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Remotely sensed hydroacoustics and observation data for predicting fish habitat suitability

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ABSTRACT

This paper investigates the use of using remotely sensed observation and full coverage hydroacoustic datasets to quantify habitat suitability for a marine demersal fish, the blue-throated wrasse. Because of issues surrounding the detection of species using remotely sensed video techniques, the application of presence-only techniques are well suited for modeling demersal fish habitat suitability. Ecological-Niche Factor Analysis is used to compare analyses conducted using seafloor variables derived from hydroacoustics at three spatial scales; fine (56.25 m^2), medium (506.25 m^2) and coarse (2756.25 m^2), to determine which spatial scale was most influential in predicting blue-throated wrasse habitat suitability. The coarse scale model was found to have the best predictive capabilities with a Boyce Index of 0.80 ± 0.26. The global marginality and specialization values indicated that, irrespective of spatial scale, blue-throated wrasse prefer seafloor characteristics that are different to the mean available within the study site, but exhibit a relatively wide niche. Although variable importance varied over the three spatial scale models, blue-throated wrasse showed a strong preference for regions of shallow water, close to reef, with high rugosity and maximum curvature and low HSI-B values. Generally the spatial patterns in habitat suitability were well represented in the Marine National Park compared to adjacent waters. However, some significant differences in spatial patterns were observed. Interspersion and Juxtaposition Indexes for unsuitable and highly suitable habitat were significantly smaller inside the Marine National Park, while the Mean Shape Index of unsuitable habitat in the Marine National Park was significantly larger.

1. Introduction

Predictive geographical modeling is increasingly being recognized as an important tool for estimating species' habitat suitability, which is a fundamental step in the planning of conservation and management programs (Franklin, 1995; Pearce and Ferrier, 2001). These techniques allow the prediction of a species' potential habitat suitability, or distribution, beyond the range of direct observation data alone. Furthermore predictive geographic modeling serves a variety of purposes in applied ecology, including identifying areas of high conservation potential, assessment of suitable habitat representativeness and spatial patterns within protected areas, identifying the best sites for species reintroductions, designing wildlife corridors, predicting sites at risk for disease or exotic species invasions, and predicting how species distributions may change in response to management decisions and climate change (Manel et al., 2001). Although originating and being applied more commonly in terrestrial environments, advances in marine remote sensing technologies and the analytical capabilities of Geographic Information System (GIS) has seen an increase in marine applications of habitat suitability modeling (Brown et al., 2005; Bryan and Metaxas, 2007; Galparsoro et al., 2009; Iampietro et al., 2005; Pittman et al., 2007; Wilson et al., 2007).

High-resolution multi-beam echo-sounder data (MBES) allows the generation of detailed full-coverage spatially explicit seafloor datasets over large geographical regions (Iampietro et al., 2005; Moore et al., 2009; Nasby-Lucas et al., 2002; Wilson et al., 2007). MBES data are ideal for the application of terrain analysis techniques which form variable datasets for input into predictive models (Wilson et al., 2007). Advances in remotely operated underwater video systems offer the ability to cost-effectively capture observation data beyond the range of traditional methods (e.g. SCUBA Assis et al., 2008) and is a viable method in estimating fish population dynamics (Lauth et al., 2004; Morrison and Carbines, 2006; Watanabe et al., 2004). Towed video techniques have produced similar results to diver transects for estimating fish population dynamics, without being restricted by depth or bottom time (Stobart et al., 2007). It also has advantages over capture methods and baited video systems as it is able to

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continuously capture data over seafloor transitional zones (Spencer et al., 2005). Morrison and Carbines (2006), for example, compared a large range of commonly used fish survey techniques (i.e. trawls, traps, nets, jigs, long-lining, baited camera and SCUBA diver) to a towed/drift video system to estimate the abundance of snapper (*Pagrus auratus* Forster) during their nighttime resting period. They found that the towed video system appeared to provide better estimates of population abundance because it was not limited by depth, deployment time or size class selectivity. The integration of high-resolution MBES data and presence records from towed video datasets provides an opportunity to develop models of fish habitat suitability over large areas of seafloor.

Different mathematical techniques have been developed for habitat suitability models (Guisan and Zimmermann, 2000); those that require presence–absence data (e.g. Generalized Linear Modeling) and more recently those that involve presence-only data (e.g. ecological-niche factor analysis (ENFA) (Hirzel et al., 2002)). Although towed video is well suited to estimating fish occurrences, obtaining reliable absence data for highly mobile demersal fishes that are closely associated with seafloor structures (e.g. kelp beds or overhanging cliff structures) from a remotely sensed video image can potentially result in an underestimate species' occurrence. Thus, the application of the latter of these two techniques will be the focus of this study. Spatially explicit presence-only models utilize some form of environmental envelope or distance approach that compares the environmental niche of a species (defined from occurrence datasets) to the ecological characteristics of the entire study area (stored as GIS layers) (Hirzel et al., 2002). While presence-only modeling is commonly used in terrestrial ecology (Brotons et al., 2004; Elith et al., 2006; Hirzel, 2001; Phillips et al., 2006; Titeux, 2006; Tsoar et al., 2007), recent marine applications have yielded promising results, particularly using ENFA. ENFA has been applied for modeling coral distribution at local (Dolan et al., 2008), regional (Bryan and Metaxas, 2007) and global (Tittensor et al., 2009) scales. It has also been applied to mobile marine species to determine cetacean distribution (Praca et al., 2009), sea bird feeding habitats (Skov et al., 2008) and suitable lobster habitat (Galparsoro et al., 2009; Wilson et al., 2007). Furthermore, because presence-only models are comparatively robust to low occurrence sample size, often reaching near optimal performance between 30 and 50 occurrences (Hernandez et al., 2006; Stockwell and Peterson, 2002; Wisz et al., 2008), they are ideal for modeling applications where observation data is limited. These characteristics make presence-only techniques well suited for marine demersal fish habitat suitability modeling.

Species can potentially respond to habitat variables at different spatial scales (Freemark and Merriam, 1986). Because each species responds to the environment at a unique range of scales (Levin,1992), there is no single correct spatial scale at which to describe species-habitat relationships (Wiens, 1989). Thus, assessing species–environment relationships at multiple scales are necessary (Cushman and McGarigal, 2003) and are becoming commonplace (Carroll et al., 1999; Fischer et al., 2004; Thompson and McGarigal, 2002; Wilson et al., 2007; Zabel et al., 2003).

Blue-throated wrasse (*Notolabrus tetricus* Richardson) are a species common to the inshore waters of southern Australia. Like numerous other wrasse species found along southern Australia, they are protogynous hermaphrodites (Barrett, 1995; Shepherd and Clarkson, 2001). Exhibiting well-defined home ranges ranging from 400 to 775 m^2 for males and 225–725 m^2 for females, they complete their life-cycle in a relatively small area (Barrett, 1995). The species has recently become the focus of a rapidly expanding commercial line and trap fishery in Victoria, south-east Australia. Coupled with likely population structuring at a localized scale and a burgeoning fishing industry, the species has been identified as being highly susceptible to over-exploitation (Smith et al., 2003). Their sedentary and highly territorial nature (Barrett, 1995) also means that they may exhibit strong associations with a particular habitat. This combined with their potential susceptibility to over-exploitation makes them an ideal candidate for habitat suitability modeling.

The objectives of this study are threefold. Firstly, we use ENFA to develop a habitat suitability model for blue-throated wrasse. Secondly, we run models using hydroacoustics sampled at three spatial scales to determine the most influential for predicting blue-throated wrasse habitat suitability. The use of the same occurrence dataset across the different spatial scale models permits a direct comparison of the model outputs. Finally, we apply landscape pattern indices using the best performing model to compare the spatial patterns of habitat suitability classes within the Discovery Bay Marine National Park with adjacent waters.

2. Materials and methods

2.1. Study area

The study area was located on the western side of Cape Duquesne, south-eastern Australia (Fig. 1) and encompassed a total area 39.8 km^2, with 26.3 km^2 of this situated in the Discovery Bay Marine National Park. The site ranged in depth from 12 to 80 m, with mean water temperatures ranging from 12 °C in winter to 18 °C in summer (CSIRO, 2009). The seafloor of the area reflects the region's rich volcanic history. Sheer basalt reef structures rise some 20 m from the seafloor and are covered in a rich array of temperate southern Australian flora and fauna. The shallow (< 20 m) reefs within this region support a high diversity of canopy dominating species (dominated by *Ecklonia radiata* Agradh, *Phyllospora comosa* Agradh and *Durvillaea potatorum* Areschoug), with understory communities dominated by mixed red algae increasing with depth. Deeper reefs were found to consist of a sponge dominated habitat with other invertebrates including ascidians, bryozoans and gorgonians (Ierodiaconou et al., 2007b).

2.2. Multi-beam echo-sounder survey and model variables

Model variables were derived from multi-beam echo-sounder (MBES) data that was acquired on the 2nd and 3rd of November (38 h), 2005 as part of the Victorian Marine Habitat Mapping Project (Ierodiaconou et al., 2007b). MBES bathymetry and backscatter information were collected using a hull-mounted Reson Seabat 8101 multi-beam system with 100% overlap of run lines to ensure full site coverage. Precise positioning was achieved using Starfix HP Differential GPS system ($\pm$0.30 m), integrated with a positioning and orientating system for marine vessels (POS MV) for heave, pitch, roll and yaw corrections ($\pm$0.02° accuracy). Navigation, data logging, real-time quality control, display and post-processing were carried out using the Starfix suite 7.1 (Fugro Survey Pty Ltd.). Sound velocity profiles were taken every 12 h during survey operations to account for variations in sound speed through the water column. Bathymetry data were corrected to the lowest astronomical tide based on reading from an Aquatec 320 tide gauge that was deployed during the survey. The XYZ data were then used to produce a bathymetric grid at 2.5 m horizontal resolution and a range resolution of $\pm$12.5 mm. Backscatter data were corrected for gain and time varied gain using the University of New Brunswick (UNB1) algorithm (Starfix suite 7.1). Data were

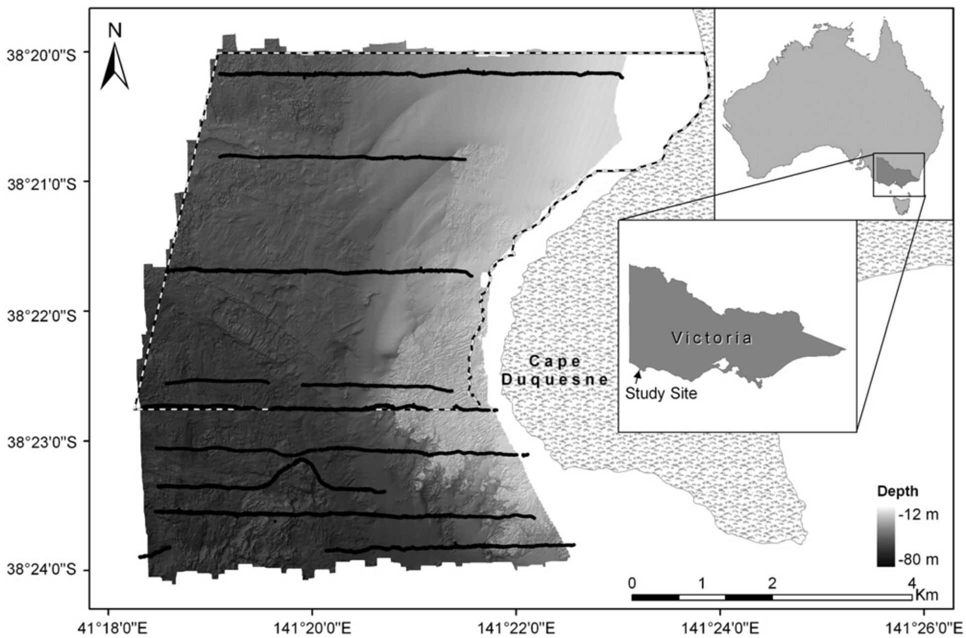

Fig. 1. Bathymetric hillshade highlighting the study area used to investigate habitat suitability. Shading indicates water depth. Dashed black line shows Discovery Bay Marine Park Boundary. Solid black lines illustrate towed video transects positions.

post-processed by trained surveyors to hydrographic standards. Backscatter processing included the correction for transmission loss, the actual area of ensonification on the bathymetric surface, source level, and transmit and receive beam patterns (see Fonseca et al., 2008). Additionally backscatter was corrected for seafloor bathymetric slope from the MBES bathymetry dataset. Final products of the MBES survey constituted cleaned 2.5 m backscatter intensity (dB) and bathymetry (m) grid layers.

The processed 2.5 m gridded backscatter and bathymetry were used to derive 10 additional variables to further characterize local variation within the MBES imagery and delineate analogous regions of morphology and signal scattering (Table 1). These derivatives were selected for their expected influence over distribution of fish as found in previous investigations (e.g. rugosity—Friedlander and Parrish, 1998; slope—Moore et al., 2009; bathymetric variance—Pittman et al., 2007; distance to nearest reef—Wedding et al., 2008). They represent variation in seafloor characteristics in terms of proximity to reef (Euclidean distance to nearest reef), exposure to wave energy and seafloor currents (aspect, benthic position index (BPI), slope), complexity and surface area of seafloor structure (complexity, rugosity, maximum curvature) and variations in high and low frequency signal scattering properties of the substratum recorded in the backscatter intensity dataset (Hue-saturation-intensity). Euclidean distance to nearest reef was calculated using Spatial Analyst tool kit in ArcGIS 9.3 based on a predicted substrata dataset using automated classification techniques as part of the Victorian Marine Habitat Mapping Project (Ierodiaconou et al., 2007a).

Variables were calculated at three spatial scales to assess which most influenced wrasse habitat suitability. The spatial scales were chosen to encompass the home range of 225–775 m^2 estimated for blue-throated wrasse (Barrett, 1995). Consequently, we included three window sizes of 3×3, 9×9 and 21×21 cells, which equates to ground areas of 56.25, 506.25, and 2756.25 m^2 (hereafter referred to as fine, medium and coarse scale models). These windows represent the finest model possible, a midpoint of the estimated home range and approximately 3.5 times larger than the home range. A correlation tree derived in Biomapper 4.0 was used to assess the correlation between variables at each spatial scale. To avoid incorporating redundant data, a default threshold of 0.5 was chosen in line with previous studies (Galparsoro et al., 2009; Hirzel et al., 2002). For each spatial scale, the same least correlated subset of the initial 13 variables (Table 1) were used to allow direct comparison of modeling results.

2.3. Towed video fish surveys

Demersal fish were surveyed using towed video transects. After visual analysis of the bathymetry dataset, nine video transects were selected perpendicular to the coast to capture the main physical and biological gradients within the site (e.g. depth, exposure, substrata, benthic biological habitat). Over four days (24th and 25th of March, and the 26th and 27th of April 2006) 20.8 h of georeferenced underwater towed video footage, covering 56 linear km of seafloor were collected (Fig. 1). The towed-camera system comprised of a micro remotely operated vehicle (VideoRay Pro 3) mounted in a custom stainless cage to protect the system from collision as well as providing a secure tow point. The camera was towed at speeds between 0.5 and 1.0 $m\,s^{-1}$ (1–2 kn) at a height approximately 1 m above the seafloor. The wide-angle camera was tilted downward to maximize a consistent field of view of the benthos immediately in front of the camera, as well as the water column ahead. This configuration facilitated an ample field of view to observe demersal fish and allowed safe navigation of the equipment. The video signals were transferred to the surface via an umbilical cable where they were monitored in real-time for navigation ease and recorded on mini-DV tape. The survey positional data were recorded (at 1 s intervals) through the integration of vessel location (Omnistar satellite dGPS), motion sensor (KVH) and acoustic camera positioning (Tracklink Ultra Short Baseline). The video imagery was time stamped with positional data prior to being recorded to tape. Subsequently, the video footage and the camera track files were visually analyzed to record the precise position of fish species occurrence within approximately

Table 1
Variables used in the ENFA models with biological relevance to blue-throated wrasse.

Model variables	Variable description	Kernels sizes	Software
Aspect			
Eastness	Because aspect is a circular variable (i.e. large values (359°) are very close to small values (1°)) the data were transformed. Aspect was transformed by trigonometric functions (Roberts, 1986). Eastness values close to 1 represent east-facing slopes, while those facing west have a value close to −1	3×3, 9×9, 21×21 cells	Spatial Analyst—ArcGIS 9.3
Northness	Northness is represented in values close to 1 if the aspect is generally northward, close to −1 if the aspect is southward	3×3, 9×9, 21×21 cells	Spatial Analyst—ArcGIS 9.3
Backscatter	Backscatter intensity is important in quantifying physical properties of the seafloor (Le Gonidec et al., 2003). Provides a proxy for seafloor hardness and softness	3×3, 9×9, 21×21 cells	Fugro Starfix suite 7.1
Bathymetry	Bathymetry provides a measure of depth for the entire site	3×3, 9×9, 21×21 cells	Fugro Starfix suite 7.1
Benthic position index	Measure of a location relative to the overall landscape. Calculated by comparing the elevation of a cell with the mean elevation of surrounding cells by the three analysis extents. Regions with positive values are higher than their surroundings, where as areas negative values are lower. Flat areas have values closer to zero (Weiss, 2001)	8, 22, 52 scale factor	BTM Tool for ArcGIS
Complexity	Complexity provides a measure of the rate of change of the slope and a measure of localized variability in seafloor structure	3×3, 9×9, 21×21 cells	ENVI 4.2
Euclidean distance to nearest reef	The Euclidean distance (in m) to nearest reef was calculated from extracting the reef class from a substratum map that was generated as a part of the Victorian Marine Mapping Project using a decision tree classifier (see Ierodiaconou et al., 2007b)		Spatial Analyst—ArcGIS 9.3
HSI-blue	A Synthetic Color Image transformation was applied to the backscatter. This transforms backscatter from a gray scale image into a synthetic color image by applying high pass and low pass filters. Low pass data are assigned to hue, while high pass is assigned to intensity, and a fixed saturation level is used. These hue, saturation and intensity data are transformed into red, green, and blue (RGB) spectrum, producing a three band color image. This transformation is commonly used with radar data to improve the display of subtle large-scale features while retaining fine detail (Daily, 1983)	3×3, 9×9, 21×21 cells	ENVI 4.2
-green			
-red			
Maximum curvature	Maximum curvature provides the greatest curve, relative to its neighbors, of either the profile (i.e. the curvature in the direction of maximum downwards slope) or plan (i.e. the shape of the surface viewed as if a horizontal plane) convexity (Gallant and Wilson, 1996)	3×3, 9×9, 21×21 cells	ENVI 4.2
Rugosity	Rugosity, or vertical relief, is the ratio of surface area to planar area within analysis window and is to represent a measure of structural complexity (Lundblad et al., 2006)	3×3, 9×9, 21×21 cells	BTM Tool for ArcGIS
Slope	Slope is the rate of change in bathymetry over the analysis window (Wilson et al., 2007)	3×3, 9×9, 21×21 cells	Spatial Analyst—ArcGIS 9.3

Kernels sizes give the number of cells or scale factor used to calculate fine, medium and coarse models.

2 m either side and 3 m into the water column above the transects. Transects were analyzed by the same observer to decrease any between operator bias. Video footage was only excluded from the analysis when the video quality was too poor to identify fish or view the seafloor. To minimize erroneously positioned fish, individuals were only counted if they were observed in the foreground (within 5 m of the camera) of the video footage.

2.4. Model formulation and evaluation

Ecological-niche factor analysis (ENFA) was used to develop the habitat suitability models using Biomapper 4 software (Hirzel et al., 2007). For each spatial scale, rasters of the least correlated subset of variables were imported into the Biomapper program along with a grid identifying which cells were classified as 'presence' for blue throated wrasse. A Box–Cox transformation was used to improve the normality of the variables (Hirzel et al., 2002). ENFA then reduces original variables to a subset of uncorrelated factors. MacArthurs broken-stick rule (MacArthur, 1957) was used to determine how many of these factors were retained in the habitat suitability calculation. The 'broken-stick' concept of MacArthur (1957) describes how species partition a resource pool in multi-dimensional space into non-overlapping niches. Based on this concept, the 'MacArthurs broken-stick' rule compares the eigenvalue distribution of the factors to ensure that there is no overlap and that only those which are necessary are retained (i.e. with eigenvalues >1). Thus, the retained factors explain most of the information related to the distributions of the original variables and constitute the dimensions of the environmental-space for the calculation of habitat suitability. The important difference between ENFA, and other data reduction techniques such as principal components analysis, is that rather than only accounting for the variance among factors the ENFA factors have ecological relevance (Hirzel et al., 2002). Marginality of the species (i.e. how species' habitat differs from the mean available conditions) is represented in the first factor, while specialization (breadth of the ecological niche) is maximized in the subsequent factors (Hirzel et al., 2001). The factor coefficients give the importance of each variable to the different factors and the relative range of the variables preferred by the species (positive coefficients indicate preference for areas above mean for that variable, and the inverse for negative coefficients). They are also used to compute a global marginality (varying between 0 and 1, with higher values indicating greater differences) and specialization (indicating some degree of specialization when greater than 1). We use the distance geometric mean algorithm to generate habitat suitability maps. This algorithm computes a smooth set of habitat suitability envelopes by relating each observation cell in such a way that the denser these are in the environmental-space, the higher the habitat suitability (Hirzel et al., 2007). A cell with a habitat suitability value of zero would have the least suitable combination of values for all variables, while a cell with a value of 100 would have the most suitable combination.

To determine which spatial scale model performed best, habitat suitability models were evaluated in Biomapper 4 using the predicted-to-expected ratio curve (p/e curve) and the continuous Boyce index (B) (Boyce et al., 2002; Hirzel et al., 2006). A perfect model would exhibit a straight increasing line p/e curve. The B is a Spearman rank correlation coefficient between the p/e ratio and the habitat suitability values. It varies from -1 to 1, a perfect model having a $B=1$. Hirzel et al. (2006), however, compared the accuracy of different validation methods and found a $B\approx0.6$ corresponds to an Area under the receiver operating characteristic (ROC) curve >0.9 (ROC evaluates the proportion of correctly and incorrectly classified predictions over a continuous range of presence–absence thresholds. The closer ROC is to 1, the better the model).

In practice, the occurrence data is partitioned into k independent subsets, and $k-1$ partitions are used as a calibration dataset, leaving the last partition for validation. We used $k=10$, together with 1 random seed, for each spatial scale model. To generate the p/e curve for each model, we used three equal-width habitat suitability windows (0–33, 34–67, and 68–100). If a model properly predicts the suitable areas, the p/e ratio should be <1 for unsuitable habitat, >1 for moderately suitable habitat and $\gg 1$ for highly suitable habitat. The p/e ratio should also exhibit a monotonic increase from unsuitable to highly suitable. B is then computed between the p/e ratio and the mean values of habitat suitability window. The p/e curve and B are then produced k (in our case 10) times, each time leaving out another validation partition, allowing the assessment of their central trend and variance (presented here as mean $\pm$ SD). Using the p/e curve, thresholds were estimated following Hirzel et al. (2006), which are the points where the curve is <1, >1 and $\gg 1$. This permits reclassification of predicted maps into meaningful habitat suitability classes, which can then be used to analyze spatial patterns.

2.5. Spatial patterns of blue-throated wrasse habitat suitability

Using the best performing model, the spatial arrangement and representation of the three habitat suitability classes (determined by p/e curve) were compared inside Discovery Bay Marine National Park with adjacent waters. PatchGrid Analyst 4 extension in ArcGIS 9.3 was used to generate six measures of landscape pattern indices. Twenty-two non-overlapping landscape analysis windows were randomly positioned in- and outside the Marine National Park. The size of the landscape analysis window was selected following recommendations by O'Neill et al. (1996), suggesting that the landscape analysis window be 2–5 times larger than the largest patch of interest. A $550\times550\,m^2$ landscape analysis window was selected because it was large enough to contain the 98th percentile of habitat suitability patches. For each landscape analysis window, interspersion and juxtaposition index (IJI), largest patch index (LPI), landscape shape index (LSI), mean patch size (MPS), mean shape index (MSI) and patch size coefficient of deviation (PSCV) were calculated (see footnotes in Table 4 for descriptions). While there are numerous landscape pattern indices available (McGarigal and Marks, 1994), these were selected based on the findings by Teixido et al. (2002), who identified them as an adequate subset of indices to describe marine landscape patterns. The differences in these indices between the Discovery Bay Marine National Park and adjacent waters were compared to assess the representativeness of the Marine National Park for blue-throated wrasse habitat suitability. A non-parametric Kruskal–Wallis test was used for comparisons as the raw and transformed data did not conform to parametric assumptions.

3. Results

3.1. Ecological-Niche Factor Analysis modeling and scale selection

A total of 83 blue-throated wrasse individuals were identified from the video analysis, as some frames included multiple individuals this equated to 61 occurrences records. To determine which variable spatial scale most influenced blue-throated wrasse habitat suitability three ENFA models were generated. The models were based on three different spatial scales (fine: $56.25\,m^2$, medium: $506.25\,m^2$, and coarse: $2756.25\,m^2$) and were constructed using the same occurrence dataset to enable direct comparison between outputs (Fig. 2). For each scale model, ENFA reduced the least correlated subset of variables (bathymetry, benthic position index, eastness, Euclidean distance to nearest reef, hue-saturation-intensity-blue, maximum curvature, northness and rugosity) to five explanatory factors (selected by comparison with the broken-stick distribution (Hirzel et al., 2002; MacArthur, 1957)). These five explanatory factors were fitted using the distance geometric mean algorithm to define blue-throated wrasse habitat suitability at each spatial scale.

Global marginality, specialization and Boyce Index values for each spatial scale investigated are presented in Table 2. Although

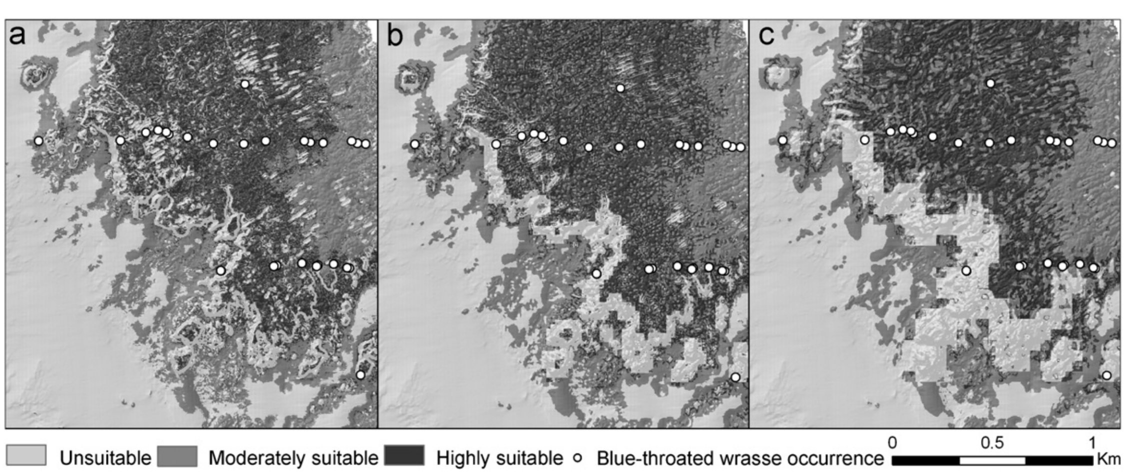

Fig. 2. Predicted blue-throated wrasse habitat suitability for the different spatial scale models and occurrences: (a) fine spatial scale model: area $56.25\,m^2$, (b) medium spatial scale model: area $506.25\,m^2$, and (c) coarse spatial scale model: area $2756.25\,m^2$. Habitat suitability models generated using the geometric mean algorithm within ENFA.

all models performed well, the Boyce Index indicated that the coarse scale model (0.80 ± 0.26) (Fig. 3) performed better than both the fine and medium scale models, 0.75 ± 0.33 and 0.60 ± 0.42, respectively. The *p/e* curves for all models showed a positive monotonic trend as suitability increased (Fig. 4). As the spatial scale increased, global marginality was found to decrease from 1.03 to 0.95, but global specialization values stayed the same (1.54). These global marginality and specialization values indicate that, irrespective of the spatial scale analyzed, blue-throated wrasse prefer regions that are different to the mean available but exhibit a relatively wide niche.

3.1.1. *Fine scale model*

The marginality factor indicated a strong relationship for areas close to reef (-0.61) and high rugosity (0.61) (Table 3). This factor also showed the importance of higher HSI-B values (0.31), shallow water (bathymetry: 0.30) and high maximum curvature (0.25). Specialization coefficients highlighted that blue-throated wrasse are restricted to regions that are shallow water (bathymetry: 0.79), low HSI-B (-0.69), east facing (eastness: 0.66), depressions (BPI: -0.59), close proximity to reef (0.55) and lower maximum curvature (-0.43). Northness at this scale did not appear to be important (Table 3).

3.1.2. *Medium scale model*

The marginality factor showed a similar trend to the fine scale model, with a strong association for areas close to reef (-0.67), whereas maximum curvature had a greater influence (0.39). High rugosity (0.39), higher HSI-B values (0.33), shallow water (bathymetry: 0.32) were also found to be important. Specialization coefficients highlighted that all eight variables were important. Blue-throated wrasse were restricted to areas that had low HSI-B (-0.92), north-west facing (eastness: -0.85, northness: 0.47), shallow water (-0.80) and high rugosity (0.24) (Table 3).

3.1.3. *Coarse scale model*

The marginality factor showed the same trend as that of the fine scale model. A strong association was evident with areas close to reef (-0.68), high rugosity (0.47), high HSI-B values (0.34), shallow water (0.33) and high maximum curvature (0.29) (Table 3). Specialization coefficients indicated that blue-throated wrasse were restricted to areas that were north-east facing (northness: 0.86, eastness: 0.78), high HSI-B (0.85), close to reef (-0.53), on top of crests (0.22) and in shallow water (0.33) (Table 3).

Table 2
Continuous Boyce Index (B, varying between –1 and 1), global marginality (M, varying generally between 0 and 1) and global specialization (S, indicating some degree of specialization when superior to 1) for the fine, medium and coarse scale models.

Scale	*B* (mean ± SD)	*M*	S
Fine	0.7 ± 0.33	1.03	1.54
Medium	0.6 ± 0.42	0.93	1.54
Coarse	0.8 ± 0.26	0.92	1.54

3.2. *Spatial patterns of blue-throated wrasse habitat suitability*

Three habitat suitability classes were predicted for the best performing ENFA model. To compare the spatial patterns in habitat suitability classes within the Discovery Bay Marine National Park with adjacent waters we applied six landscape pattern indices to the coarse scale model. Interspersion and juxtaposition index (IJI) exhibited significantly lower values in the Marine National Park compared to adjacent waters for unsuitable ($H=13.20$, df$=1$, $p<0.001$) and highly suitable ($H=10.24$, df$=1$, $p<0.001$) habitat classes indicating that they are both unevenly distributed (Table 4). Although statistically non-significant in- and outside the Marine National Park, IJI for moderately suitable habitat exhibited much greater values compared to unsuitable and highly suitable habitats, indicating a more even arrangement of patches. In contrast, the mean shape index (MSI) for unsuitable habitat was significantly larger ($H=4.88$, df$=1$, $p<0.05$) in the Marine National Park. All habitat suitability classes exhibited

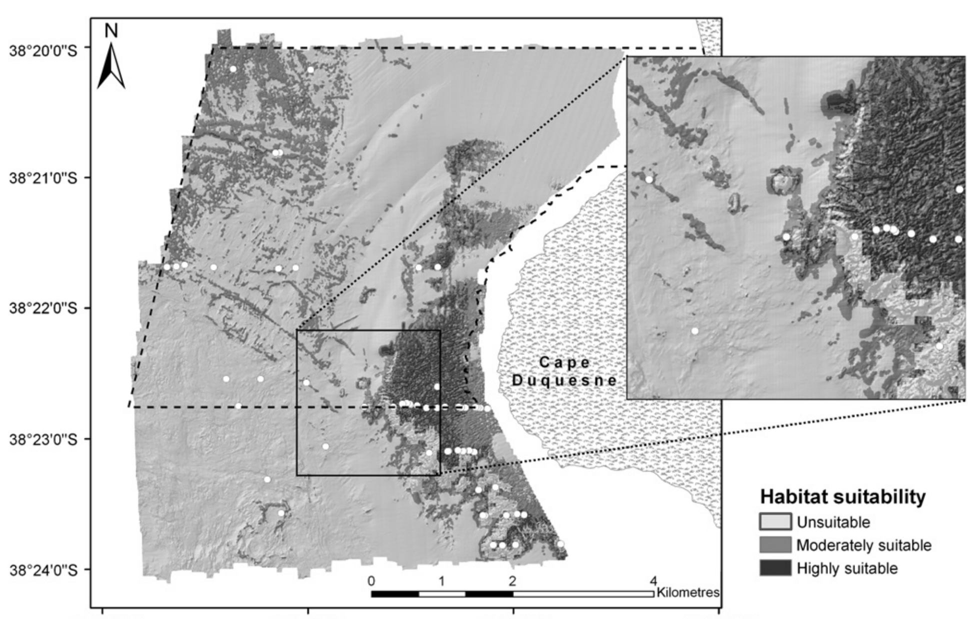

Fig. 3. Predicted habitat suitability for blue-throated wrasse over the whole study area using the coarse scale model. Inset map shows how presence cells (white dots) mainly fall within pixels with high habitat suitability. A few observations are in pixels with moderate-unsuitable habitat reflecting the fact that blue-throated wrasse may not always occur in optimal habitat as indicated by the specialization value. Heavy dashed black line delineates the Discover Bay Marine National Park boundary.

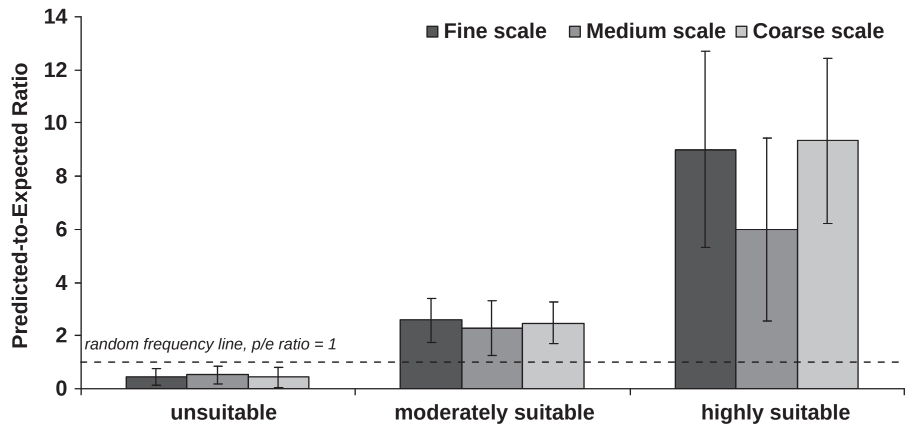

Fig. 4. Cross-validation results for habitat suitability models for blue-throated wrasse produced using the geometric mean in ENFA. Predicted-to-expected ration indicates the number of species occurrence cells encountered between cross-validation runs ($k=10$). Error bars indicate the standard deviation. Values are shown for three habitat suitability windows ranging from low habitat suitability scores (0–33) through to high habitat suitability (67–100).

Table 3
Contribution of the variables to the factors generated by ENFA used to build the coarse scale model of blue-throated wrasse habitat suitability.

Fine scale variables	**Factor 1 *M* (100%) *S* (43%)**	**Factor 2 *S* (24%)**	**Factor 3 *S* (15%)**	**Factor 4 *S* (6%)**	**Factor 5 *S* (4%)**
Distance to nearest reef	−**0.61**	**0.55**	−0.10	0.39	0.02
Rugosity	**0.61**	0.00	0.05	0.04	0.02
HSI-B	**0.31**	0.34	−**0.69**	0.41	−0.17
Bathymetry	**0.30**	**0.76**	0.36	−0.01	0.27
Maximum curvature	**0.25**	0.01	0.10	0.26	−**0.43**
Eastness	0.09	0.00	0.15	0.49	**0.66**
BPI	0.03	0.07	−**0.59**	−0.59	0.52
Northness	−0.01	−0.03	−0.04	−0.10	0.09
Medium scale variables	**Factor 1 *M* (100%) *S* (46%)**	**Factor 2 *S* (27%)**	**Factor 3 *S* (10%)**	**Factor 4 *S* (6%)**	**Factor 5 *S* (6%)**
Distance to nearest reef	−**0.67**	−0.54	−0.26	−0.27	0.17
Maximum curvature	**0.39**	−0.02	0.09	−0.07	0.01
Rugosity	**0.39**	−0.02	0.03	−0.14	**0.24**
HSI-B	**0.33**	−0.25	−**0.92**	0.15	0.07
Bathymetry	**0.32**	−**0.80**	0.26	−0.25	−0.01
BPI	−0.14	−0.01	−0.05	−0.09	**0.47**
Eastness	0.11	0.06	−0.06	−**0.85**	0.24
Northness	0.05	0.03	−0.01	0.29	**0.79**
Coarse scale variables	**Factor 1 *M* (100%) *S* (44%)**	**Factor 2 *S* (28%)**	**Factor 3 *S* (11%)**	**Factor 4 *S* (7%)**	**Factor 5 *S* (5%)**
Distance to nearest reef	−**0.68**	−**0.53**	0.12	0.44	0.22
Rugosity	**0.47**	0.04	−0.14	0.18	0.13
HSI-B	**0.34**	0.22	**0.85**	0.27	0.05
Bathymetry	**0.33**	**0.81**	−0.33	0.19	0.11
Maximum curvature	**0.29**	0.01	−0.02	0.05	0.10
BPI	−0.07	−0.01	0.03	0.04	**0.22**
Eastness	0.06	−0.05	−0.33	**0.78**	0.35
Northness	0.00	−0.09	0.14	−0.24	**0.86**

Coefficients are sorted by decreasing value of coefficients on the marginality factor (M). Specialization values for each factor are represented (in brackets) by S. Variables that make the largest contribution (< -0.2 or > 0.2) to each factor are highlighted in bold.

mean MSI values greater than one, indicating that they all exhibit noncircular patch shapes. Largest patch index (LPI) and mean patch size (MPS) showed similar trends with high values being recorded for unsuitable habitat monotonically decreasing to highly suitable habitat but were statistically non-significant between regions. Low LPI and MPS values for highly suitable habitat indicate that the largest and mean patches are smaller than other suitability classes presented. Landscape shape index (LSI) and patch size coefficient of deviation (PSCV) exhibited higher values for moderately suitable habitat compared to unsuitable and highly suitable but were not significantly different (Table 4).

4. Discussion

The geometric mean algorithm within ENFA provided a prediction of blue-throated wrasse habitat suitability. Models were based on high-resolution multi-beam echo-sounder (MBES) derived variables and towed video observations at three spatial scales. The present study confirms other findings that presence-only models can provide good predictions of habitat suitability for marine species (Dolan et al., 2008; Galparsoro et al., 2009; Praca et al., 2009; Tittensor et al., 2009). Based on our results, we will discuss four main points: First, we

Table 4
Landscape indices used to assess the spatial arrangement and configuration blue-throated wrasse habitat suitability for inside and out of Discovery Bay Marine National Park (MNP).

Landscape pattern index	Region	Suitability class	Mean ± SD
LPI	Inside MNP	Unsuitable	64.04 ± 37.32
		Moderately	23.79 ± 23.98
		Highly	11.05 ± 22.44
	Outside MNP	Unsuitable	78.73 ± 30.71
		Moderately	11.95 ± 17.78
		Highly	6.44 ± 13.13
LSI	Inside MNP	Unsuitable	3.11 ± 1.96
		Moderately	6.38 ± 3.72
		Highly	4.21 ± 4.18
	Outside MNP	Unsuitable	2.50 ± 1.76
		Moderately	4.81 ± 4.28
		Highly	4.77 ± 3.14
IJI	Inside MNP	Unsuitable	**0.48 ± 0.51****
		Moderately	42.13 ± 33.37
		Highly	**0.17 ± 0.43****
	Outside MNP	Unsuitable	**7.35 ± 12.30****
		Moderately	39.06 ± 45.04
		Highly	**17.51 ± 18.21****
MSI	Inside MNP	Unsuitable	**1.39 ± 0.32***
		Moderately	1.47 ± 0.25
		Highly	1.56 ± 0.16
	Outside MNP	Unsuitable	**1.19 ± 0.16***
		Moderately	1.42 ± 0.25
MPS	Inside MNP	Unsuitable	10.42 ± 13.57
		Moderately	0.52 ± 1.04
		Highly	0.14 ± 0.41
	Outside MNP	Unsuitable	15.03 ± 14.53
		Moderately	0.10 ± 0.08
		Highly	0.05 ± 0.07
PSCV	Inside MNP	Unsuitable	277.58 ± 330.84
		Moderately	471.87 ± 374.69
		Highly	342.56 ± 325.53
	Outside MNP	Unsuitable	226.65 ± ± 238.20
		Moderately	354.81 ± 330.58
		Highly	308.51 ± 224.32

Significant difference between the Marine National Park and adjacent region are shown in bold and denoted by *$p<0.05$. **$p<0.001$. Descriptions of indices are given in footnote. Descriptions modified from McGarigal and Marks (1994). Largest patch index (LPI) is the percentage of the landscape window comprised by the largest patch. With low values indicating the largest patch in the landscape is increasingly small. Landscape Shape Index (LSI) is the sum of the all edge segments (m) within the landscape boundary involving the corresponding patch type, divided by the square root of the total landscape area (m^2), and adjusted by a constant for square raster cell edges. The larger the LSI the more irregular the patch shape. Mean Shape Index (MSI) is the patch perimeter (m) divided by the square root of patch area (m^2) for each corresponding patch type, adjusted by a constant for a square raster cell edge, divided by the number of patches of the same type. When MSI equals one all patches of the corresponding patch type are circular. Mean patch size (MPS) is the total landscape area (m^2), divided by the total number of patches, divided by 10000 (to convert to hectares). Interspersion and juxtaposition index (IJI) is the observed interspersion (%) over the maximum possible interspersion for the given number of patch types. When IJI approaches 100% all patches are equally and maximally adjacent to all other patch types. Patch size coefficient of deviation (PSCV) is the variability in patch size relative to the mean patch size (Note, this is the population mean, not the sample mean).

address some issues surrounding the use of presence-only models on remotely sensed datasets. Second, we discuss the importance of spatial scale for predicting blue-throated wrasse habitat suitability. Third, we discuss the habitat parameters identified by the models as being important. Fourth, we discuss the spatial patterns in habitat suitability classes.

4.1. Predictive ability of models

All three variable scales yielded model performances that were comparable with other good performing ENFA models in the literature (e.g. Hirzel and Arlettaz, 2003; Wilson et al., 2007). While these models exhibit variability among cross-validation results, even the lower end of these ranges produced adequate p/e ratio values and good separation between suitability windows. This supports the idea that the ENFA technique appears to be well matched to modeling habitat requirements of marine demersal fish based on remotely sensed datasets. A presence-only modeling approach was chosen over presence/absence methods because there are difficulties in obtaining reliable absence data from remotely sensed video datasets. While we acknowledge that to attain 'perfect detection' (i.e. probability of 1) is unrealistic, obtaining 'true' absence data (when animals are actually absent) is problematic for mobile or inconspicuous species, such as demersal fishes. Kéry (2002), for example, estimated that 12–34 visits to a site are needed before assuming a 95% probability that a site is unoccupied. 'False' absence data, when animals are present but not detected, can significantly bias the generated model. This shortcoming can be avoided using presence-only methods, such as ENFA (Hirzel et al., 2002). Because of the use of presence-only data, however, such methods tend to overestimate the area of suitable habitat (Zaniewski et al., 2002). Overestimating, however, might be more preferable to underestimating their existence, particularly when considering a commercially- or ecologically important species that is likely to be targeted by management (Fielding and Bell, 1997). Indeed, presence-only methods predict the potential distribution (fundamental niche), whereas presence/absence methods reflect the present distribution (realized niche) of the species (Brotons et al., 2004; Zaniewski et al., 2002). Even though presence-only methods have limitations, they are increasingly being shown to be a useful approach for predictive habitat modeling in marine environments.

Another important factor that influences the predictive performance of these models is variable selection (Araujo and Guisan, 2006). We generated models based on seafloor variables because of availability of data (multi-beam echo-sounder data) and the known ecology of the species (strong seafloor associations) (Johnson and Gillingham, 2005). While the models performed well, the addition of other variables may further improve their predictive capabilities. Bottom shear stress, for example, has been found to have significant influence on fish community structure (Vaz et al., 2007).

4.2. Spatial scale

By comparing the three different scale models in this study, our results indicate the coarse model (2756.25 m^2) produced better suitability results compared to fine and medium. The value of 2756.25 m^2 is substantially larger than the home range estimates of 400–775 m^2 for males and 225–725 m^2 for females (Barrett, 1995). Our results, however, support the suggestion that habitat selection of space-demanding species may be dominated by variables operating at or above the home-range scale (Carroll et al., 1999).

While the coarse-scale model performed better overall, variable importance differed at the three spatial scales analyzed. Maximum curvature, for example, was found to have a stronger influence at the medium scale compared to fine and coarse scales. This is in agreement with the idea that the species respond to their environment at multiple spatial scales. Similar scale-dependence of single habitat variables has been found for reptiles (Fischer et al., 2004), eagles (Thompson and McGarigal, 2002), lobster (Wilson et al., 2007) and marine fish (Moore et al., 2009). Consequently, we recommend that variables in habitat suitability models should be included at different spatial scales so that subtle, but important, habitat preferences can be detected.

4.3. Variables selected by the models

Our results confirm that landscape-scale variables can explain blue-throated wrasse habitat preferences. They also support the idea that factors operating at the landscape scale could explain the variance of species occurrence that may not be explained by small-scale habitat preferences (Stroch, 2002).

The ENFA models indicated which variables best explained blue-throated wrasse habitat suitability. Although varying slightly over the three scale models, blue-throated wrasse showed a strong preference for regions of shallow water, close to reef, with high rugosity and maximum curvature and low HSI-B. Mature blue-throated wrasse preferably live on relatively deep and exposed reef-dominated habitats, while juveniles occur in large numbers on shallow seaweed-dominated reefs (Edgar, 2000). This general habitat preference is confirmed by the strong correlations with low values of Euclidean distance to nearest reef and bathymetry and high values of rugosity and maximum curvature in our models. As expected, we found that models predicted the largest areas of highly suitable habitat to be shallow reef areas. These regions are dominated by large stands of kelp (mainly *Ecklonia radiata*) (Ierodiaconou et al., 2007b), and perhaps reflect the habitat use of juveniles. Models also predicted smaller patches of highly suitable habitat in deeper regions at the northern end of the site, and may reflect more isolated adult populations (Fig. 3). This is only speculative as model models did not take into account different size-class fish. Given adequate data, and building similar models based on different size-class fish we may be able to detect differences in habitat uses throughout the blue-throated wrasse life history. While the towed video system utilized here is not capable of providing accurate length measurements, the incorporation of data derived from other video methods, such as stereo baited remote underwater video systems that are able to provide accurate length measurements of fishes (Harvey et al., 2003), is worthy of further investigation.

4.4. Spatial patterns of blue-throated wrasse habitat suitability

The decline of many species has been linked directly to habitat loss and fragmentation (Fahrig, 2003). Conservation strategies now frequently consider not only the amounts of habitat that must be retained, but also the spatial configurations of habitat across landscapes of concern (O'Neill et al., 1996; Pulliam et al., 1992). By generating spatially continuous models of habitat suitability and applying a suite of landscape pattern indices, we are able to provide management agencies with accurate information that not only indicates where habitat suitability patches are located, but also an indication of size, variability, isolation, juxtaposition, spatial arrangement and boundary characteristics (McGarigal and Marks, 1994). We found that there were few significant differences in spatial patterns of habitat suitability classes between the Marine National Park and surrounding area. We observed that unsuitable patches exhibited more complex shapes inside the Marine National Park. Furthermore, both unsuitable and highly suitable habitat classes were more unevenly distributed inside the Marine National Park. It is not surprising that we only observed a few differences in the spatial characteristics in habitat suitability classes between the two regions. Recent habitat mapping studies along the Victorian coastline have revealed complex, spatially heterogeneous reef systems that support a diversity of benthic habitats (Holmes et al., 2008; Ierodiaconou et al., this issue; Rattray et al., 2009). Intuitively, with blue-throated wrasse showing such strong associations with seafloor structure, it is likely that the adjacent seafloor regions exhibiting similar heterogeneous spatial patterns reflect this in terms of habitat suitability.

5. Conclusions

The present research highlights the benefits of having spatially continuous layers of environmental data rather than the categorical or linear descriptors relied on by earlier studies (Babcock et al., 1999; Friedlander and Parrish, 1998; Westera et al., 2003). By providing spatially continuous coverage across an entire site we are able to predict habitat suitability based on video occurrence records and variables derived from hydroacoustics over large regions of seafloor. Through these models we were able to identify the variables and spatial scale that most influence blue-throated wrasse habitat suitability. Furthermore, we can begin to quantify the spatial arrangement and representation of habitat suitability to provide marine managers with a level of information that has historically been limited to coarse spatial resolutions. Practitioners should remember, however, that these models predict a species potential habitat suitability, or distribution, and should not replace but compliment empirical research.

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