

Spatial prediction of demersal fish distributions: enhancing our understanding of species–environment relationships

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We used species distribution modelling to identify key environmental variables influencing the spatial distribution of demersal fish and to assess the potential of these species–environment relationships to predict fish distributions accurately. In the past, predictive modelling of fish distributions has been limited, because detailed habitat maps of deeper water (>10 m) have not been available. However, recent advances in mapping deeper marine environments using hydroacoustic surveys have redressed this limitation. At Cape Howe Marine National Park in southeastern Australia, previously modelled benthic habitats based on hydroacoustic and towed video data were used to investigate the spatial ecology of demersal fish. To establish the influence of environmental variables on the distributions of this important group of marine fish, classification trees (CTs) and generalized additive models (GAMs) were developed for four demersal fish species. Contrasting advantages were observed between the two approaches. CTs provided greater explained variation for three of the four species and revealed a better ability to model species distributions with complex environmental interactions. However, the predictive accuracy of the GAMs was greater for three of the four species. Both these modelling techniques provided a detailed understanding of demersal fish distributions and landscape linkages and an accurate method for predicting species distributions across unsampled locations where continuous spatial benthic data are available. Information of this nature will permit more-targeted fisheries management and more-effective planning and monitoring of marine protected areas.

Keywords: classification trees, generalized additive models, spatial ecology, species distribution models.

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Introduction

Species distribution modelling is an important, rapidly developing area of ecological research (Guisan and Zimmermann, 2000; Austin, 2002, 2007; Guisan *et al.*, 2005). It not only provides a better understanding of species–environment relationships, but also allows the prediction of a species' distribution across unsampled locations. In this research, species distribution modelling was employed to provide detailed information on the spatial ecology of a key group of marine species, demersal fish, within one of the most pristine and remote marine national parks (MNPs) in Victoria, Australia. Cape Howe MNP, representative of the Twofold Shelf Bioregion, is one of the least well researched MNPs in Australia (Plummer *et al.*, 2003). With very little known about the system, species distribution models offer detailed baseline information on the spatial ecology of a species that can be incorporated into species management strategies to permit more effective monitoring and protection of individual species and communities (Maravelias, 1999; Maravelias *et al.*, 2000).

Two species distribution modelling approaches were employed; classification trees (CTs) and generalized additive models (GAMs). CTs and GAMs were compared for their ability to define key species–environment relationships and to predict species distributions across unsampled locations accurately. These statistical

approaches were chosen because they are both well suited to exploring and modelling complex ecological data (Breiman *et al.*, 1983; Chambers and Hastie, 1993; Austin, 2002).

The research, which extends detailed marine species distribution modelling, was made possible by the recent availability of detailed habitat maps (1:25 000), derived from hydroacoustic surveys of deeper marine waters (10–100 m), and of very accurate predicted habitat mapping techniques. At Cape Howe MNP, high-resolution hydroacoustic data were collected by Fugro Pty Ltd in 2006 as part of a collaboration between Parks Victoria and the Coastal and Estuarine Waterway Cooperative Research Centre. Holmes *et al.* (2008) linked benthic information from towed videos with these high-resolution bathymetry (1:25 000) data using classification and regression tree models to develop predictive habitat models for each of the major substratum and sessile benthic communities present. The models were then used to develop complete predicted maps of site benthos (Holmes *et al.*, 2007, 2008). Having high resolution, spatially explicit, continuous data is rare in marine environments, even more so in deeper marine environments. However, it is this detailed environmental information, in conjunction with more flexible species distribution modelling approaches, that has provided comprehensive understanding of the spatial ecology of demersal fish.

The aims of our research were to use species distribution modelling to identify key environmental variables from the predicted habitat maps produced by Holmes *et al.* (2007, 2008) that may influence the spatial distribution of demersal fish and to use the species–environment relationships defined to predict fish distributions accurately. Species distribution models were developed for four demersal fish species recorded at Cape Howe. The models were produced at two scales of analysis to examine the exact nature and scale of the species' relationships with measured environmental variables. Our research explored the extent to which the environmental variables measured have a significant influence on demersal fish distributions and whether fish distributions can be predicted accurately across unsampled locations, based on the species–environment relationships defined.

Material and methods

The research was conducted within Cape Howe MNP located on the easternmost point of the Victorian coastline in southeastern Australia. Covering an area of 4050 ha and extending offshore to 3 nautical miles (Figure 1), Cape Howe MNP is characterized by granite outcrops and the intermixing of upwelled cold water with the warmer waters of the East Australian Current (Plummer *et al.*, 2003). Floral and faunal assemblages include eastern temperate, southern temperate, and cosmopolitan species (Hutchins and Swainston, 2002; Plummer *et al.*, 2003).

Fish sampling

The fish assemblage was sampled using stereo-Baited Remote Underwater Video Systems (stereo-BRUVS). This technique was implemented to provide a consistent and comparable, non-extractive method for estimating demersal fish diversity. The video systems consisted of a pair of Sony HC15 digital camcorders within waterproof housings. Bait consisted of ~800 g of crushed pilchard, *Sardinops sagax*, for each deployment. Sampling sites were separated by a minimum of 500 m on a given day to preclude the overlap of bait plumes and to reduce the likelihood of measuring the same fish in adjacent samples (Harvey *et al.*, 2007). The stereo-BRUVS were set between 08:00 and 17:00 to minimize the effects of diurnal changes in fish behaviour (Willis *et al.*, 2006) and retrieved after recording at each station for 1 h. As the available light was extremely low, the stereo-BRUVS were set to record on night shot at some of the deeper sites, with additional

light being provided by two Pelican SabreLite dive torches with diffusers. For a detailed description, comparative analysis, and review of this method, the reader is referred to Harvey and Shortis (1996), Harvey *et al.* (2001a, b, 2002), Cappo *et al.* (2003, 2004), and Watson *et al.* (2005).

Demersal fish were sampled using both systematic random and stratified random sampling. Sample points were allocated utilizing the bathymetry and predicted habitat maps available for the park (Holmes *et al.*, 2007) and defined in Cartesian coordinates (spatially explicit). This sampling strategy was chosen to ensure good spatial coverage and adequate representation of predicted habitat types and to ensure that the data were robust for modelling. Demersal fish were sampled from October to December 2006, with a total of 247 1-h stereo-BRUVS drops collected (Figure 2). Species distribution models were developed for four of the species sampled (Table 1). Species chosen to be modelled were recorded at a minimum of 15 sites and represent a diversity of demersal fish prevalence, life history, size, and mobility.

Environmental variables

Detailed habitat maps (1:25 000) were available for each of the major substratum and sessile benthic communities present. Broad-scale environmental variables mapped included reef, sediment, macroalgae, and sessile invertebrates. Fine-scale environmental variables provided a more detailed breakdown of the major substratum and benthic communities, namely solid reef, boulders, broken reef, gravel, sand, caulerpa, sponges, seahips, ascidians, and *Tethya* spp. Derived geophysical data from the habitat mapping were also used to reveal textural differences, or topographic complexity, across the seafloor. These derived datasets were produced by applying algorithms (detailed in Table 2) to the bathymetry data, using a moving window kernel of 12.5 m (fine scale) or 25 m (broad scale) radius. These environmental variables were obtained for each of the 247 stereo-BRUVS drops by intersecting the sample locations with each of the environmental layers within ArcGIS.

Model formulation and evaluation

CTs and GAMs were developed in S-Plus® 6.2 for Windows, Academic Site-Edition (Insightful Corporation). Separate models were developed for each of the four demersal fish species (Table 1) at two scales of investigation, using the broad- and

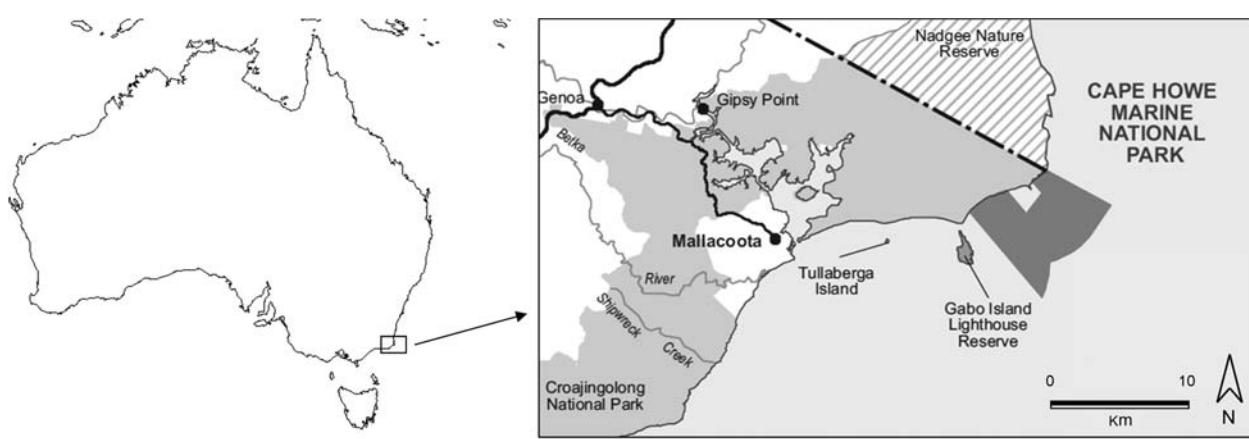


Figure 1. Location of the study area, Cape Howe MNP, on the east coast of Victoria, Australia.

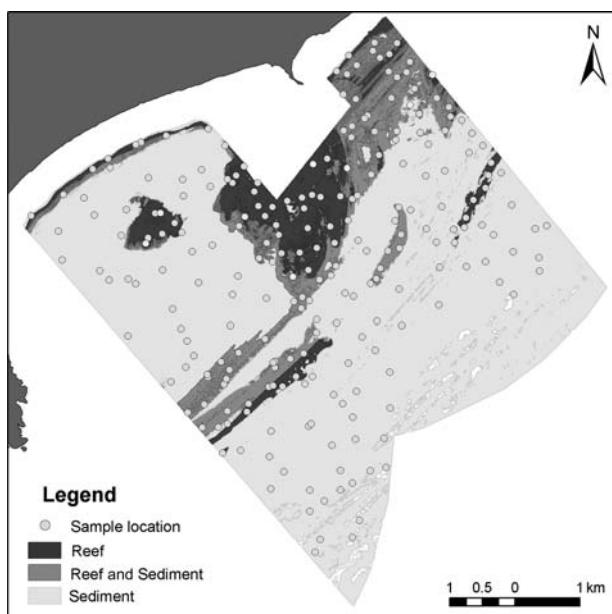


Figure 2. Predicted substratum map of Cape Howe MNP (Holmes *et al.*, 2007) displaying all 247 1-h stereo-BRUVS samples used to survey demersal fish occurrence.

Table 1. Fish species modelled and their prevalence (the proportion of sites at which they were recorded).

Family	Species	Common name	Prevalence
Labridae	<i>Achoerodus viridis</i>	Eastern blue grouper	0.06
Muraenidae	<i>Gymnothorax prasinus</i>	Green moray	0.20
Platycephalidae	<i>Platycephalus caeruleopunctatus</i>	Eastern blue-spotted flathead	0.31
Scyliorhinidae	<i>Cephaloscyllium laticeps</i>	Draughtboard shark	0.55

fine-scale habitat data and geophysical data (Table 2). Models were developed using 75% of the data, 25% being withheld from model development for model evaluation. CTs were developed using the rpart routine (Therneau and Atkinson, 1997). Tree size was selected using tenfold cross-validation to establish the model with the lowest estimated error. GAMs were developed using the GRASP (generalized regression analysis and spatial prediction) routine developed by Lehmann *et al.* (1999, 2002). The GAMs were based on a backward, stepwise selection using the Bayesian information criterion, and fivefold cross-validation to determine the most parsimonious model.

To establish the amount of variance in the species distributions explained by the models, the adjusted deviance ($\text{Adj}D^2$) was calculated for each model (Table 3) and for each contributing environmental variable (Table 4). This measure is used to establish the deviance accounted for by the model (Weisberg, 1980). A perfect model is one with no residual deviance and a D^2 of 1 (Weisberg, 1980; Guisan and Zimmermann, 2000). The $\text{Adj}D^2$ value was chosen because it accounts for differences in the number of observations and parameters used in the models (Guisan and Zimmermann, 2000). Although valuable in examining

Table 2. Geophysical data obtained from Holmes *et al.* (2007, 2008).

Geophysical parameter	Description
Depth	Elevation relative to the Australian Height Datum (m)
Aspect	Azimuthal direction of steepest slope
Curvature	Combined index of profile curvature and plan curvature
Slope	First derivative of elevation: average change in elevation/distance
Range	A measure of local relief: maximum minus the minimum elevation in a local neighbourhood of 12.5 and 25 m kernel radius
Profile curvature	Second derivative of elevation: concavity/convexity parallel to the slope
Plan curvature	Second derivative of elevation: concavity/convexity perpendicular to the slope
Hypsometric index	Indicator of whether a cell is a high or a low point within the local neighbourhood of 12.5 and 25 m kernel radius
Rugosity	Surface area of the local neighbourhood (eight neighbouring pixels)

species–environment relationships, however, $\text{Adj}D^2$ is not an unbiased and independent method of comparing approaches (Franklin, 1998; Vayssières *et al.*, 2000). Instead, models were compared based on their predictive accuracy or their ability to classify new cases correctly.

Model predictive accuracy was evaluated using 25% blind validation and assessing the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot, model sensitivity (percentage of correctly predicted presences), and specificity (percentage of correctly predicted absences) using the P_{fair} threshold (Fielding and Bell, 1997; Austin, 2007; Lobo *et al.*, 2007). AUC assesses a model's ability to discriminate between predicted presence and absence. An AUC value of 1.0 indicates that the model can discriminate perfectly between presence and absence, whereas a value <0.6 indicates that the model has no discriminatory power or that discrimination is by chance alone. For this analysis, AUC values >0.9 were interpreted as excellent, 0.8–0.9 as good, 0.7–0.8 as fair, 0.6–0.7 as poor, and <0.6 as having no discrimination (Araujo *et al.*, 2005). A bootstrap method was also employed to measure the significance of the discriminatory power of the models.

Results

Species distribution modelling was successful in defining key species–environment relationships. It was also established that the species–environment relationships defined can be used to predict fish distributions across unsampled locations accurately.

Explained deviance

Of the four species modelled, three of the CTs and one of the GAMs explained $>50\%$ of the total deviance ($\text{Adj}D^2$) in the species distribution (Table 3). The species models providing the greatest deviance explained were *Achoerodus viridis* (blue grouper) and *Cephaloscyllium laticeps* (draughtboard shark). *Achoerodus viridis* had the highest $\text{Adj}D^2$, with 79.6% explained by the broad-scale GAM, and *C. laticeps* had 63.1% of its deviance attributed to the broad-scale CT. The broad-scale variables

Table 3. Discriminatory power of the statistical models, CTs, and GAMs, in relating species presence/absence to measured environmental variables.

Species	Model	AdjD ² (%)	AUC	Sensitivity	Specificity
<i>Achoerodus viridis</i>	CT _F	74.0	0.9717***	100.0	96.2
	GAM _B	79.6	0.8899**	83.3	83.0
<i>Gymnothorax prasinus</i>	CT _B	43.7	0.8775***	100.0	66.7
	GAM _B	43.0	0.9191**	87.5	86.3
<i>Platycephalus caeruleopunctatus</i>	CT _B	58.6	0.8020	63.2	80.0
	GAM _B	29.7	0.8908**	89.5	82.5
<i>Cephaloscyllium laticeps</i>	CT _B	63.1	0.7879	72.4	73.3
	GAM _B	23.1	0.8305*	72.4	73.3

The adjusted D² (AdjD²) reflects the percentage deviance accounted for by each model. Fish species model evaluation used 25% of the dataset withheld from model development. Discriminatory power was based on the AUC of the ROC plot, and model sensitivity and specificity. The most accurate model, either fine scale (subscript F) or broad scale (subscript B), is displayed for each species and for each modelling approach. AUC < 0.5, no discrimination; 0.6 < AUC < 0.7, poor discrimination; 0.7 < AUC < 0.8, fair discrimination; 0.8 < AUC < 0.9, good discrimination; AUC > 0.9, excellent discrimination. *p < 0.05, **p < 0.01, ***p < 0.0001, all based on the results of bootstrapping.

Table 4. Summary of relative contributions (%) of predictor variables for the most accurate CTs and GAMs produced for each of the four demersal fish species investigated at the fine (subscript F) and broad (subscript B) scales.

Species	Model	Predictor	Relative contribution (%)	AdjD ² (%)
<i>Achoerodus viridis</i>	CT _F	Solid (≥ 0.5)	54.1	74.0
		Boulders (≥ 0.5)	19.9	
<i>Gymnothorax prasinus</i>	GAM _B	Reef	79.6	79.6
		Reef (≥ 0.5)	5.7	43.7
<i>Platycephalus caeruleopunctatus</i>	CT _B	Range (≥ 0.79)	38.0	
		Hypsometric index	34.9	42.9
<i>Cephaloscyllium laticeps</i>	GAM _B	Reef	8.0	
		Algae (≥ 0.5)	17.3	58.6
		Depth (≤ 67.7)	4.8	
		Slope (< 0.72)	3.1	
		Range (< 0.80)	24.3	
		Hypsometric index (< 0.02)	9.2	
		Depth	20.6	29.7
		Sediments	5.6	
		Invertebrates	3.5	
		Depth (< 58.6)	43.3	63.1
	CT _B	Profile curvature (less than -0.75)	2.6	
		Depth (> 16.4)	6.0	
	GAM _B	Hypsometric index (≥ 0.03)	2.6	
		Range (≤ 0.40)	2.6	
		Rugosity (≥ 1.00)	6.0	
		Depth	23.1	23.1

explained a greater portion of deviance for all but one of the eight models, with the distribution of *A. viridis* better explained by the CTs, at the fine scale.

Model evaluation

The predictive performance of the eight models developed for the four species, based on the AUC, was excellent for two models (AUC > 0.9), good for five models (AUC 0.8–0.9), and fair for one model (AUC 0.7–0.8; Table 3). These values were unaffected by prevalence, with examples of good predictive performance for species with high prevalence, *C. laticeps* and *Platycephalus caeruleopunctatus* (eastern blue-spotted flathead), and low prevalence, *A. viridis* and *Gymnothorax prasinus* (green moray). The bootstrap procedure revealed six of the eight models to have a discriminatory

power significantly better than by chance alone. Sensitivity (percentage of correctly predicted presences) ranged from 63.2 to 100%, and specificity (percentage of correctly predicted absences) from 66.7 to 96.2%.

Species–environment relationships

Species–environment relationships for each of the four species modelled were explored by investigating the relative contribution (percentage of deviance explained) of each variable to each model (Table 4). The distributions of the four species were better represented by the broad-scale variables, with only one model, the CT for *A. viridis*, providing a better fit with the fine-scale environmental variables. The distribution of *A. viridis* was highly correlated with reef, with 79.6% of the deviance in its distribution

attributed to reef by the broad-scale GAM, and 74% attributed to solid reef and boulders by the fine-scale CT. *Gymnothorax prasinus* also responded positively to reef and broad-scale topographic complexity. The CT found range, a measure of local relief, to explain 38% of this species' distribution, and reef to explain 5.7%. The GAM for that species found a slightly different measure of broad-scale topographic complexity. The hypsometric index (an indicator of whether a cell is a high or low point within the local neighbourhood) accounted for 34.9% of its distribution, and reef for 8%.

The distribution of *P. caeruleopunctatus* was better explained by the CT, with 58.6% of its distribution explained by this model, as opposed to just 29.7% explained by the GAM. The GAM provided a slightly more robust model, though. The CT was also acceptable, however (Table 3). The CT was better able to describe the complex distribution of the species, which included being present in relatively flat, unvegetated areas, while also being present in relatively flat, shallow, vegetated areas. *Cephaloscyllium laticeps* was also better described by the CT. Again, that modelling approach was able to describe the complex interaction of that species' distribution with depth and broad-scale measures of topographic complexity. The species was mainly affiliated with depths of 16.4 m (6.0%) and 58.6 m (43.3%) and with some broad-scale topographic complexity: hypsometric index (2.6%), range (2.6%), and rugosity, or surface area (6.0%).

Predicting species distributions

Our research found the CTs consistently to explain more of the deviance in the species distributions. Although the predictive performance of the CTs was slightly less than that of the GAMs, they remained adequate to produce robust predicted models. CTs are readily transferred into the GIS software where predictions across unsampled locations are computationally efficient. Therefore, the CTs were deemed best for that part of the analysis.

To aid interpretation of the predicted distributions of the four species, the reader is referred to the predicted substratum map for Cape Howe MNP shown in Figure 2. That map details the distribution of the three broad substratum categories, reef, reef and sediment, and sediment. When comparing the predicted distribution of *A. viridis* (Figure 3a) with the substratum map (Figure 2), the strong link this species has with the areas of continuous reef is clear. The distribution of *G. prasinus*, the other strongly reef-affiliated species, was predominantly defined by topographic complexity. Absences in that species' predicted distribution were observed in the middle, flatter areas of reef (Figure 3b). *Platycephalus caeruleopunctatus*, a sand-affiliated species (Hutchins and Swainston, 2002), was predicted to be present in depths of <67.7 m, over sediment areas and some reef-and-sediment areas (Figure 3c). *Cephaloscyllium laticeps* was predicted to be present across all substrata in depths of <59 m (Figure 3d), but also predicted to be present out to the deepest regions of the park (which is up to 110 m deep).

Discussion

Establishing robust methods to understand and define marine species distributions is critical to good fisheries management and marine protected area planning and monitoring. We have presented two such methods. Contrasting advantages and disadvantages were represented by the two modelling approaches. The CTs provided greater deviance explained in three of the four species distributions. The CTs were also better able to represent interactions between environmental variables in a species'

response. In contrast, GAMs provided better predictive accuracy for three of the four species modelled. However, just one method was employed to define species distributions: as, in general, the CTs provided greater deviance explained and their predictive performance was still considered adequate, the CTs were employed to define the distributions of the four species.

Our research has also extended marine species distribution modelling, clearly demonstrating the additional information on a species' spatial ecology that may be obtained from detailed predicted habitat maps (1:25 000) and from continuous derived geophysical data. Strong associations were detected between species distributions and the environmental variables measured. For three of the four species modelled, >50% of the variation in their distributions could be explained by the environmental variables alone, confirming their importance in dictating species distributions. The remaining 26.0–56.3% of unexplained deviance for the four species may be attributed to unmeasured environmental variables found important in influencing fish distributions, such as temperature, exposure to currents or wave action, light, salinity, and dissolved oxygen (Ebeling *et al.*, 1980; Martini *et al.*, 1997; Babcock *et al.*, 1999; García-Charton and Pérez-Ruzafa, 2001; Rueda, 2001; Fulton and Bellwood, 2004). Other causes of unexplained deviance may be attributed to unaccounted for ecological characteristics, life history, and behavioural traits such as diet, size, mobility, predation, and competition (Choat and Ayling, 1987; Lincoln Smith, 1989; McCormick, 1994; Babcock *et al.*, 1999; García-Charton and Pérez-Ruzafa, 2001; Curley *et al.*, 2002; Willis and Anderson, 2003; Willis *et al.*, 2003). This outcome requires further research, with additional explanation likely to come from a combination of additional environmental and ecological variables.

Environmental variables that were important in describing species distributions were the continuous measures of depth, substratum, and broad-scale measures of topographic complexity. That these environmental measures are important in themselves is not surprising, because many studies have demonstrated their influence on fish assemblage structure and spatial distribution (Luckhurst and Luckhurst, 1978; Choat and Ayling, 1987; McCormick and Choat, 1987; Friedlander and Parrish, 1998; Preide and Merrett, 1998; Rueda, 2001; Harman *et al.*, 2003; Jones *et al.*, 2003; Anderson and Millar, 2004). For example, they reflect important physiological, environmental, or ecological limitations, such as the availability of refuge, territory, and food, or the existence of competition or predation (Ebeling *et al.*, 1980; Choat and Ayling, 1987; McCormick, 1994; Friedlander and Parrish, 1998; García-Charton and Pérez-Ruzafa, 2001; Anderson and Millar, 2004). What is demonstrated by our research, however, is the value of having continuous layers of environmental data rather than the categorical or linear descriptors of habitat or relief relied on by earlier studies (Ebeling *et al.*, 1980; Cole, 1994; McCormick, 1994; Friedlander and Parrish, 1998; Moser *et al.*, 1998; Babcock *et al.*, 1999; Willis, 2001; Curley *et al.*, 2002; Westera *et al.*, 2003; Willis and Anderson, 2003). These continuous layers of bathymetric, biological, and terrain data clearly have the additional advantage of providing spatially explicit, three-dimensional, environmental measures. The measures reflect subtle, but important, differences in biological and topographic complexity and have been demonstrated as important in structuring species distributions.

Additional insight into demersal fish distributions and spatial ecology provided by this analysis includes greater understanding

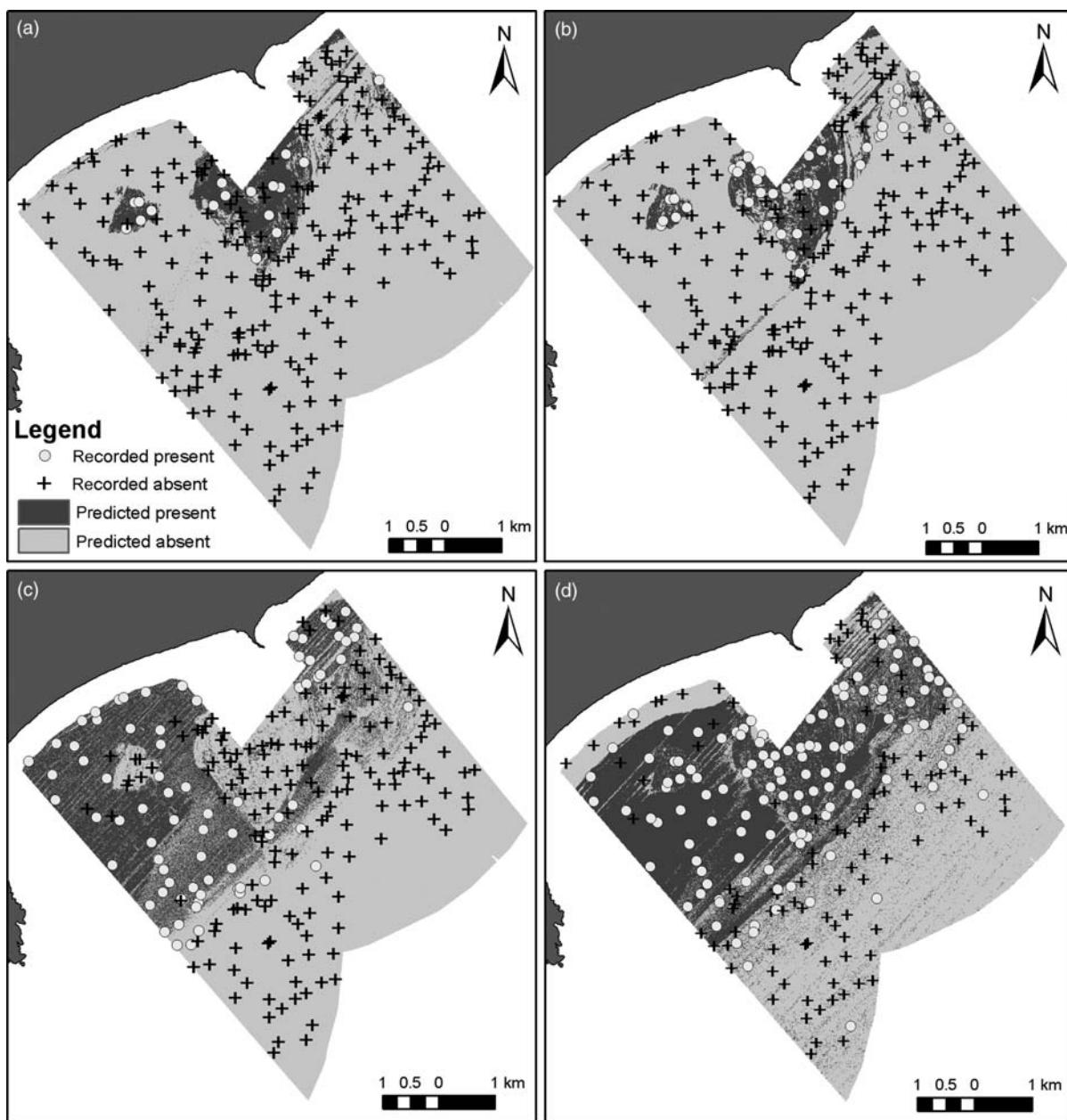


Figure 3. Predicted distributions defined by the CTs for (a) *Achoerodus viridis*, (b) *Gymnothorax prasinus*, (c) *Platycephalus caeruleopunctatus*, and (d) *Cephaloscyllium laticeps*.

of the two reef-affiliated species. Species distribution models for *A. viridis* and *G. prasinus* highlighted an important difference in the ecological requirement of the two. *Achoerodus viridis*, a benthic carnivore consuming a variety of prey, is the largest wrasse of the southeast coast, growing up to a metre long (Gillanders, 1995; Hutchins and Swainston, 2002). The CT defined its distribution by the presence of solid reef and boulders. In contrast, the distribution of *G. prasinus* was correlated with reef and the hypsometric index. *Achoerodus prasinus* is a nocturnally active opportunistic predator that feeds mainly on fish and crabs and is reliant on crevices and holes for refuge during the day (Russell, 1983; Yukihira *et al.*, 1994). Examining the predicted distributions of these two species, *G. prasinus* was predicted to be present in areas of reef with high topographic complexity where

many crevices and holes are available for it to find refuge during the day. *Achoerodus viridis*, however, had a less patchy distribution, which included most of the predicted reef substratum.

Models of the other two species also provided additional insights into their spatial ecology. *Platycephalus caeruleopunctatus* grows to 90 cm, is a benthic ambush predator of crustaceans and fish, and is affiliated with sandy, less-vegetated habitats (Coleman and Mobley, 1984; Humphries *et al.*, 1992; Edgar and Shaw, 1995; Hutchins and Swainston, 2002). Its distribution was found by the CT to be correlated with flat, unvegetated areas, and also with relatively flat, shallow, vegetated areas. Some of its predicted distribution was over reef. Predicting a sand-affiliated species to be present over reef was unexpected. Closer examination revealed, however, that these areas are a mixture of reef and sand-inundated reef,

with sparse macroalgae (including caulerpa and turf algae), more closely matching the species' known distribution and so explaining its unexpected predicted distribution over reef in the northeast corner of the park. This highlights the ability of CTs to detail two important, but distinct, areas inhabited by this species. *Cephaloscyllium laticeps* had the broadest predicted distribution of the four species investigated. It grows to a maximum length of 1.5 m and is a common predatory species of the southeast coast, recorded as preferring deeper offshore areas (Hutchins and Swainston, 2002; Awruch *et al.*, 2008). Here, we found it to be affiliated mainly with depths of 16–59 m, with some broad-scale topographic complexity, and it was predicted to be present over all substrata shallower than 59 m. In addition, *C. laticeps* was predicted to be present down to the deepest waters of the park (to 110 m). This species is significantly larger and more mobile than the other three, so can be expected to range over a greater area and in turn over a greater range of substratum and habitat types. Again, the CT modelling approach was more effective than the GAM at describing its complex distribution interaction with depth and broad-scale measures of topographic complexity.

To conclude, our findings have demonstrated clearly that more-detailed, continuous, spatially explicit environmental data result in better understanding of the factors that determine the distributions of individual species. The two modelling techniques we used provided a comprehensive understanding of demersal fish distributions and landscape linkages, and also provided an accurate method of predicting species distributions across unsampled locations where continuous spatial benthic maps were available. Having accurate information on the factors driving the spatial distribution of demersal fish at Cape Howe MNP is important for effectively monitoring and managing this key group of marine organisms. The predicted distributions provide a solid baseline against which future changes in species distributions, management practices, and the effects of climate change may be monitored and compared. Information of this nature will facilitate more-effective planning and monitoring of this unique, biologically important, but relatively unknown marine protected area.

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