Integrating distribution models and habitat classification maps into Marine Protected Area planning

Renata Ferrari^{1,2}, Hamish Malcolm³, Joe Neilson⁵, Vanessa Lucieer⁴, Alan Jordan⁶, Tim Ingleton⁷, Will Figuera¹, Nicola Johnstone⁸, Nicole Hill⁴

¹ University of Sydney, School of Life and Environmental Sciences, Edgeworth David Bld, Science Road, NSW 2006, Australia. Renata.ferrari@sydney.edu.au will.figueira@sydney.edu.au

² Australian Institute of Marine Sciences, PMB No. 3, Townsville, Queensland 4810, Australia

³ Fisheries Research, NSW Department of Primary Industries, 32 Marina Drive Coffs Harbour NSW 2450, Australia. Hamish.malcolm@dpi.nsw.gov.au

⁴ Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, TAS 7001, Australia. Nicole.hill@utas.edu.au vanessa.lucieer@utas.edu.au

⁵ Marine Planning, NSW Department of Primary Industries, 84 Crown St, Wollongong, NSW 2520, Australia. joe.neilson@dpi.nsw.gov.au

⁶ Fisheries Research, NSW Department of Primary Industries, Port Stephen Fisheries Institute, Locked Bag 1, Nelson Bay, NSW 2315, Australia. alan.jordan@dpi.nsw.gov.au

⁷ NSW Office of Environment and Heritage, 59-61 Goulburn St, Sydney, NSW 2000, Australia. Tim.Ingleton@environment.nsw.gov.au

⁸ Marine Strategy, NSW Department of Primary Industries, 32 Marina Drive Coffs Harbour NSW 2450, Australia. nicola.johnstone@dpi.nsw.gov.au

Short running title: *Maps and models for conservation planning*

Keywords: ecological and functional surrogates, endemic and threatened species, fish, habitat classification scheme, habitat maps, stakeholders, local knowledge and expertise, marine protected areas, Marxan, conservation prioritization, spatial management, conservation planning, data-deficient ecosystems.

Type of article: *Letter*

Number of words (abstract and manuscript): 5215

Number of references: 58

Number of figures: 6

Number of tables: 4

Corresponding author: Australian Institute of Marine Sciences, PMB No. 3, Townsville, Queensland 4810, Australia. Mobile: +(61) 425 676 050 R.Ferrari@aims.gov.au or renata.ferrari@gmail.com

Abstract

Effective conservation planning requires biotic data across an entire region. In data-poor ecosystems conservation planning is informed by using environmental surrogates (*e.g.* temperature) predominantly in two ways: to develop habitat classification schemes (1) or develop species distribution models (2). We test the utility of both approaches for conservation planning of marine ecosystems, and rank environmental surrogates, such as depth and distance from shore, according to their power to predict the distribution and abundance of biotic species. Specifically, we compared a habitat classification scheme; based on coarse levels of habitat types derived from depth and distance from shore; against species distribution models, which predict fish abundance and prevalence as a function of environmental surrogates (depth, distance from shore, latitude, reef area, zoning, and several metrics of habitat structural complexity). We consistently set conservation target levels to 21% of each conservation feature, following global standards and a sensitivity analyses. Thus when running scenarios to protect fish species we aimed to protect at least 21% of each species, and when running scenarios of habitat classes, we aimed to protect at least 21% of each habitat class. We found that when aiming to protect 21% of the chosen conservation targets, distribution models protected 21% of the predicted abundance/occurrence of all modelled species and functional groups, but did not protect most habitats. Contrastingly, using a habitat classification scheme protected 21% of all habitat types and 34% of all species and functional groups, but required protecting three times more area. Thus, using only distribution models as targets in data-poor ecosystems could be a risky conservation planning strategy. Ultimately the best conservation outcomes were achieved by incorporating local knowledge to synthesize the conservation outcomes of both scenarios.

Introduction

Systematic conservation planning approaches, such as Marxan (Watts and Possingham 2013), have been used extensively as a decision support tool for spatial planning over the past 30 years to improve conservation benefits and outcomes (see full explanation of systematic conservation approaches in Margules & Pressey 2000; Pressey & Cowling 2001) and inform adaptive management (McCook *et al.* 2010; Levin *et al.* 2013). Modern conservation planning uses systematic approaches to increase the probability of achieving conservation objectives; which improve integration of biotic, social and environmental data (Groves and Game 2016), especially compared to *ad-hoc* or even “expert” selection approaches (Cowling *et al.* 2003; Stewart, Noyce & Possingham 2003; Leslie 2005). Spatial systematic conservation planning approaches objectively select areas most likely to maximise representation of conservation features (*e.g.* biodiversity), avoiding biases where datasets and areas are large (Margules & Pressey 2000; Ferrier 2002; Sarker *et al.* 2006). Additionally, systematic conservation planning can be used to maximise conservation benefits whilst reducing socioeconomic opportunity costs, such as restricting areas from fisheries (Klein *et al.* 2008a; Klein *et al.* 2008b).

Although lagging behind terrestrial conservation efforts, systematic conservation planning approaches have increasingly been used in planning Marine Protected Areas (MPAs) over the past 15 years (Leslie *et al.* 2003; Fernandes *et al.* 2005; Cook & Auster 2006; Klein *et al.* 2015). However, there are strong constraints (*e.g.* restricted time underwater, difficulty for remote sensing methods to penetrate the water surface, depth limits in SCUBA diving restrict most studies to shallow reefs)_associated with obtaining biological information at scales suitable for undertaking systematic planning in the

marine environment (Stevens & Connolly 2004). Systematic planning is most effective when data are available across the entire planning area, which often does not exist in marine ecosystems (Ban 2009; Elith and Leathwick 2009). This can constrain effective systematic conservation planning due to missing data within the majority of the planning area. For instance, where there are few spatial data points, an algorithm will select those planning units where data is available, potentially misrepresenting planning units without data. Where biotic data are sparsely available their spatial distributions can be inferred by establishing their relationship with environmental data (Stevens and Connolly 2004; Johnston et al. 2015). This includes the use of habitat classification schemes where environmental surrogates, such as temperature or depth, represent biotic patterns (Sarker *et al.* 2005; Moore, Van Niel & Harvey 2011) and modelling approaches that enable spatial predictions of individual species distributions based on their relationships with environmental variables (Guisan et al. 2013).

The differential effort required to develop robust classification schemes and distribution models has led to many studies comparing these approaches for systematic conservation planning. In terrestrial ecosystems, distribution models can improve conservation planning outcomes compared to classification schemes (Guisan et al. 2013). Yet, developing robust distribution models that are adequate for conservation planning requires statistical expertise that may not always be accessible to managers (Elith and Graham 2009). Designing classification schemes that represent biotic distributions is more feasible because certain environmental surrogates, such as depth, are strongly related to biotic communities (Malcolm et al. 2011). Evidence supporting the use of distribution models in marine conservation planning is lacking (Ballantine and Langlois

2008; Klein et al. 2015) and classification schemes have been more readily applied (Barrett et al. 2003; Jordan et al. 2005; Malcolm et al. 2011). Consequently, there are limited guidelines for integrating the results of multiple conservation scenarios that use distribution models and classification schemes in marine ecosystems (Ballantine and Langlois 2008).

This study tested the benefit of using distribution models against using habitat classification schemes to inform conservation planning of marine ecosystems. We used an MPAs in south-eastern Australia, the Solitary Islands Marine Park (SIMP), as a case study to advance marine systematic conservation planning in three ways. Firstly, we ranked environmental variables according to how strong they relate to the biological data of conservation interest, also referred to as predictive power. This allows for the prioritization of data collection, which is essential to managers with limited resources. Secondly, we quantitatively compared conservation trade-offs between conservation planning scenarios using classification schemes and distribution models, for instance we compared the output of scenarios that use a habitat classification scheme as a conservation feature against scenarios that use the predicted species distribution models as a conservation feature. Thirdly, we developed a decision framework to incorporate local knowledge with the results of conservation scenarios using classification schemes and distribution models.

Methods

Study site

The study was conducted in the SIMP on the east Australian coast. The SIMP was established in 1991 as a multiple use MPAs that contains ‘no take’ zones (Sanctuary

Zones: SZ) and zones where fishing is permitted. It has undergone adaptive management twice through rezoning, with the representation of biodiversity a key objective for rezoning. The subtropical MPAs has high biological diversity due to being in a tropical-temperate transition with extensive reef habitats (Harriott, Smith & Harrison 1994; Malcolm, Jordan & Smith 2010).

The SIMP covers 720 km² of coastal waters, in this study the SIMP was separated into northern (132.5 km²) and southern (85.01 km²) regions to reflect the coverage of high-resolution seabed mapping conducted in the area (Fig. 1) (Jordan et al. 2010; Malcolm et al. 2010).

Figure 1 Map of the study area with the Habitat Classification Scheme (HCS) highlighted in colour. The grey line denotes the marine park boundary. Islands were clipped-out for the Marxan analyses.

Sampling methods

Field methods and video processing of fish data

Fish were surveyed on reefs using Baited Remote Underwater Video (BRUV), with 56 deployments at 19 sites in the northern region and 103 deployments at 34 sites in the south (totalling 159 thirty-minute BRUV deployments). Each BRUV unit consisted of a digital video camera with wide-angle lens in an underwater housing, an attachment frame, a bait-pole with bait, and a rope and float system linking the BRUV to the surface (Malcolm, Jordan & Smith 2011). Baits were used to attract fish to a viewing area in front of the camera with 1 kg of mashed pilchard *Sardinops neopilchardus*, attached to the end of a bait-pole at a distance of 1.5 m from the lens (Hardinge et al. 2013).

Data were analysed post-survey using EventMeasure-stereo software (SeaGIS Pty. Ltd.) with the identity of each fish species and an index of its relative abundance (MaxN) recorded from each replicate. MaxN was the maximum number of individual fish of each species in the frame at any one time during the 30-min record. This eliminated the chance of recounting individual fish. The field-of-view was standardized to a distance of approximately 3 m behind the bait to minimize the effects of water visibility on the measure of relative abundance, further details of sampling methodology can be found in Cappo et al. (2003) and Harasti et al. (2015).

A restricted number of targeted fish were selected (Table 1) using a combination of species lists from recreational fishing competitions in SIMP (Henry, Matthews & Kelly 1996), commercial fishing data for NSW (Rowling, Hegarty & Ives 2010), and BRUV surveys undertaken extensively throughout the SIMP (Malcolm, Jordan & Smith 2011). Additionally five fish functional groups were selected to run SDMs, these groups

included fish from the entire assemblage (Table 1). The first two groups were trophic functional groups of high commercial value. The third group was particularly vulnerable to fishing impacts, the fourth group included species with high-conservation value in relation to global representation within this subtropical marine park, and the fifth group, wrasse family (Labridae), was included as a surrogate for overall fish diversity. The Labridae account for ~17% of the reef fish species recorded from the SIMP (Malcolm, Jordan & Smith 2010) and is an effective surrogate to represent reef-fish diversity in the SIMP (Malcolm & Smith 2010).

Table 1 Eight fish species and five functional groups of commercial and/or conservation importance selected in this study for SDMs. Details of species placement in functional groups in Table S1.

Species	Common Name	Rationale
<i>Chrisophrys auratus</i>	Snapper	Key target fished species
<i>Nemadactylus douglasi</i>	Grey morwong	Key target fished species
<i>Notolabrus gymnogenis</i>	Crimson banded wrasse	Key target fished species
<i>Ophthalmolepis lienolatus</i>	Maori wrasse	Key target fished species
<i>Rhabdosargus sarba</i>	Tarwhine	Key target fished species
<i>Glaucosoma scapulare</i>	Pearl perch	Key target fished species
<i>Choerodon venustus</i>	Venus tusk fish	Key target fished species
<i>Brachaelurus waddi</i>	Blind shark	By catch species & subtropical endemic
Functional Group*		Rationale
Target predator fish		Targeted trophic group
Target piscivore fish		Targeted trophic group
Benthic sharks		Vulnerable group
Subtropical endemics		High conservation value
Labrids		Surrogate group

*See Supplementary Information for species lists per group

Swath mapping

Subtidal reefs were digitised from swath-acoustic data and spatial variables were calculated for the reef areas in both northern and southern regions: latitude, distance from mainland, management zone ('no-take' vs fished), reef area, depth, standard deviation of depth, curvature, slope, fractal dimensions and surface rugosity (Table 2).

Swath acoustic mapping was conducted over the two survey areas using a 125 kHz GeoSwath interferometric sidescan sonar (Jordan et al. 2010). Bathymetric and seabed reflectance (backscatter) data were gridded at 5 x 5 m grid cell resolution and the spatial layers were created in ArcMap10 (ESRI, USA). Areas of rocky reef were digitised by hand at a constant scale of 1:2000 using a combination of the bathymetry and backscatter. Overall, rocky reef areas were generally characterised by regions of relief, relatively higher backscatter reflectance and grey scale heterogeneity (texture). In contrast, unconsolidated substratum were characterised by regions of relatively little relief, homogeneous textural complexity and weaker seafloor reflectance (see Jordan et al., 2010, for details). Spatial variables (Table 2) were then calculated on a 5 x 5 cell basis for the 5 x 5 m gridded data using Fledermaus (QPS, USA) and ArcMap10 (ESRI, USA).

Habitat classification scheme (HCS)

The HCS used in our study was designed for the SIMP based on assemblage patterns of fishes and prevalence patterns of major benthic habitat formers (Malcolm et al. 2011). The assemblage patterns of fishes are mostly reflected on depth and distance from shore, thus HCS considers depth (shallow 0-25 m, intermediate 25-50 m, deep >50 m) and distance from mainland (inshore 0-1.5 km, midshelf 1.5-6 km, offshore >6 km);

resulting in seven categories: shallow inshore; shallow midshelf, shallow offshore, intermediate inshore, intermediate midshelf, intermediate offshore, deep offshore (Fig. 1) (Malcolm et al. 2012). This reflects the presence of islands and adjacent reefs on the midshelf and offshore waters.

Species distribution models (SDM)

The relationship between the prevalence/abundance of fish, for nine species and five functional groups (Table 1), and the spatial variables (Table 2) and management zone was assessed using generalized and generalized hierarchical models in R (R Core Team, 2014). First, the spatial variables (Table 2) were explored followed by model refining and assessment, third final models were used to predict fish distributions across each of the studied regions, all models used empirical data.

Table 2 Spatial variables tested as potential predictors in the SDMs, those used in the habitat classification scheme are marked with a ^. Some of these variables were collinear (i.e. surface rugosity and standard deviation of depth), in which case we used only one of the variables in the SDMs. Variables not used in the SDMs are greyed out. Variables that were log transformed in analyses are marked with an asterisk *.

Variable	Description
Depth	Mean depth at each cell in the 5 m grid (range 14.6 – 73.7 m).
Distance	Distance from the 5 m grid cell where the BRUV were deployed to the coastline (km).
Zoning	Inside or outside no take zone, no fishing allowed.
Latitude	Latitude
Curvature	The slope of each cell in the 5 m grid in relation to a 3 x 3 cell analysis.
Depth standard deviation	Standard deviation of depth, represents the dispersion of depth values (in meters) around the mean depth within a square 3 x 3 cell window. In this analyses the cell values are 5 x 5 m so the analysis window is 15 x 15 m.
Fractal dimension	This is a measure of the 2 dimensional complexity of the shape of the reef. Mean fractal dimension approaches one for shapes with simple

	perimeters and approaches two when shapes are more complex.
*Reef area	Total area of reef in each planning unit (m ²).
Fractal perimeter	The length of the perimeter of each reef fraction (m).
Surface rugosity	Surface rugosity is a measure of the variation in three dimensional orientation of grid cells within a 3 x 3 cell neighbourhood. This variable captures variability of aspect and slope in a single measure. Rugosity values can range from 0 (no seafloor variation) to 1 (complete seafloor variation). Typical values are between 0 and 0.4.
Slope	Identifies the slope (gradient, or rate of maximum change in z value) from each cell of a raster surface.
^Depth categories	Depth of seabed from bathymetric charts (0-25 m, 26 – 50 m, > 50 m).
^Distance categories	Distance from the shore measured perpendicularly from the coastline (km).

221

222 During data exploration explanatory variables were assessed for correlation and
223 where two variables were correlated at Pearson's $r > 0.7$, the variable likely to be most
224 proximal in determining the distribution of fish was chosen (Table 2). The distribution of
225 variables was also checked and highly skewed variables were log transformed (Table 2).
226 As a preliminary step, Generalised Additive Models (GAM) of each predictor variable
227 against the prevalence of each species was used to assess the form of each response using
228 package *mgcv* (Wood 2011). The following interactions were considered: depth *
229 standard deviation of depth, depth*fractal dimensions, and depth*latitude.

230 Not all functional groups or species were abundant enough to run abundance
231 models (see Supplementary Information Fig 5). Predictions from abundance models are
232 better than prevalence models as conservation feature layers in Marxan, because they
233 contain more information about how good the habitat is for supporting the species of
234 conservation interest. Thus, we used abundance models when possible and prevalence
235 models otherwise. We considered using prevalence models for all groups, but chose to

use a combination of both given that: (1) abundance models allow the selection of areas of high abundance to protect groups that are abundant enough, (2) prevalence models allow the protection of rare places where non-abundant species occur, (3) many of the species and groups for which we modelled prevalence were recorded in very low abundances at individual sites (mostly less than 3), which in essence is not very different to presence-absence.

The abundance (when possible) or prevalence of fish was modelled as a function of the environmental variables and management zone using packages *mass*, *stats* and *lme4* in R (Venables, 2002, Venables and Ripley 2002, R Core Team 2014, Bates et al. 2015). Predictor variables were scaled and centred for analysis. The choice of model was informed by the potential need to account for (i) random effects of site, (ii) zero inflated or over dispersed data (i.e. poisson, negative binomial or zero inflated glm), and (iii) spatial autocorrelation. Model forward selection was based on Akaike Information Criteria (AIC) (Bolker et al. 2009) and final model adequacy was assessed using residual plots (Bjornstad 2013). Assumptions of independence (to ensure no spatial autocorrelation was present) were checked for all final models, by plotting the correlation between model residuals to a distance of 4.5 km (the average inter reef distance) using the *spline.correlogram* function in the package *ncf* (Bjornstad, 2013) with 200 bootstrap samples.

“Site” was tested as a random effect in the original models to account for potential spatial autocorrelation. If no significant ($p > 0.05$) improvement of model fitness resulted from including “Site” as random effect and if no evidence of spatial autocorrelation was found in residual correlograms of models without the random effect, “Site” was removed

from the model following the parsimony principle (Bates, 2015). Fish abundance data were spread across the different management zones within the SIMP (general use (fishing and trawling permitted): north region 6, south region 18 sites; habitat protection (only fishing permitted): north region 8, south region 9 sites; and no take zones (fishing and trawling not permitted): north region 5, south region 8 sites).

The final model for each species and group was used to generate predictions of the average prevalence / abundance across each region as a function of the spatial variables and management zones. The predictive performance of models was assessed using 5 fold cross validation. Assessment for prevalence models was based on the mean value across the folds of the Area Under the Receiver Operator Curve (AUC). The AUC quantifies the ability of the model to discriminate between presences and absences in the dataset. AUC values >0.9 indicate excellent model performance, 0.7- 0.9 moderate to high performance, 0.5-0.7 low performance and ~ 0.5 indicates performance was no better than random (Barbosa et al. 2013). Estimates of the error of these predictions (AUC standard error) were also generated. Assessment for abundance model was based on the mean value across folds of the proportion of variance explained by the final model, here after referred to as D-squared (Guisan and Zimmerman, 2000). Both the AUC and the D-squared were calculated using the modEvA package (Barbosa et al. 2013).

Integrating approaches to systematic conservation planning

1) Ranking environmental surrogates

The mean distribution of fish across each region was predicted for each species and functional group. Environmental variables were ranked according to the number of final models in which each variable was retained (i.e. a variable retained in all final models would rank 100%).

2) *Conservation planning scenario comparison*

Marxan is the most widely used software for spatial conservation planning globally (Ball 2009). Marxan is a tool to guide systematic planning, it works by allowing an objective spatial optimisation of the areas that should be protected and assessing the trade-offs between the proportion of species conserved successfully and the related cost (Ball et al. 2009). Marxan.io is a web application where users can use Marxan and upload their datasets, run Marxan, edit parameters, run parameter tests, visualise output maps, figures and tables, and publicly share datasets (Watts 2016). We compared seven different conservation scenarios that used either HCS (% area of each habitat) or SDM (% abundance/occurrence of each species/functional group) as conservation targets in Marxan.io (Watts and Possingham 2013), (Table 3).

North and south regions were merged together and the non-reef areas (i.e. islands, unconsolidated substrata) were excluded. Data available at finer scales than that of the planning units (250 x 250 m) were averaged across all cells within each planning unit (total 1603 planning units), and values were standardized proportionally on a scale from 0 – 1. The boundary length modifier, which controls the amount of clumping (0.04); the target, which sets the amount of a species/habitat to protect (21%); and the penalty factor, which penalizes not meeting the target (0.3); were held constant across scenarios. The key question this study investigated was comparing the type of conservation target used (SDMs vs HCS), rather than the variation in conservation scenarios due to variation in either of these values, thus these values were held constant to avoid confounding effects. These values were selected following both global standards, such as the Convention on Biological Diversity Aichi Target 11, which calls for at least 10% of marine and coastal zones to be protected by 2020 (UNEP 2012, <https://www.cbd.int/sp/targets/>), and a

sensitivity analyses performed in marxan.io, which tested the trade-off between different levels of protection (target) and the cost of protecting that proportion of the conservation feature (Watts 2016). We allowed the sensitivity analyses to test values between 10% - 30%, and the optimal value was 21%. Existing zones were not taken into account and 10,000 iterations were run for each scenario.

Table 3 Summary of the seven scenarios tested in this study. The dashed lines separate the types of scenarios (HCS, SDMs and combined). HCS: habitat classification scheme, SDM: species distribution model.

Scenario	Details of conservation feature	Rational
1. HCS	HCS based on three depth regions, and three distances from shore, resulting in 7 classes.	All variables required can be obtained at negligible expense to managers.
2. HCS + bathymetry	HCS plus a bathymetric map of the standard deviation of depth, a proxy of habitat structural complexity.	The HCS does not include any metric of structural complexity.
3. HCS + SDM _{all}	HCS plus SDMs for 9 species of fish and 5 functional groups (Table 1).	Scenario comparison
4. HCS + SDM _{groups}	HCS plus SDMs for 5 fish functional groups (Table 1).	Scenario comparison
5. SDM _{all}	SDM for 9 fish species and 5 functional groups (Table 1).	Scenario comparison
6. SDM _{groups}	SDMs for 5 fish functional groups (Table 1).	Scenario comparison
7. SDM _{species}	SDMs for 9 fish species (Table 1).	Scenario comparison

Scenarios were compared in three ways. Firstly, we visualized differences between scenarios using the Marxan frequency output maps and a nonmetric multidimensional scaling plot (nMDS). Secondly, we statistically assessed selection frequency differences between scenarios by planning unit using paired Wilcoxon non-parametric pair-difference test. Thirdly, we compared scenarios using the proportion of

targets protected (species, functional groups and habitat types) and the total area required for conservation under each scenario. The larger the area required for conservation the higher the cost of that scenario.

3) Integrating multiple scenarios with local knowledge

It is crucial to involve stakeholders to interpret the results of the quantitative analyses if conservation of any area is to be successful. Using expert knowledge to interpret and integrate the results of spatial quantitative approaches like the one presented here has several advantages: it allows for flexibility in discussions about which areas to protect, it allows for the incorporation of knowledge that was not captured during the quantitative process, it increases the probability of compliance by stakeholders once zoning is implemented.

We developed a conceptual decision framework to guide the integration of outputs from multiple scenarios using SDM and HCS as conservation targets with local knowledge. This framework included developing spatial layers that showed important areas for conservation values and extractive uses. These layers were based on local knowledge synthesised during meetings and from use databases. Local knowledge was derived from a broad range of scientists, natural resource managers with at least 10 years of experience working in the SIMP region and local stakeholders. Local knowledge helped guide the integration of the results from multiple scenarios following four steps: conservation objectives definition (Brown et al. 2015), spatial solutions assessment, solution integration with local knowledge, and adaptation (Game et al. 2013; Mangubhai et al. 2015).

Results

All focal species and functional groups were recorded across both regions. A total of 152 fish species were recorded across both regions (96 species in the north and 114 in the south). From these, 24 were target predators, nine piscivores, eight benthic sharks, 22 subtropical endemics, four threatened and protected, 18 Labrids, and 67 were not allocated to any of our focal functional groups. Maps of the predicted distribution of nine species and five functional groups (Table 1) were produced (Supplementary Fig. S1).

1) Ranking environmental surrogates

Predictive performance was consistent between regions. AUC, which indicate the ability of a model to distinguish presences from absences, for individual SDMs ranged from low (0.60) to excellent (0.97). The AUC for benthic sharks SDMs had high performance (0.80), while the piscivores SDM performed moderately (0.66). D-squared, which indicates the predictive accuracy of abundance SDM through cross-validation, ranged from just good (0.10) to excellent (0.67) for species and functional groups (Table 4).

Despite the strong relationship between fish distributions and environmental variables, the direction and magnitude of responses varied for each response and predictor combination, for example depth had a positive influence on target predators, but a negative influence on target piscivores. Generally, the nine fish species were more abundant/prevalent at greater depths and further from shore. Three of the five fish functional groups were more abundant in shallower waters (target predators, benthic sharks and Labrids), target piscivores were more abundant in deeper waters, and endemics abundance was unrelated to depth. Abundance and prevalence of piscivores, predators and Labrids was greater around more complex reefs (Table S2, Fig. 2).

Table 4 Statistics for the distribution models for five fish groups and nine species of commercial or conservation importance (separated by solid line). Values of deviance explained by model are D^2 expressed as percentage, and for predictive accuracy evaluated by cross-validation are mean (SD), and coloured according to model predictive accuracies: bold font excellent, black font high and grey font low (see methods).

Summary statistics of distribution models			Deviance explained	Predictive accuracy	
Species or group	Model type	Region	Adjusted D^2	D^2	AUC
Target predators	Abundance (negative binomial)	N	11%	0.16 (0.10)	NA
		S	25%	0.10 (0.05)	NA
Subtropical endemics	Abundance (negative binomial)	N	20%	0.25 (0.21)	NA
		S	12%	0.23 (0.12)	NA
Labrids	Abundance (poisson)	N	57%	0.46 (0.24)	NA
		S	49%	0.57 (0.02)	NA
Target piscivores	Prevalence	N	20%	NA	0.67 (0.03)
		S	5%	NA	0.65 (0.11)
Benthic sharks	Prevalence	N	24%	NA	0.80 (0.1)
		S	25%	NA	0.79 (0.15)
Snapper	Abundance (negative binomial)	N	10%	0.17 (0.18)	NA
	Abundance (hierarchical poisson)	S	34%	0.22 (0.21)	NA
Black spotted goatfish	Abundance (negative binomial)	N	34%	0.28 (0.29)	NA
		S	26%	0.26 (0.07)	NA
Maori wrasse	Abundance (poisson)	N	74%	0.67 (0.11)	NA
		S	63%	0.54 (0.09)	NA
Crimson banded wrasse	Abundance (poisson)	N & S	48%	0.48 (0.14)	NA
Blind shark	Prevalence (binomial)	N	25%	NA	0.87 (0.1)
		S	30%	NA	0.94 (0.07)
Pearl perch	Prevalence (binomial)	N	39%	NA	0.72 (0.17)
		S	13%	NA	0.72 (0.14)
Venus tuskfish	Prevalence (binomial)	N	55%	NA	0.89 (0.08)
	Prevalence (quasibinomial)	S	52%	NA	0.85 (0.08)
Tarwhine	Prevalence (binomial)	N	21%	NA	0.76 (0.19)
	Prevalence (quasibinomial)	S	49%	NA	0.73 (0.12)
Grey morwong	Prevalence (binomial)	N	40%	NA	0.81 (0.12)
		S	48%	NA	0.83 (0.15)

All eight variables tested were important predictors of fish distributions (both prevalence and abundance), however, depth was the most important variable and was retained in 80% of all final models (Fig. 2). Distance from shore influenced 66% of species and 40% of functional groups; while latitude and zone were related to 55% of the species and 40% of the functional groups. Fractal dimensions influenced 66% of the species, but only 20% of the functional groups. Other habitat structure metrics were also important predictors: depth standard deviation and reef area were significantly related to 44% of the species, and 40% and 20% of the functional groups, respectively. Curvature was the variable of least influence, retained in 40% of the functional groups and 22% of the species' models (Table 4, Fig. 2).

Figure 2 Relative importance of explanatory variables of both prevalence and abundance models. The numbers inside each bar represent the ranking of each environmental variable according to the number of final models each variable was retained in. For instance, if a variable had been retained in all final models it would have a value of 100%, indicating it was significantly related to all focal fish species / functional groups. Thus

the higher the x-axis value, the more useful a variable is to describe fish spatial patterns of abundance and prevalence. Management zone = no take.

2) *Conservation planning scenario comparison*

The seven scenarios clearly separated in two groups, those using the HCS and those using SDM as conservation targets (Fig. S2-S4). When both the HCS and the SDM were combined into one scenario (Table 3) the resulting selection was similar to that of scenarios with only HCS (Fig. 3), because the HCS scenarios required more area to achieve the conservation target.

The Wilcoxon-test found no significant difference between the three scenarios including SDM ($W = 1266300$, $p\text{-value} = 0.4535$), nor between the four scenarios including HCS ($W = 1288900$, $p\text{-value} = 0.8763$); but detected strong significant differences between any combination of SDM vs HCS scenarios ($W = 691200$, $p\text{-value} < 0.05$). Thus, we focus our discussion and results on two scenarios: the HCS and the SDM.

Scenarios using only the HCS applied a blanket approach to biodiversity representation and required the protection of three times more area than the SDM scenarios to achieve the conservation target (18% vs. 6.5% total area); but achieved protecting at least 21% of all habitat types, and 24 – 43% of focal species and functional groups (Fig. 3, 4 and Fig. S4). The SDM scenario protected at least 21% of the predicted abundance/occurrence of the focal species and functional groups, but only protected 21% of one habitat type, with less than 7% of any other habitat receiving protection (Fig. 4). For example, when protecting all focal species and functional groups, none of the intermediate inshore reef was protected, potentially threatening species that live there but

were not recorded in this study. The SDM scenarios adequately represented fish of commercial and conservation importance, including a biodiversity surrogate group (Labrids), by protecting a much smaller area; yet at the risk of failing to protect biota that was not captured by the SDM (i.e. benthic biota). The SDM solution provided less spatial flexibility than the HCS solution.

Figure 3 Comparison of Marxan.io scenarios using habitat classification scheme (HCS) and species distribution models (SDM) as conservation targets. Map denotes areas

419 frequently selected (in at least 40% of the 10,000 iterations) for conservation by each
 420 scenario (HCS – blue, SDM – green), and areas selected by both scenarios (red). The
 421 HCS selected 18% of the area, while the SDM scenario selected 6.5% of the area, and
 422 there was an overlap of 5.8% between scenarios (Table S3).

423
 424 **Figure 4** Percent of conservation feature protected by scenarios using (a) habitat
 425 classification scheme or (b) distribution models as conservation targets. The dashed line
 426 in both graphs denotes the target 21% to be protected by that scenario. The bars represent
 427 the additional percent protected for other conservation features not considered in that

scenario, for instance in (a) only 21% of each habitat type was targeted for conservation, but also 25 – 42% of each fish species and functional group were protected. SIR: shallow inshore reef, SMR: shallow mid shelf reef, SOR: shallow offshore reef, IIR: intermediate inshore reef, IMR: intermediate mid shelf reef, IOR intermediate offshore reef, and DOR: deep offshore reef.

No scenario protected known biodiversity hot-spots (~0.1% of total area). Thus, given there are advantages and disadvantages to both approaches and that they are not mutually exclusive, a conceptual framework to integrate HCS and SDM solutions with local knowledge was developed (Fig. 5).

Figure 5 Conceptual decision framework to guide the integration of outputs from multiple systematic spatial planning scenarios using species distribution models and habitat classification schemes as conservation targets in marine ecosystems.

3) Integrating multiple scenarios with local knowledge

We integrated conservation solutions by identifying overlapping areas with high-frequency selection across scenarios. In this study, the 5.8% overlap (of the total study area) between scenarios highlighted the core area with high-priority for conservation (Fig. 3). The decision framework included using this map alongside maps of important areas

for extractive and non-extractive uses (Fig. 6), as identified by local knowledge through stakeholder meetings. This identified gaps and guided further prioritization of areas to be protected amongst the remaining ~13% frequently selected areas in the HCS scenario (Fig. 3). Thus, the core area identified as high-priority for conservation was then extended to 10%, as per Convention on Biological Diversity recommendations of at least 10% of each habitat type be represented in highly protected areas (UNEP 2012). In an actual planning situation, these integrated maps showing core areas for protection (Fig. 3 and 6), would provide an effective platform for on-going discussion and negotiations at stakeholder meetings held to spatially plan conservation zones in a marine park.

Figure 6 (a) Extractive (i.e. fishing) and (b) non-extractive (i.e. diving) uses of the SIMP, as per stakeholder meetings and use data, numbers denote the number of users.

Discussion

This study advanced systematic conservation planning of marine ecosystems on three fronts. Firstly, it ranked surrogates and assessed their utility in conservation planning; secondly, it quantitatively compared conservation trade-offs between scenarios using HCS and SDM as targets; and thirdly, it developed a decision framework to guide

the integration of both approaches with local knowledge. Here, we demonstrate how these three steps can be applied to a data-poor highly biodiverse marine ecosystem using conservation aims that are globally common: to protect biodiversity and species of commercial and conservation importance (UNEP 2012).

Ranking environmental surrogates

The predictive performance of models was consistently good across all species and functional groups. Depth was the most important surrogate, although fractal dimensions and distance from shore were also important. Habitat structure metrics consistently had a positive relationship to fish abundance/occurrence confirming recent findings (Moore et al. 2011). Interestingly, surrogates that are readily obtained (i.e. distance) predicted fish distributions as accurately as surrogates that require high-resolution mapping information (i.e. fractals). This has important practical applications because obtaining high-resolution variables requires relatively expensive data, while quantifying a set of variables from low-resolution datasets has negligible cost. We used high-resolution depth and distance in the SDM, but low-resolution data in the HCS. While the high-resolution variables did improve the models, both robust HCS and SDM could be achieved if these are unavailable using low-resolution data (Malcolm et al. 2011; Moore et al. 2011; Stevens and Connolly 2004).

Integrating conservation solutions and local knowledge

Using SDM to set conservation targets in data-poor ecosystems can improve conservation planning (Beger et al. 2003), but in isolation SDM also have some conservation risks as not all species can be adequately captured by the models, or the data underlying the models. For example, if the biotic data and associated models only

represent fish assemblages, important benthic biota and invertebrates would not be represented in the SDM scenarios. On the other hand, using only the HCS to set biodiversity targets can be cost-effective compared to collecting raw biotic data (Guisan et al. 2013), but it could also result in a solution that requires a large area to be protected to achieve conservation objectives (Jackson and Lundquist 2016). Additionally, HCS based solely on abiotic surrogates will only coarsely approximate real biodiversity patterns (Giakoumi et al. 2015; Rubidge et al. 2016). Using local knowledge to synthesise conservation planning results obtained by multiple scenarios (both SDM and HCS) can ameliorate these hurdles, and is more likely to cost-effectively represent biodiversity and achieve secondary conservation goals simultaneously (Klein et al. 2008).

Combining the outputs of multiple scenarios and socio-economic uses highlighted overlapping areas. This offers flexibility at the planning negotiation table, for discussion between managers and stakeholders, creating room for negotiation while ensuring the protection of the most important areas simultaneously. For instance, in this study the 5.8% areas frequently selected by both the HCS and the SDM scenarios would be prioritised for protection in ‘no take’ zones, and stakeholders could negotiate around the remaining identified areas (in this study remaining 13% identified for protection by the HCS) using the maps that highlight extractive and non-extractive uses (Fig. 6).

None of the seven scenarios protected unique sites of known high biodiversity (Malcolm et al. 2010). This is not unexpected, as these sites have not been sampled as part of this study so their biotic and environmental features were not captured by either the HCS or the SDM. Such sites should be fully protected to maximise the chance of including rare species or functional groups that may inhabit only these areas (Beger et al.

2003). We suggest managers protect unsurveyed, but known, biodiversity hotspots regardless of the systematic spatial conservation solutions.

It is important to highlight that when SDM are not available, effective conservation planning scenarios can be achieved using only HCS, which are essential for correcting biases and filling gaps in knowledge (Brooks et al. 2004). Applying a precautionary approach to conservation planning is advised, especially in data-poor ecosystems (Groves and Game 2016).

Game et al. (2017) showed the need for methodologies that enable the rapid incorporation of both local and expert knowledge, particularly in data-poor systems, such as the fuzzy logic models. This study developed advanced SDM and a robust HCS to inform conservation planning. We tested and ranked eight environmental surrogates of fish distributions, including fish functional groups, which can be transferred to other marine ecosystems (Brown and Mumby 2014). Combining both scenario types, particularly interpreted in the context of local knowledge, will identify effective conservation solutions and add flexibility to negotiations between managers and stakeholders. In turn, these discussions will maximize the likelihood of successful conservation planning by involving stakeholders early in the planning process (Groves and Game 2016) and allow rapid responses to environmental and social changes (Brown et al. 2012).

Acknowledgements

This project was supported by the University of Sydney, the NSW Department of Primary Industries and Australia's Integrated Marine Observing System (IMOS), partially funded by the Department of Innovation, Industry, Science and Research

through the National Collaborative Research Infrastructure Scheme and the Education Investment Fund, and the Marine Biodiversity Hub, a collaborative partnership supported through funding from the Australian Government's National Environmental Research Program (NERP).

Data availability: all environmental data are available at <https://catalogue-imos.aodn.org.au/geonetwork/srv/eng/metadata.show?uuid=60160b01-8ffc-45ce-a6f4-ee70ce391ec6>

References

1. Ball, I.R., H.P. Possingham, and M. Watts. 2009. Marxan and relatives: Software for spatial conservation prioritisation. Chapter 14: Pages 185-195 in Spatial conservation prioritisation: Quantitative methods and computational tools. Eds Moilanen, A., K.A. Wilson, and H.P. Possingham. Oxford University Press, Oxford, UK.
2. Ballantine W., Langlois T. (2008) Marine reserves: the need for systems. *Hydrobiologia* **606**, 35-44.
3. Ban N.C. (2009) Minimum data requirements for designing a set of marine protected areas, using commonly available abiotic and biotic datasets. *Biodivers Conserv* **18**, 1829-1845.
4. Barbosa M.A., Real R., Muñoz A., Brown J.A. (2013) New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Divers Distrib* **19**, 1333-1338.
5. Barrett N., Edgar G., Morton A., Buxton C. (2003) A decade of study in Tasmanian MPAs-Part 2. *Fishing Today* **16**, 2.
6. Beger M., Jones G.P., Munday P.L. (2003) Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biol Conserv* **111**, 53-62.
7. Bjornstad O.N. (2013) ncf: spatial nonparametric covariance functions. *R package version 11-5*.
8. Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H., White J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* **24**, 127-135.
9. Brooks T., Fonseca D.A., Gustavo A.B., Rodrigues A.S. (2004) Species, data, and conservation planning. *Conservation Biology* **18**, 1682-1688.
10. Brown C.J., Bode M., Venter O., Barnes M.D., McGowan J., Runge C.A., Watson J.E., Possingham H.P. (2015) Effective conservation requires clear objectives and prioritizing actions, not places or species. *Proceedings of the National Academy of Sciences* **112**, E4342- E4342.
11. Brown C.J., Fulton E.A., Possingham H.P., Richardson A.J. (2012) How long can fisheries management delay action in response to ecosystem and climate change? *Ecological Applications* **22**, 298-310.
12. Brown C.J., Mumby P.J. (2014) Trade-offs between fisheries and the conservation of ecosystem function are defined by management strategy. *Front Ecol Environ* **12**, 324-329.
13. Cappel M., Harvey E.S., Malcolm H., Speare P. (2003) Potential of video techniques to monitor diversity, abundance and size of fish in studies of Marine Protected Areas. pp. 455-464 in J.P. Beumer, A. Grant, D.C. Smith

- 581 editors. *Aquatic Protected Areas - what works best and how do we know?*
582 World Congress on Aquatic Protected Areas proceedings, Cairns, Australia.
- 583 14. Cook, R. & Auster, P. (2006) Developing alternatives for optimal
584 representation of seafloor habitats and associated communities in
585 Stellwagen Bank National Marine Sanctuary. *Marine Sanctuaries Conservation*
586 *Series* pp. 24. U.S. Department of Commerce, National Oceanic and
587 Atmospheric Administration, Office of National Marine Sanctuaries
- 588 15. Cowling, R.M., Pressey, R.L., Sims-Castley, R., le Roux, A., Baard, E., Burgers,
589 C.J. & Palmer, G. (2003) The expert or the algorithm?—comparison of priority
590 conservation areas in the Cape Floristic Region identified by park managers and
591 reserve selection software. *Biological Conservation*, **112**, 147-167.
- 592 16. Elith J., Graham C.H. (2009) Do they? How do they? WHY do they differ? On
593 finding reasons for differing performances of species distribution models.
594 *Ecography* **32**, 66-77.
- 595 17. Elith J., Leathwick J.R. (2009) Species distribution models: ecological
596 explanation and prediction across space and time. *Annual Review of Ecology,*
597 *Evolution, and Systematics* **40**, 677-697.
- 598 18. Fernandes, L., Day, J., Lewis, A., Slegers, S., Kerrigan, B., Breen, D., Cameron,
599 D., Jago, B., Hall, J., Lowe, D., Innes, J., Tanzer, J., Chadwick, V., Thompson, L.,
600 Gorman, K., Simmons, M., Barnett, B., Sampson, K., De'ath, G., Mapstone, B.,
601 Marsh, H., Possingham, H., Ball, I., Ward, T., Dobbs, K., Aumend, J., Slater, D.
602 & Stapleton, K. (2005) Establishing representative no-take areas in the Great
603 Barrier Reef; large-scale implementation of theory on marine protected areas.
604 *Conservation Biology*, **19**, 1733-1744.
- 605 19. Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional
606 conservation planning: Where to from here? *Systematic Biology*, **51**, 331-363.
- 607 20. Game E.T., Bremer L.L., Calvache A., Calvache A., Moreno P.H., Vargas A.,
608 Rivera B., Rodriguez, L.M. (2017) Fuzzy Models to Inform Social and
609 Environmental Indicator Selection for Conservation Impact Monitoring.
610 *Conserv Lett*, doi: 10.1111/conl.12338.
- 611 21. Game E.T., Kareiva P., Possingham H.P. (2013) Six common mistakes in
612 conservation priority setting. *Conservation Biology* **27**, 480-485.
- 613 22. Giakoumi S., Brown C.J., Katsanevakis S., Saunders M.I., Possingham H.P.
614 (2015) Using threat maps for cost-effective prioritization of actions to
615 conserve coastal habitats. *Mar Policy* **61**, 95-102.
- 616 23. Groves C., Game E.T. (2016) *Conservation Planning: Informed Decisions for a*
617 *Healthier Planet*. W. H. Freeman, United Kingdom.
- 618 24. Guisan A., Tingley R., Baumgartner J.B., Naujokaitis-Lewis, I. Sutcliffe, P.R.,
619 Tulloch A.I., Regan T.J., Brotons L., McDonald-Madden E., Mantyka-Pringle C.,
620 Martin T.G., (2013) Predicting species distributions for conservation
621 decisions. *Ecology letters* **16**, 1424-1435.

25. Guisan A., Zimmermann N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-186.
26. Harasti D., Malcolm H., Gallen C., Coleman M.A., Jordan A., Knott N.A. (2015) Appropriate set times to represent patterns of rocky reef fishes using baited video. *Journal of Experimental Marine Biology and Ecology* **463**, 173-180.
27. Hardinge J., Harvey E.S., Saunders B.J., Newman S.J. (2013) A little bait goes a long way: the influence of bait quantity on a temperate fish assemblage sampled using stereo-BRUVs. *Journal of Experimental Marine Biology and Ecology* **449**, 250-260.
28. Harriott, V.J., Smith, S.D.A. & Harrison, P.L. (1994) Patterns of coral community structure of subtropical reefs in the Solitary Islands Marine Reserve, Eastern Australia. *Marine Ecology Progress Series*, **109**, 67-76.
29. Henry, G., Matthews, J. & Kelly, E. (1996) Recreational fishing competition - survey of Solitary Islands Marine Park. *NSW Fisheries Report to the National Fishcare Program*.
30. Jackson S.E., Lundquist C.J. (2016) Limitations of biophysical habitats as biodiversity surrogates in the Hauraki Gulf Marine Park. *Pac Conserv Biol* **22**, 159-172.
31. Johnston A., Fink D., Reynolds M.D., Hochachka W.M., Sullivan B.L., Bruns N.E., Hallstein E., Merrifield M.S., Matsumoto S., Kelling, S. (2015) Abundance models improve spatial and temporal prioritization of conservation resources. *Ecological Applications* **25**, 1749-1756.
32. Jordan A., Davies P., Ingleton T., Foulsham E., Neilson J., Pritchard T. (2010) Seabed habitat mapping of the continental shelf of NSW. p. 207. Sydney, NSW.
33. Jordan A., Lucieer V., Lawler M. (2005) Linking habitat mapping with fisheries assessment in key commercial fishing grounds.
34. Klein C.J., Brown C.J., Halpern B.S., Segan D.B., McGowan J., Beger M., Warson J.E. (2015) Shortfalls in the global protected area network at representing marine biodiversity. *Scientific reports* **5**, 17539.
35. Klein, C.J., Chan, A., Kircher, L., Cundiff, A.J., Gardner, N., Hrovat, Y., Scholz, A., Kendall, B.E. & Airame, S. (2008a) Striking a Balance between Biodiversity Conservation and Socioeconomic Viability in the Design of Marine Protected Areas. **22**, 691-700.
36. Klein, C.J., Steinback, C., Scholz, A.J. & Possingham, H.P. (2008b) Effectiveness of marine reserve networks in representing biodiversity and minimizing impact to fishermen: a comparison of two approaches used in California, *Conservation Letters*, **1**, 44-51.
37. Leslie, H. (2005) A Synthesis of Marine Conservation Planning Approaches. *Conservation Biology*, **19**, 1701-1713.
38. Leslie, H., Ruckelshaus, M., Ball, I., Andelman, S. & Possingham, H. (2003) Using siting algorithms in the design of marine reserve networks. *Ecological Applications*, **13**, S185-S198.

39. Levin, N., Watson, J.E.M., Joseph, L.N., Grantham, H.S., Hadar, L., Apel, N., Perevolotsky, A., DeMalach, N., Possingham, H.P. & Kark, S. (2013) A framework for systematic conservation planning and management of Mediterranean landscapes, *Biological Conservation*, **158**, 371-383.
40. Malcolm H.A., Foulsham E., Pressey R.L., Jordan A., Davies P.L., Ingleton T., Johnstone N., Hessey S., Smith S.D (2012) Selecting zones in a marine park: Early systematic planning improves cost-efficiency; combining habitat and biotic data improves effectiveness. *Ocean and Coastal Management* **59**, 1-12.
41. Malcolm H.A., Jordan A., Smith S.D.A. (2010) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. *Marine Biodiversity* **40**, 181-193.
42. Malcolm H.A., Jordan A., Smith S.D.A. (2011) Testing a depth-based Habitat Classification System against the pattern of reef fish assemblages (15 - 75m) in a subtropical marine park. *Aquatic Conservation: Marine and Freshwater Ecosystems* **21**, 173-185.
43. Malcolm H.A., Smith S.D.A. (2010) Objective selection of surrogate families to describe reef fish assemblages in a subtropical marine park. *Biodiversity and Conservation* **19**, 3611-3618.
44. Mangubhai S., Wilson J.R., Rumetna L., Maturbongs Y. (2015) Explicitly incorporating socioeconomic criteria and data into marine protected area zoning. *Ocean & Coastal Management* **116**, 523-529.
45. Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243-253.
46. McCook, L.J., Ayling, T., Cappo, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B., Marsh, H., Mills, M., Molloy, F.J., Pitcher, R.C., Pressey, R.L., Russ, G.R., Sutton, S., Sweatman, H., Tobin, R., Wachenfeld, D.R. & Williamson, D.H. (2010) Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Science*, **107**, 18278-18285.
47. Moore C.H., Van Niel K., Harvey E.S. (2011) The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. *Ecography*, **34**, 425-435.
48. Pressey, R.L. & Cowling, R.M. (2001) Reserve selection algorithms and the real world. *Conservation Biology*, **15**, 275-277.
49. RCoreTeam. (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
50. Rowling, K., Hegarty, A. & Ives, M. (2010) Status of fisheries resources in NSW, 2008/09. Industry and Investment NSW.
51. Rubidge E.M., Gale K.S.P., Curtis J.M.R. (2016) Community ecological modelling as an alternative to physiographic classifications for marine conservation planning. *Biodivers Conserv* **25**, 1899-1920.

52. Sarker, S., Justus, J., Fuller, T., Kelley, C., Garson, J. & Mayfield, M. (2005) Effectiveness of Environmental Surrogates for the Selection of Conservation Area Networks. *Conservation Biology*, **19**, 815-825.
53. Sarker, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H. & Andelman, S. (2006) Biodiversity conservation planning tools: Present status and challenges for the future. *Annu. Rev. Environ. Resour.*, **31**, 123-159.
54. Stevens, T. & Connolly, R. (2004) Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management. *Biological Conservation*, **119**, 351-362.
55. Stewart, R.R., Noyce, T. & Possingham, H.P. (2003) Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. *Marine Ecology Progress Series*, **253**, 25-38.
56. UNEP. (2012) Global Environmental Outlook 5. Available from <http://web.unep.org/geo/assessments/global-assessments/global-environment-outlook-5>. Accessed 30 April 2017.
57. Venables W.N., Ripley B.D. (2002) *Modern Applied Statistics with S*, Fourth Edition, Springer, New York pp. 27-300.
58. Watts M., Possingham H.P. (2013) Marxan.net: Cloud infrastructure for systematic conservation planning. Available from <http://marxan.net/>. Accessed 30 April 2017.
59. Watts, M.E. 2016. marxan.io: A web app for systematic conservation planning. Revision 46. URL <http://marxan.net/marxanio>
60. Wood S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **73**, 3-36.

Figure Legends

Figure 1 Map of the study area with the Habitat Classification Scheme (HCS)

highlighted in colour. The grey line denotes the marine park boundary.

Figure 2 Relative importance of explanatory variables. The numbers inside each bar

represent the ranking of each environmental variable according to the number of final

models each variable was retained in. For instance, if a variable had been retained in all

final models it would have a value of 100%, indicating it was significantly related to all

focal fish species / functional groups. Thus the higher the x-axis value, the more useful a

variable is to describe fish spatial patterns of abundance and prevalence. Management

zone = no take.

Figure 3 Comparison of Marxan.io scenarios using habitat classification scheme (HCS)

and species distribution models (SDM) as conservation targets. Map of the areas

frequently selected (in at least 40% of the 10,000 iterations) for conservation by the HCS

(blue) and the SDM (green) scenarios. Red areas were selected by both scenarios at least

40% of the iterations. Only 20% of the area was selected by either scenario more than

40% of the time, the HCS selected 18% of the area, while the SDM scenario selected

6.5% of the area, and there was an overlap of 5.8% between scenarios (Table S3).

Figure 4 Percent of conservation feature protected by scenarios using (a) habitat

classification scheme or (b) distribution models as conservation targets. The dashed line

in both graphs denotes the target 21% to be protected by that scenario. The bars represent

the additional percent protected for other conservation features not considered in that

scenario, for instance in (a) only 21% of each habitat type was targeted for conservation,

but also 25 – 42% of each fish species and functional group were protected. SIR: shallow

inshore reef, SMR: shallow mid shelf reef, SOR: shallow offshore reef, IIR: intermediate

inshore reef, IMR: intermediate mid shelf reef, IOR intermediate offshore reef, and DOR: deep offshore reef.

Figure 5 Conceptual decision framework to guide the integration of outputs from multiple systematic spatial planning scenarios using species distribution models and habitat classification schemes as conservation targets in marine ecosystems.

Figure 6 (a) Extractive (i.e. fishing) and (b) non-extractive (i.e. diving) uses of the SIMP, as per stakeholder meetings and use data, numbers denote the number of users.

Supplementary information

Table S1 Species placed in each functional group for this study. We looked at threatened and protected species but they were not numerous enough to model, they were considered in the last step of our decision framework when considering unique areas that were not properly represented by the conservation targets.

Functional Group	Common name	Scientific name
Target piscivores	Samsonfish Amberjack Yellowtail kingfish Pearl perch Jewfish, mullet Teraglin, trag Black cod Scribbled rockcod Bonito	<i>Seriola hippo</i> <i>Seriola dumerili</i> <i>Seriola lalandi</i> <i>Glaucosoma scapulare</i> <i>Argyrosomus hololepidotus</i> <i>Atractoscion aequidens</i> <i>Epinephelus daemeli</i> <i>Epinephelus undulatostratus</i> <i>Sarda australis</i>
Target predators	Eastern blue groper Foxfish Goldspot hogfish Pigfish Venus tusk fish Crimson-banded wrasse Maori wrasse Moses perch Blackspot goatfish Bream Snapper Tarwhine Chinaman leatherjacket Sergeant baker Wirrah Red morwong Emperor Hussar Southern fusilier Goldspotted sweetlips Sweetlips Cobia Silver trevally Grey morwong	<i>Achoerodus viridis</i> <i>Bodianus frenchii</i> <i>Bodianus perditio</i> <i>Bodianus unimaculatus</i> <i>Choerodon venustus</i> <i>Notolabrus gymnogenis</i> <i>Opthalmolepis lineolata</i> <i>Lutjanus russelli</i> <i>Parupeneus spilurus</i> <i>Acanthopagrus australis</i> <i>Chrysophrys auratus</i> <i>Rhabdosargus sarba</i> <i>Nelusetta ayraudi</i> <i>Aulopus purpurissatus</i> <i>Acanthistius ocellatus</i> <i>Cheilodactylus fuscus</i> <i>Lethrinus sp.</i> <i>Lutjanus adetii</i> <i>Paracaesio xanthura</i> <i>Plectorhinchus flavomaculatus</i> <i>Plectorhinchus sp</i> <i>Rachycentron canadum</i> <i>Pseudocaranx dentex</i> <i>Nemadactylus douglasi</i>
Benthic sharks	Gulf wobbegong Ornate wobbegong Spotted wobbegong Blindshark	<i>Orectolobus halei</i> <i>Orectolobus ornatus</i> <i>Orectolobus maculatus</i> <i>Brachaelurus waddi</i>

	Gummy shark Created port jackson Shark Cat shark grey nurse shark	<i>Mustelus antarcticus</i> <i>Heterodontus galeatus</i> <i>Asymbolus sp</i> <i>Carcharias taurus</i>
Subtropical endemics	Eastern blue devil Broadband anemonefish Australian damsel Maori cod/ scribbled rockcod Happy moment Bream Three bar porcupinefish	<i>Paraplesiops bleekeri</i> <i>Amphiprion latezonatus</i> <i>Pomacentrus australis</i> <i>Epinephelus undulatostratus</i> <i>Siganus nebulosus</i> <i>Acanthopagrus australis</i> <i>Dicotylichthys punctulatus</i>
Labrids	Eastern blue groper Diamond wrasse Bluetail wrasse Black-spotted wrasse Foxfish Goldspot hogfish Pigfish Striped pigfish Venus tuskfish Comb wrasse Cloud wrasse Cleaner wrasse Crimson banded wrasse Maori wrasse Gunther's wrasse Luculent wrasse Moon wrasse Green moon wrasse	<i>Achoerodus viridis</i> <i>Anampses caeruleopunctatus</i> <i>Anampses femininus</i> <i>Austrolabrus maculatus</i> <i>Bodianus frenchii</i> <i>Bodianus perditio</i> <i>Bodianus unimaculatus</i> <i>Bodianus izuensis</i> <i>Choerodon venustus</i> <i>Coris picta</i> <i>Halichoeres nebulosus</i> <i>Labroides dimidiatus</i> <i>Notolabrus gymnogenis</i> <i>Opthalmolepis lineolata</i> <i>Pseudolabrus guentheri</i> <i>Pseudolabrus luculentus</i> <i>Thalassoma lunare</i> <i>Thalassoma lutescens</i>
Threatened and protected	Black cod Grey nurse shark Blue devilfish Spiny pipehorse	<i>Epinephelus daemeli</i> <i>Carcharias taurus</i> <i>Paraplesiops bleekeri</i> <i>Solegnathus spinosissimus</i>

Table S2 Summary of species distribution model statistics. Values are p-values with coefficient symbol (positive or negative), which indicates a positive or negative effect of that explanatory variable on that fish spp. / group (for depth, a negative value indicates there are more fish deeper). AUC is the predictive accuracy metric used for prevalence models. Explanatory variables are removed if not significant ($p > 0.05$), marginally significant ($p = 0.06 - 0.1$) are shown in gray text if retained in final model. N = North, S = South.

Variable	Snapper Abundance		Black spotted goatfish Abundance		Maori wrasse Abundance		Crimson banded Wrasse Abundance	
	N	S	N	S	N	S	Both N & S	
Northing					- 0.009		0.001	
Depth		- 0.001		- 0.02				
Distance Coast		- 0.001	0.009		- 0.001	- 0.001	- 0.002	
Zone (SZ)					- 0.01	- 0.001		
Zone (HPZ)			0.06					
Zone (GUZ)			- 0.002					
Reef area			-0.003					
Depth SD		- 0.003				- 0.01		
Curvature	0.02							
Fractal dimensions		0.03		- 0.007	- 0.01			
Site as random (SD)		1.054						
Pearson D ²	10 %	34 %	34%	26 %	74 %	63 %	48 %	
AUC mean	0.69	0.71	0.74	0.70	0.97	0.91	0.91	

Variable	Blind shark Prevalence		Pearl perch Abundance		Venus tuskfish Abundance		Tarwhine Prevalence		Gray morwong Prevalence	
	N	S	N	N	S	N	N	S	N	S
Northing				0.04	- 0.04	-0.001				0.03
Depth		0.05		- 0.001		-0.001	0.08	0.009	- 0.009	- 0.005
Distance Coast					-0.001	-0.009	0.06		0.04	
Zone (SZ)		0.03	0.08		-0.03					0.05
Zone (HPZ)			- 0.05				- 0.04	- 0.005		
Zone (GUZ)	- 0.01	- 0.01						- 0.07		
Reef area			0.04			0.005		- 0.01		
Depth SD							0.01		0.05	
Curvature										- 0.02
Fractal dimensions						- 0.002		0.01		- 0.02
Depth* Depth SD									- 0.03	-0.02
Depth*Northing			- 0.008							
Pearson D ²	25%	30 %	39 %	13 %	55 %	52 %	21%	49%	40%	48 %
AUC mean	0.86	0.94	0.83	0.78	0.88	0.85	0.76	0.73	0.81	0.81

782

Variable Model type	Target piscivores Prevalence		Target predators Abundance		Benthic sharks Prevalence		Subtropical endemics Abundance		Labrids Abundance	
	N	S	N	S	N	S	N	NA	N	S
Northing						0.004		- 0.04		
Depth		-0.02	0.31	0.001	-0.01	0.001			0.003	0.001
Distance Coast					-0.01				0.001	
Zone (SZ)							0.001	0.001	0.001	
Zone (HPZ)	- 0.007							0.001	0.001	
Zone (GUZ)	- 0.03						0.06	0.03	0.001	
Reef area									- 0.06	
Depth SD	- 0.07			0.58						
Curvature	0.03								0.02	
Fractal dimensions			0.001							
Depth* Fractal			0.001							
Depth* Depth SD				- 0.05					- 0.001	
Site as random									0.309	
Pearson D ²	20 %	5 %	11 %	25 %	24 %	25 %	20 %	12 %	57 %	49 %
AUC mean	0.65	0.63	NA	NA	0.78	0.80	0.73	0.66	NA	0.81

783

784

Table S3 Table comparing the area selected at least 40% of the 10,000 iteration runs by the habitat classification scheme (HCS) and the species distribution models (SDM) scenario. Comparison of Marxan.io scenarios using habitat classification scheme (HCS) and species distribution models (SDM) as conservation targets: 80% of the area was not selected by either scenario more than 40% of the 10,000 iterations, the HCS selected 18% of the area at least 40% of the time, while the SDM scenario selected 6.5% of the area and there was an overlap of 5.8% between scenarios. See Figure 2 in manuscript.

Class	Hectares (total 2855)	Percent
Neither > 40%	2289	80.5%
only HCS > 40%	372	13%
only SDM_grp > 40%	20	0.7%
Both HCS and SDM_grp > 40%	165	5.8%

Supplementary Figures

Figure S1 Figure with maps of the 28 species distribution models – see attached

Figure S2 Figure with frequency maps of 7 scenarios – see attached

Figure S3 Relation between the SDM scenario frequency of election and the other six scenarios. Note the very high correlation with the SDM groups and the SDM species, and weak but significant relation to the HCS scenarios.

Figure S4 Non-metric multidimensional scaling plot of the distance between the frequency selection for each of the seven scenarios. The two clusters are significantly different.