWA: National Institute of Water and Atmospheric Research

Predictors	Unit	Mean ± SD	Range	Data provider	Contributions in model 1 Mean (%)	CV (%)
SST	°C	20.7 ± 0.7	18.9 to 22.0	NASA	22.6	4.8
TURBIDITY	−	0.9 ± 0.8	−1.9 to 3.8	NASA	22.2	3.9
DIST_MAJWATERSHED	km	18.6 ± 20.6	0.1 to 125.1	LINZ	17.0	5.1
DEPTH	m	12.6 ± 7.1	−0.1 to −62.3	NIWA	14.5	5.0
DIST_MINWATERSHED	km	4.3 ± 7.7	0.02 to 44.4	LINZ	13.3	4.0
DIST_COAST	km	1.2 ± 1.7	0.01 to 16.4	LINZ	10.4	4.3

Daily estimates of SST were obtained from the National Aeronautics and Space Administration (NASA) multi-scale ultra-high resolution SST (MURSST) dataset with 1 km resolution (http://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST.html). Furthermore, to test the relationship between Māui dolphin presence and water turbidity, we used remotely sensed chl *a* concentration (mg m^{-3}) obtained from 8 d composite datasets with 4 km resolution (NASA, Aqua MODIS; http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMBchla8day.html). The moderate resolution imaging spectroradiometer (MODIS) algorithm calculates the spectral absorption properties of surface waters and, based on the measured water-leaving radiance, it estimates phytoplankton and coloured dissolved organic matter concentrations, ultimately deriving chl *a* concentration (Savtchenko et al. 2004). In coastal waters, the isolation of the chl *a* absorption signal is challenging due to increased suspended sediments and dissolved organic matter (Gitelson et al. 2008). Yet, this technical bias can be advantageous when trying to record turbidity remotely in coastal environments. The relationship between *in situ* Secchi disk measurements taken during 2015 and MODIS chl *a* concentrations was examined. We recognize the difference in scale of these 2 oceanographic measurements, but no satellite product other than MODIS chl *a* was available at a finer spatial scale across the study area. Therefore, we assessed the potential of this readily accessible remotely sensed dataset as an index of coastal water turbidity at a kilometric scale (see Supplement 1). Based on a near-linear relationship between Secchi disk measurements and log-transformed remotely sensed chl *a* concentration (see 'Results'), the latter measure was included in our SDM (hereafter referred to as TURBIDITY).

Modelling methods

The relationship between Māui dolphin occurrences and environmental predictors was modelled using a boosted regression tree framework (BRT; Friedman 2001). BRTs differ fundamentally from traditional regression methods as they do not require assumptions about the appropriate data model. BRTs are based on a decision tree algorithm that partitions the predictor space into homogeneous response categories, and a boosting algorithm that iteratively optimizes the predictive performance of the model by combining a large number of decision trees (Elith et al. 2008). In this study, the BRT approach was preferred over a linear or additive regression approach

because of its ability to detect complex interactions among predictors and to model non-linear ecological relationships between response and predictor variables (Elith et al. 2008).

BRTs were fitted using the gbm v.2.1.1 (Ridgeway 2007) and dismo v.1.0-12 (Hijmans et al. 2011) libraries in R statistical software. Models were optimized through a 4-fold cross-validation following the Elith et al. (2008) procedure that balanced the number of trees (nt) with the learning rate (lr), bag fraction (bf) and tree complexity (tc; see Supplement 2 at www.int-res.com/articles/suppl/m551p261_supp.pdf). As recommended by De'ath (2007), cross-validation folds were specified to reflect the internal structure of our dataset and were each composed of one year of presence/absence data.

Presence and pseudo-absence were divided into a training dataset (1626 points) and an evaluation dataset (180 points) using a stratified random split (i.e. balancing year and presence/absence in each strata). Calibration of the BRT algorithm was run on the training dataset, while the evaluation dataset was withheld for external validation. Model validation was conducted through 4 metrics to achieve minimum predictive error (see Supplement 2): the percent deviance explained in the training dataset (int.dev) or in the evaluation dataset (ext.dev), and the area under the receiver operating curve averaged during cross-validation (cv.AUC) or calculated in the evaluation dataset (ext.AUC). AUC measures the model's ability for binary classification between presence and absence points (range between 0 and 1, with >0.7 considered a useful model; Swets 1988). The percent deviance explained is a measure of deviance reduction (Guisan & Zimmermann 2000), which can be calculated internally to illustrate descriptive performance of the model or externally to illustrate predictive performance.

The relative contribution of a predictor to a BRT model is measured by the number of times it is selected for tree splitting, and variable selection occurs automatically as non-informative predictors are ignored. Yet, manually removing redundant variables may be desirable when working with small datasets (Elith et al. 2008). Based on internal and external performance metrics, 5 models including either DIST_COAST or DEPTH or neither of the 2 variables were compared, as these predictors showed a significant correlation (Spearman's rho = 0.79) and were likely to be redundant (see Supplement 2, Fig. S3). This comparison was repeated for each model over 1000 bootstrap samples of the training dataset. These random samples included 90% of the training dataset

that were balanced to include a constant presence: pseudo-absence ratio (i.e. 7% of presences). The mean effect of each predictor on the probability of dolphin presence was described in partial dependency plots. These fitted functions are a useful basis for ecological interpretation (Friedman 2001).

Comparison of spatial predictions to historical data

Using the 1000 bootstrapped repetitions of the optimal BRT model, Māui dolphin habitat suitability was predicted on a grid with 1 km^2 cells covering all North Island coastal waters. Using the outputs from these 1000 models, the mean value of habitat suitability and the associated coefficient of variation (CV) was calculated for each grid cell. For this purpose, turbidity and depth layers were re-sampled to 1 km resolution using a bilinear interpolation method. Cells within harbours or with a turbidity index under −0.5 were excluded (equivalent to a 0.61 mg m$^{−3}$ chl *a* concentration). This method limited prediction to nearshore waters where turbidity conditions were within the range of our chl *a* index. Dynamic predictors were averaged over 5 summer months (December 2013 and January to the end of April 2014) to create average summer grids of SST and turbidity. SST in the south of North Island tends to be lower than the temperatures experienced in our study area during this time period. In order to limit our predictions to areas where the SST was similar to the conditions of our training dataset, we removed grid cells with summer SST outside the interval [min(training SST) − SD(training SST): max(training SST) + SD(training SST)] (with minimum, maximum and SD from Table 2). This approach ensured a conservative geographical extrapolation of our model to North Island that was within the range of our sampled predictor variables.

The mean predicted values of habitat suitability were rescaled to range between 0 and 1, and grid cells with predicted values above the fourth quantile of the overall mean were selected as highly suitable habitat. This relatively low threshold was applied because the distribution of predicted habitat suitability values was zero-skewed and heavy-tailed. High habitat suitability cells were clumped together and suitable areas with surface areas >80 km^2 were selected (threshold based on the overlap of core areas of presence across years; Fig. 1). This surface threshold reduced the noise produced by small suitable areas and let the ecologically meaningful larger areas stand out. These zones were spatially com-

pared to current management areas along the west coast of North Island and to historical dolphin sightings. A dataset of 452 observations was derived from public sightings and dedicated survey sightings (acoustic boat-based, land-based and aerial surveys excluding sightings used in our model) collected between 1970 and 2012 in the warm season (December to April; data provided by the New Zealand Department of Conservation; http://www.doc.govt.nz/our-work/our-work-with-maui-dolphin/maui-dolphin-sightings/). Visual species identification is difficult between Māui and Hector's dolphins, so this dataset may include both species. Most historical sightings were not scored using a consistent validation process but were conserved in the dataset because they provide information on the past distribution of Māui and Hector's dolphins. Overall, we selected sightings from the most reliable validation categories (scores 1 to 3) or not validated (score 0). Dolphin positions were plotted against the North Island map of predicted habitat suitability, and the degree of overlap was assessed between highly suitable patches and sightings that were included within the prediction range. All analyses were conducted using QGIS v.2.6.1 (QGIS Development Team 2015) and R statistical software v.3.1.1 (R Core Team 2014).

RESULTS

Annual distributions

The effort of the boat-based surveys was relatively similar between 2010, 2011 and 2015, and lower in 2013. A total of 4226 km were surveyed during 296 h across the 4 years, with 119 dolphin group encounters recorded (Table 1). Most sightings were concentrated between Manukau Harbour and Port Waikato (72%); 13% of sightings were made in the northern part of the study area, towards Kaipara Harbour, while 14.3% were made between Port Waikato and Raglan Harbour. Sightings were located at a distance of 0.80 ± 0.39 km from the coast, with a maximum of 2.53 km. There was no significant difference in group size across years (Kruskal-Wallis test: $H = 8.927$, p = 0.03) and groups averaged about 5 individuals (Table 1).

The kernel density estimates scaled by effort illustrate that across 4 years, the area between Manukau Harbour and Port Waikato was consistently occupied, with Māui dolphins sighted south of Waikato in 2010 and 2011 (n = 17 groups; Fig. 1). The area of overlap between the 4 annual core areas of use was

873 km². The ratio of the number of presence points over the distance covered during surveys was stable over the years (Table 1), but the spatial extent of the sightings was smaller in 2013, and particularly small in 2015, even though the spatial extent of the survey effort was relatively consistent.

Habitat selection model

Secchi disk values from 110 measurements in 2015 ranged from 0.8 to 14.0 m (3.8 ± 2.4 m). Despite the difference in scale between the log-transformed chl *a* concentrations and Secchi disk measurements, they showed a linear relationship (adjusted R^2 = 0.43, df = 107, regression coefficient = 2.12 ± 0.24 SE) and were significantly correlated (Pearson's coefficient = 0.65, paired sample 2-sided *t*-test: t = −8.906, df = 107, p < 0.0001; see Fig. S1 in Supplement 1). As a result, the log-transformed chl *a* concentration was included in BRT models to describe turbidity.

We generated 12 cross-validated BRT models from the different combinations of parameters. After comparing these models, we selected a set of parameters (tc = 4, lr = 5×10^{-4}, bf = 0.1) allowing the production of the model with highest predictive performance (model 1, 6 predictors, nt = 1025). This model explained 31.3% of the deviance in the training dataset on average (int.dev, bootstrap CV = 7.7%) and 20.3% of the evaluation dataset deviance on average (ext.dev, bootstrap CV = 6.4%). AUC scores were relatively high, both when calculated within the cross-validation stage (cv.AUC = 0.803, bootstrap CV = 1.9%) and within the evaluation dataset (ext.AUC = 0.870, bootstrap CV = 0.9%). Models including fewer predictors (models 2 to 5: without DIST_MINWATER-SHED and/or DEPTH and/or DIST_COAST) did not perform better on average, either in terms of explicative power or of predictive power (see Supplement 2, Table S2). Therefore, model 1 was considered our best model, with the following influential predictors contributing in the model in descending order: SST, TUR-BIDITY, DIST_MAJWATERSHED, DEPTH, DIST_MINWATERSHED and DIST_COAST (Table 2).

Species–environment relationships are described by the partial response plots (Fig. 2). SST displayed a positive relationship to probability of dolphin presence, which peaked at about 21.8°C, then slightly decreased for higher temperatures. A predominantly positive asymptotic relationship was found between TURBIDITY and dolphin presence. Partial responses to DIST_MAJWATERSHED, DIST_COAST and DEPTH displayed clear peaks and reached their maximum at 15 km, 700 m and −10 m, respectively. The response to DIST_MINWATERSHED is more complex as it displays a small peak for distances of 0 to 5 km and then reaches a plateau for distances over 20 km. This pattern is likely to result from the heterogeneous distribution of minor rivers on the west coast. In 2010, 2011 and 2013, several groups of dolphins were observed in an area free from minor rivers south of Kaipara Harbour, whereas the core area of use across all study years was located between Manukau Harbour and Port Waikato, where the river network is relatively dense (see Fig. S2 in Supplement 1).

Predicted habitat suitability

Mean predicted habitat suitability based on model 1 was high in the kernel density core area between Manukau Harbour and Port Waikato, and other hotspots were correctly identified farther south: between Port Waikato and Raglan Harbour; south of Kawhia Harbour; and south of Hawera (Fig. 3). When applying our bootstrapped BRT model to North Island and selecting grid cells with high average predicted suitability (>0.10 after rescaling values to range between 0 and 1), we predicted 21 patches of high nearshore habitat suitability, with area sizes ranging from 92 to 1456 km² (Fig. 4a). There was variability in the shape of these patches, with some extending over more than 100 km of the coast (e.g. South Taranaki Bight), while others were restricted inside bays (e.g. Hauraki Gulf). A halo effect was commonly observed around major watersheds, reflecting the strong peak in the functional relationship at 15 km. The CV of predicted habitat suitability varied between 10 and 19% over our area of geographical extrapolation. Grid cells with highest uncertainty were globally located further from the coast and from major watersheds (Fig. 4b). Due to the restriction on predictions for waters outside our sampled SST range, no predictions were made in the Wellington region (Fig. 4).

Of the 452 historical and contemporary Māui and Hector's dolphin sightings, 391 were located inside our prediction range. Evaluation of these 391 sightings indicated that 76.2% were located within high habitat suitability patches around North Island (Fig. 4a, yellow points). The remaining 93 points (23.8%) were located at a distance of 25.2 ± 13.2 km from the closest patch. Overlap cannot be measured for sightings located outside the prediction range (either too far offshore, or in harbours, or in the Wellington
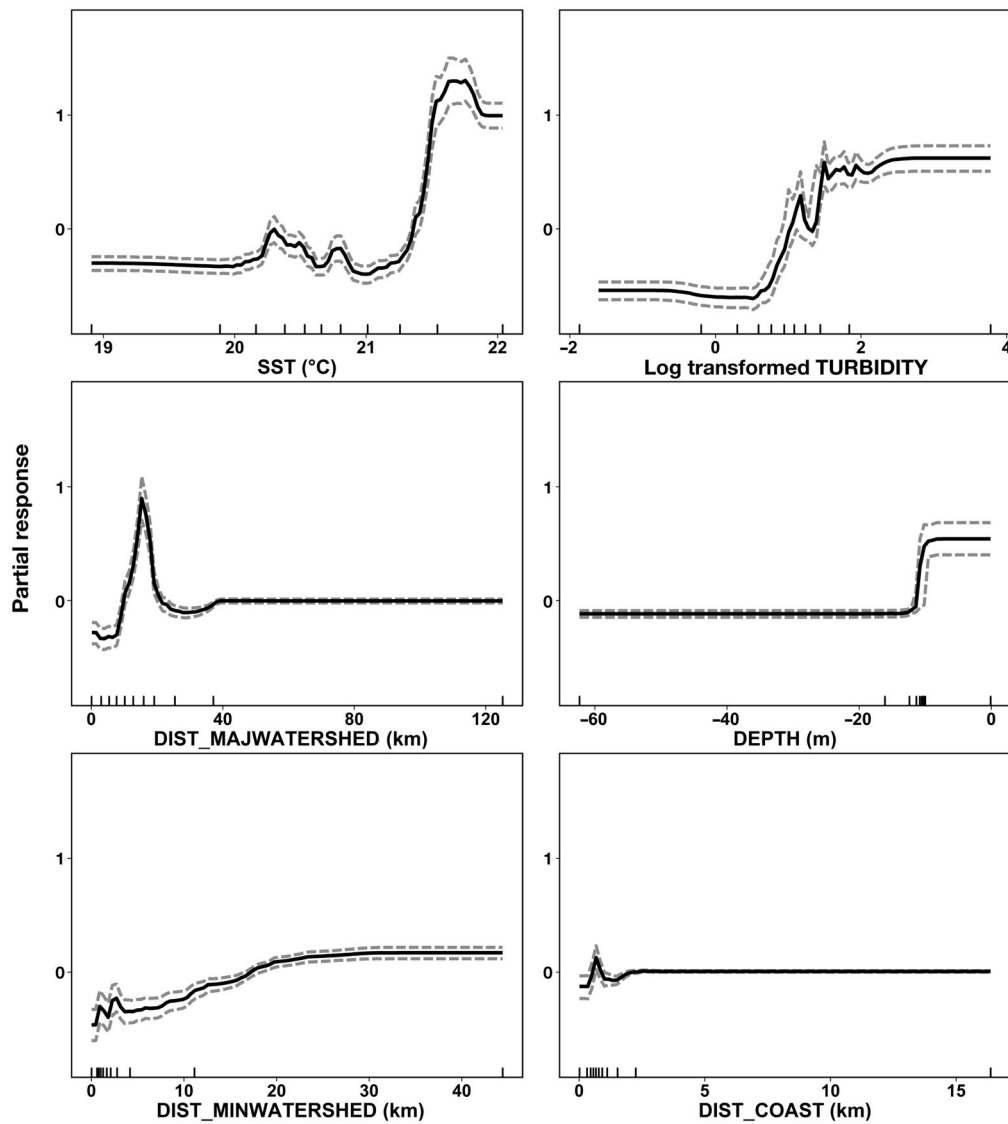
Fig. 2. Boosted regression trees (BRT) partial dependency plots for the predictor variables of Māui dolphin habitat use. Each plot shows the effect of a variable on the probability of presence while fixing other variables to their mean value. The *y*-axes are centred to have a common 0 mean over each variable distribution. Rug plots show distribution of values across that variable, in deciles, and provide a measure of confidence on the fitted response. Grey dashed lines correspond to the 5 and 95% confidence intervals calculated over 1000 BRT models fitted to bootstrap samples of the training dataset

region), but it is evident that many reported sightings occurred relatively close to predicted suitable habitat (50% occurred within 40 km of the nearest highly suitable patch; Fig. 4a, blue points).

DISCUSSION

For the first time, we quantified the relationship between Māui dolphin nearshore distribution and environmental predictors. Using a BRT modelling approach, we showed that the distribution of Māui

dolphins is related to SST, water turbidity, distance to major watersheds, depth and, to a lesser extent, distance from the coast and to minor watersheds (Fig. 2). Applying this model outside the current known range of the species, we highlighted other areas of potentially suitable habitat, which show close spatial distribution with historical sightings of Hector's and Māui dolphins around North Island.

The current nearshore distribution of Māui dolphins is centred between Manukau Harbour and Port Waikato. Māui dolphins were generally observed in pods of less than 5 individuals that were clustered
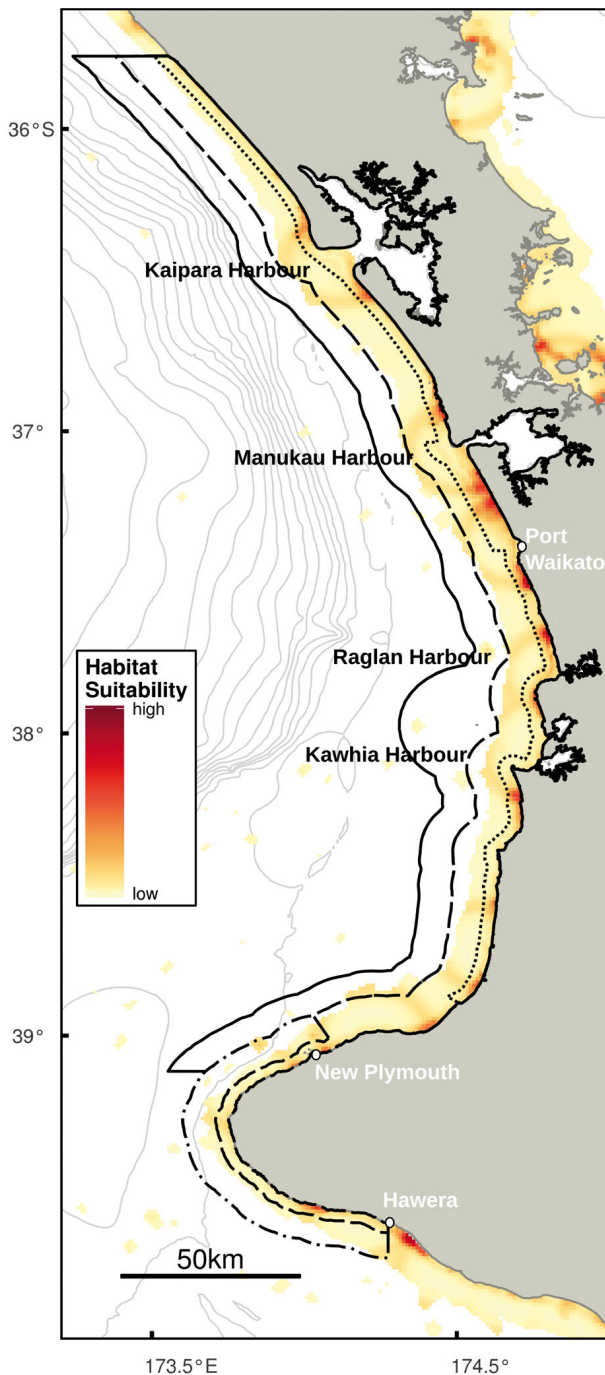
Fig. 3. Nearshore relative habitat suitability for Māui dolphins predicted by BRT models for west coast North Island, New Zealand. Habitat suitability is averaged over 1000 BRT models using a bootstrap resampling approach and scales on a colour gradient. Areas in white correspond to offshore waters where no predictions were made because turbidity dropped below the −0.5 limit of reliability between chl *a* concentration and Secchi disk relationship. Limits of Marine Mammal Sanctuary (solid line), set net prohibition area (dashed lines), conditional commercial set net prohibition area (dashed-dotted line) and trawl prohibition area (dotted line) are shown in black. Light grey lines represent 50 m isobaths

along the coast. Although annual changes in distribution are hard to estimate, given the variation in effort across study years, we observed a restriction of the encounter range between 2011 and 2015. In 2015, despite a spatially extensive survey effort, all groups were observed within a 20-km-long portion of the coast just south of Manukau Harbour. The preference for this restricted zone probably results from a combination of 2 scenarios: (1) habitat in this zone best meets the ecological and physiological needs of Māui dolphins compared to habitats along the rest of the west coast North Island; and (2) other factors prevent dispersion to the rest of the west coast, thus limiting Māui dolphin occurrence to this zone. Among other factors, the Allee effect (i.e. depensatory feedback operating only at low numbers) has likely contributed to the current distribution of Māui dolphins by favouring the aggregation of individuals for social interactions, cooperative feeding and/or predator avoidance (Courchamp et al. 1999). As observed in other species, social animals such as Māui dolphins may preferentially concentrate in patches of habitat already occupied, even if other areas of equal or higher habitat suitability exist at close range (Stephens & Sutherland 1999, Clapham & Zerbini 2015). Unfortunately, these social behaviours are difficult to quantify within a habitat distribution model.

While our results provide insight into the nearshore, summer habitat of Māui dolphins, caution is warranted in model extrapolation to other seasons and habitats. First, although our application of easily accessible remotely sensed chl *a* data to describe turbidity enabled us to use 3 years of survey data when *in situ* water clarity data were not collected, the linear relationship between *in situ* Secchi disk measurements and chl *a* concentration is only valid in a restricted range (>0.6 mg m^{-3}), limiting predictions to turbid nearshore waters within this range. Second, the limited extent of model calibration data relative to habitat availability in areas of geographical extrapolation is an inherent problem when applying SDMs, and can highlight variation between fundamental and realized habitat use patterns (e.g. Torres et al. 2015). The limited extent of our sightings and survey effort data to nearshore habitats of the west coast of North Island resulted in higher uncertainty of predictions in geographical areas in which habitats were not sufficiently represented in the training dataset, and should be regarded with more caution. Yet, by limiting predictions based on SST, we ensured that no environmental extrapolation was made beyond our predictive data range (e.g. Fig. 4b,
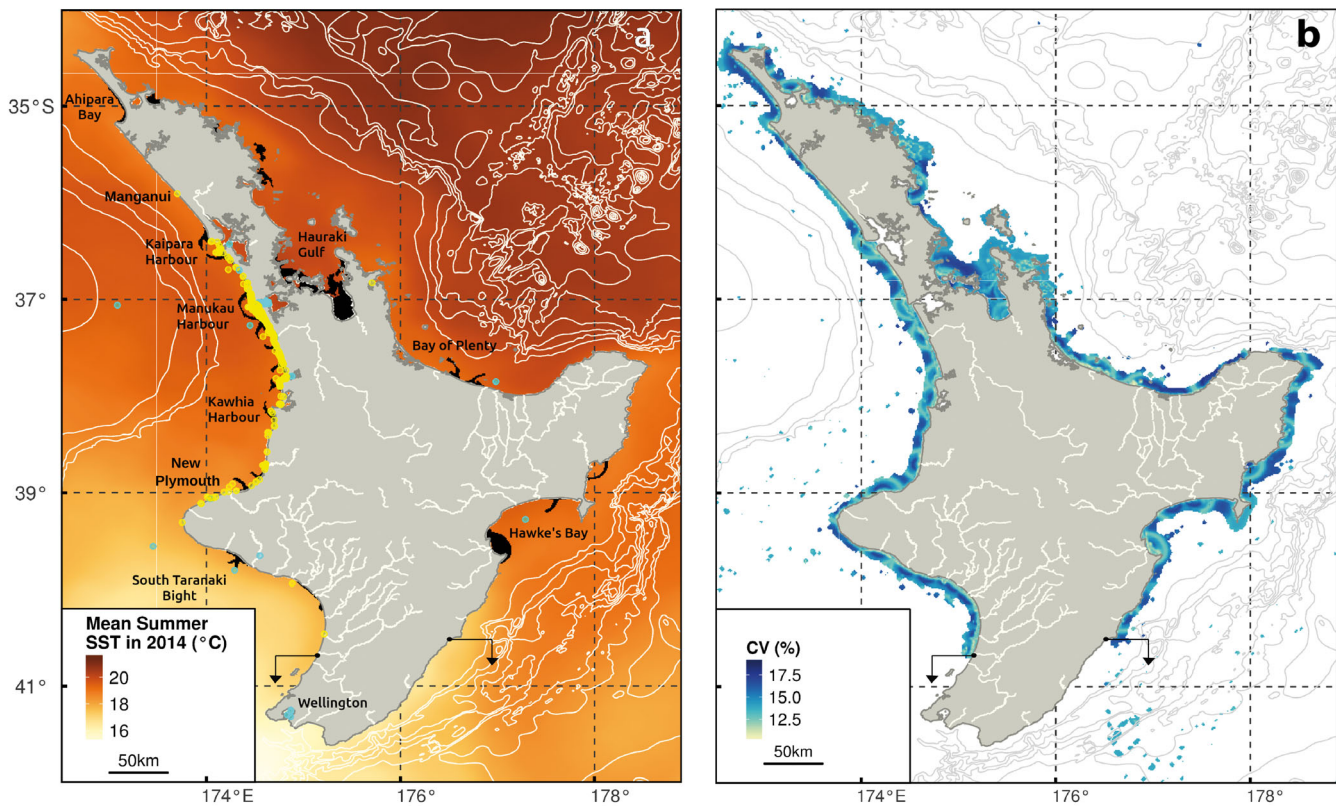
Fig. 4. Predictions of habitat suitability for Māui dolphins and historical sightings of Māui and Hector's dolphins in North Island, New Zealand. (a) Mean predicted patches of high habitat suitability. Black zones show areas of high habitat suitability with surface area greater than 80 km^2. Historical sightings of Māui and Hector's dolphins included within (⬤) and outside (⬤) our prediction range are shown. Background shows SST average values for December 2013 to April 2014. Although obscured by many sightings, the area between Kaipara Harbour and Kawhia Harbour is covered by several patches of high habitat suitability. (b) CV of the predicted habitat suitability. The coefficient is calculated over 1000 BRT model runs using a bootstrap resampling approach. It ranges from 10 to 19% and provides a spatial measure of uncertainty for our predictions. Areas in white were excluded from our predictions because they are outside the data calibration range (i.e. offshore waters in general, harbours and nearshore waters of the Wellington region). Light grey lines represent isobaths from depth 100 to 10 000 m, with a 400 m increment. Black arrows indicate the latitudinal limit under which no predictions were made

Wellington region excluded from our predictive range). Lastly, seasonally biased calibration data must be considered when making habitat predictions. Indeed, SST and turbidity along the west coast of North Island vary greatly throughout the year and the habitat preferences of Māui dolphins are likely affected by the resulting seasonal changes of their prey and predator distributions (Heithaus & Dill 2002). Hector's dolphins extend their distribution offshore during winter (Rayment et al. 2010) and Māui dolphins may display the same behaviour (Du Fresne 2010). As all 2010–2015 surveys took place during summer, we only predicted habitat suitability in warm months and used historical sightings collected during this time period, but future research should include winter surveys to ascertain whether there are seasonal differences.

Like other habitat studies of marine predators (e.g. Block et al. 2011), SST was the main factor describing Māui dolphin occurrence. Due to its accessibility using remote sensing, SST is commonly included in marine SDMs. Furthermore, SST integrates the spatial and temporal patterns of many abiotic and biotic parameters such as prey abundance, frontal location and productivity. In our study, Māui dolphin probability of presence increased in relatively warm waters. This relationship may be a function of prey abundance, but there is currently no direct evidence for such a relationship. Little is known about the diet of Māui dolphins, but it may resemble the generalist diet of Hector's dolphins, which eat various species of fish throughout the water column and often target juveniles. Miller et al. (2012) analysed 2 Māui dolphin stomach contents, and found only ahuru *Auche-*

noceros punctatus and red cod *Pseudophycis bachus*, 2 species that are common in coastal waters of New Zealand and also consumed by Hector's dolphins around South Island. More information about the diet and distribution of Māui dolphins is required to improve our mechanistic understanding of their spatial relationship with SST.

The occurrence of Māui dolphins was also explained by turbidity, depth, distance to the coast and distance to watersheds, which agrees with previous qualitative studies (Ferreira & Roberts 2003, Slooten et al. 2005, Rayment & Du Fresne 2007, Childerhouse et al. 2008, Dawson 2009, Du Fresne 2010). The relationship between turbidity and the occurrence of Māui dolphins revealed an overall preference for turbid waters but was relatively complex in its shape. This non-linear pattern may be due to the dynamic nature of turbidity, which fluctuates as a result of multiple factors such as concentrations of chl *a*, dissolved organic matter and suspended sediment. The latter two are mainly supplied by rivers and are transported by oceanic currents. We found that the probability of dolphin occurrence was optimized by a distance of 15 km from major watersheds, suggesting that (1) turbid waters are transported by currents away from major watersheds, providing optimal turbidity levels at a distance of 15 km, or (2) other unconsidered sources of turbidity exist in the area of highest dolphin density south of Manukau Harbour.

During the 2010–2015 surveys, Māui dolphins were observed feeding in turbid plumes between Manukau Harbour and Port Waikato, suggesting that their distribution is linked to prey availability. However, predation is also known to be a driver of species distribution patterns and may add to the complexity of the ecological relationships displayed by Māui dolphins. New Zealand is one of the world's hotspots for white sharks *Carcharodon carcharias*, and they are reported in the nearshore waters of west coast North Island (Malcolm & Warrick 2012). Shark bite scars have been observed on stranded (Russell 1999) and live Māui dolphins (R. Constantine pers. comm.), but it is likely that some shark attacks are simply fatal and do not leave scars. Since vision is one of the major senses white sharks rely on while foraging at close range (Strong 1996), Māui dolphins could actively seek turbidity plumes to avoid predation. Overall, an optimal level of turbidity could provide Māui dolphins with the best trade-off between prey availability and predation risk.

The relatively high overlap rate (76.2%) between the predicted patches of high habitat suitability and historical sightings supports the relevance of our

model, but also raises questions about the past and future dynamics of Māui dolphin distribution patterns. Given that the Māui dolphin population currently occupies a small subset of its historical range (Russell 1999, Ferreira & Roberts 2003, Slooten et al. 2006, Du Fresne 2010, Oremus et al. 2012), our model predictions are likely to underestimate the real extent of suitable habitat in North Island. Yet, these predictions indicate that during summer months, pockets of suitable habitat currently exist all around North Island, and historical sightings suggest that Māui or Hector's dolphins may have previously occupied these areas (Du Fresne 2010). However, these pockets are separated by relatively great distances (maximum of about 200 km without considering the Wellington region), and by deep and cold waters that might act as natural barriers to population connectivity, contributing to the species' isolation and decline. Given the small home ranges observed for Māui and Hector's dolphins (Rayment et al. 2009, Oremus et al. 2012), this lack of connectivity is a matter of concern for the recovery of the North Island population. However, there is also evidence of long-distance dispersal in Hector's dolphins (Hamner et al. 2014b), suggesting that while they usually live in restricted areas with very specific habitat requirements, the species may also be able to migrate to new areas.

This and previous studies suggest that the realized ecological niche of the Māui dolphin is very restricted. Protection measures successfully cover the small nearshore area currently occupied by the population in summer. Although our model predictions may not be appropriate to evaluate habitat suitability in offshore waters outside the set net prohibition zone, high suitability habitats were predicted in the shallowest waters that are well covered by fishing and mining restriction zones. Yet, bringing Māui dolphins back from the brink of extinction may require increased conservation measures specifically tuned towards their habitat use. It is critical to assess whether the offshore extent of their range increases in the winter and whether current conservation efforts are adequate for protecting Māui dolphins all year round. Also, the relatively low deviance explained by our model underlines the lack of data that is essential to distinguish their fundamental niche (i.e. free of interference from other species; Hutchinson 1957) from their realized niche (i.e. accounting for biotic interactions and competition). Including prey–predator and intra-specific relationships in models will improve our mechanistic understanding of habitat selection and help clarify the niche of Māui dolphins. Nonetheless, we believe the methods used

here to describe Māui dolphin distribution (kernel density estimate generated using modified smoothing factors and shifted coordinate system) and habitat use (turbidity derived via remotely sensed data and BRT modelling) may be applicable to other marine species living in coastal environments. Indeed, several dolphin species preferentially occupy turbid, coastal waters near rivers (e.g. Commerson's dolphin, Garaffo et al. 2011; Indo-Pacific humpback dolphin *Sousa chinensis*, Lin et al. 2015; Chilean dolphin, Viddi et al. 2015) and our methods may improve our understanding of their spatial ecology. More generally, this study illustrates how habitat modelling may be used to predict the distribution patterns of endangered marine species and provide valuable ecological knowledge necessary for their conservation.

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