Remotely sensed habitat variables are poor surrogates for functional traits of rocky reef fish assemblages

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SUMMARY

Conservation planning often relies on measures such as species richness and abundance to prioritize areas for protection. Nonetheless, alternative metrics such as functional traits have recently been shown to be useful complementary measures for detecting biological change. Timely conservation planning often precludes the collection of such detailed biological data relying instead on remotely-sensed habitat mapping as a surrogate for diversity. While there is evidence that habitat maps may predict taxonomic species richness and diversity in some coastal ecosystems, it is unknown whether similar strong relationships exist for functional traits and functional multimetrics. We compared the performance of physical habitat structural complexity obtained from high definition swath mapping in explaining variation in traditional taxonomic metrics as well as functional traits (e.g., maximum length, trophic level, gregariousness) and functional multimetrics (e.g., functional richness, dispersion) of fish assemblages. Reef complexity measures were good surrogates for fish species richness and abundance but not for functional traits or multimetrics, except functional richness at the scale of 1 m. Remotely sensed habitat maps may not be a good surrogate for predicting functional traits and multimetrics of fish assemblages, and must be used with caution when maximizing such aspects of assemblages is a priority for conservation planning.

Keywords: conservation planning, fish, mapping, marine protected areas, reef, reserve, surrogate

INTRODUCTION

A primary goal of many conservation initiatives is to protect biological diversity and ecological processes. The size, placement and spatial arrangement of areas selected for protection are therefore often designed to maximize biological diversity (Pressey *et al.* 2007). To achieve this, conservation planning often relies on the use of surrogates for species richness and diversity, particularly where biological information or resources are lacking or when the extent or spatial scale of protection exceeds the feasibility of ecological surveys (Sarkar *et al.* 2005).

In marine environments, remotely-sensed habitat mapping that characterizes the physical structural complexity of habitats (hereafter 'habitat complexity') has been widely used as a predictor or surrogate for fish and invertebrate species diversity on coral reefs (Pittman *et al.* 2009; Pitman & Brown 2011), temperate reefs (Rees *et al.* 2013), deep reefs (Schlacher *et al.* 2007; Guinan *et al.* 2009) and soft sediments (Huang *et al.* 2014). Strong relationships between habitat structural variables and species diversity have been attributed to habitat complexity providing a greater number or diversity of resources or niches (Bell *et al.* 1991; Friedlander & Parrish 1998). Thus, in the absence of biological data, marine conservation planning often aims to select a suite of areas that maximizes habitat types and then structural complexity within habitats to protect the largest number of species.

Recently, traditional taxonomic metrics of biological change such as species diversity and richness have been outperformed by functional traits and multimetrics at showing early response to conservation measures (Coleman *et al.* 2015) and disturbance (Mulliot *et al.* 2013), previously hidden global diversity patterns (Stuart-Smith *et al.* 2013) and ecosystem resilience to climatic change (Bates *et al.* 2014). Functional traits including size, trophic and behavioural characteristics of species, may thus more accurately reflect subtle assemblage characteristics that are important for conservation outcomes. For example, high functional richness of fishes may confer resilience to communities against stressors including climatic change (Bates *et al.* 2014), and a greater range of functions within an assemblage may confer a greater breadth of ecological goods and services that an assemblage can provide (Worm *et al.* 2006). Thus, functional multimetrics and functional traits can be desirable characteristics to consider, and even maximize, in conservation planning. In contrast to species richness and diversity, it remains unknown the extent to which functional traits can be inferred when using

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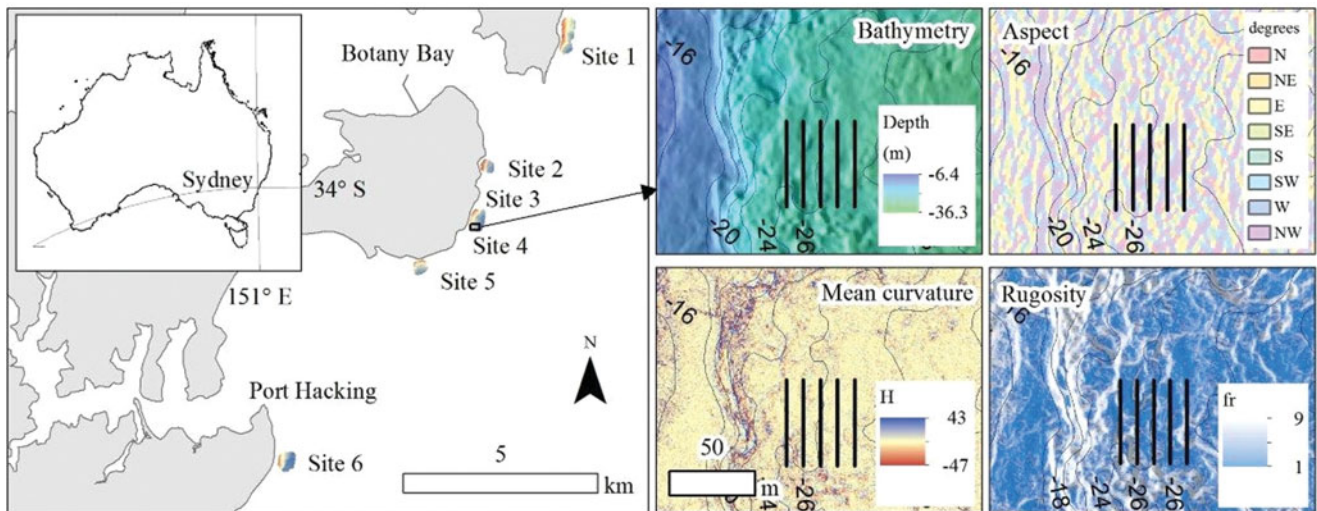
Figure 1 Location of fish assemblage sampling sites and multibeam survey areas off Sydney, Australia and example of hillshaded and depth contoured spatial layers over transect lines (n = 5) for Site 4 at 0.5 × 0.5 m bin scale.

remotely sensed habitat mapping as surrogates or predictors for biological metrics important for conservation (Parsons *et al.* 2014).

Here, we assessed novel relationships between fish functional traits and multimetrics and potential habitat surrogates on rocky reefs by testing the hypothesis that habitat structural variables derived from remotely sensed habitat mapping are good surrogates for functional traits and multimetrics of fish assemblages in addition to traditional taxonomic metrics (e.g., species richness, abundance). We also examined patterns over a range of remote sensing spatial scales to determine which scale is the optimal surrogate for representing functional and taxonomic metrics.

METHODS

Sampling fish assemblages

Fish assemblages were sampled on rocky reefs off the Sydney region at 25–35 m depth, 12 times (approximately four times annually) from 23rd March 2009 to 10th May 2012. At each of six sites (distributed over 12 km of rocky coastline; Fig. 1), five transects were sampled with 10 m spacing and north–south orientation. All sites were relatively similar, in that they consisted of a mixture of low lying sandstone reef (sometimes covered in sand and sometimes exposed), a variety of boulders, small caves and overhangs. The transect size was 50 × 1 m and sampling was with high-definition video footage taken from 2 m above the bottom. The video was played back on a computer and all species of fish were identified and quantified to the lowest possible taxonomic level. Because it was often difficult to accurately quantify large schools of fish, no species was enumerated beyond 100 individuals per transect, although few schools of fish surpassed this estimate. The video method (2 m from the substratum) meant that very small and cryptic species

were generally not enumerated unless they were visible. Most other reef species were commonly encountered using this method and species composition was comparable to other methods (e.g., baited remote underwater video; Kelaher *et al.* 2014; Coleman *et al.* 2015) for which functional traits have proven useful for detecting change relevant to conservation.

Six functional traits were assigned for each species from the global reef fishes trait database of Stuart-Smith *et al.* (2013) because these traits were available for all species sampled here. Other potentially useful traits available from Fishbase (Froese & Pauly 2014) were not used because at the time of this study, they were unavailable for many of the species sampled. The traits used related to body size, trophic position and behaviour (Table 1). They cover species attributes relevant to various aspects of spatial variation and types of resource use relevant to habitat characteristics, and collectively allow finer partitioning of species functional similarities, according to this set of characteristics. While all traits were used to generate functional similarities and thus included in functional richness and dispersion metrics, we also explored patterns in three traits separately (maximum length [L_{Max}], trophic level [TL] and gregariousness), because these traits respond to conservation measures (Coleman *et al.* 2015). L_{Max} represents the theoretical maximum size of a given species based on its growth curve, rather than being a measure of individual body size measured from survey data. The actual size of fish seen in surveys could not be accurately estimated because videos were not equipped with stereo cameras and aspects such as visibility and distance and angle of a fish relative to the camera position would have biased size estimates. TL is a continuous index representing the position of each species in the food chain, and as for L_{Max}, was also obtained for each species from Fishbase (Froese & Pauly 2014). Values for other traits came from a combination of FishBase (Froese & Pauly 2014), published studies and biological knowledge of the authors here and in

Table 1 Traits used to calculate functional richness and dispersion. Data from Fishbase (Froese & Pauly 2014) are indicated with an asterix. Other traits were from author knowledge and Stuart-Smith *et al.* (2013).

Functional trait	*Category*	*Units*
Maximum length*	Body size	Total potential length a fish species can grow (cm), continuous
Trophic level*	Trophic	Index. Range 2–4.1, continuous
Trophic breadth*	Trophic	Number of prey phyla consumed. Range 1–6
Gregariousness	Behaviour	Index from 1–3 indicating solitary found in pairs or sometimes aggregating and schooling species
Water column position	Behaviour	Benthic, demersal, site-attached pelagic, roaming pelagic
Diel activity pattern	Behaviour	Diurnal, nocturnal

Stuart-Smith *et al.* (2013). Trophic diversity was calculated as the number of different trophic positions per sample. We calculated functional dispersion (F_{Dis}) and functional richness as the convex hull volume (F_{Ric}) with the R package 'FD' using the function dpFD (Laliberté & Shipley 2011). For statistical analyses, all metrics were averaged over the 12 times to match habitat variables for each transect and site (therefore n = 30). This ensured that each value used in the analyses was independent and that the relationships established were not based on a single diversity snap shot in time, but instead on longer-term estimates more useful to effective conservation planning.

Multibeam surveying of habitat variables

High resolution bathymetric data were acquired using swath acoustic surveying in February 2013 over the same site and transect positions where fish were surveyed (Fig. 1). Depth soundings were acquired using a pole-mounted Geoswath 125 kHz interferometric side-scan sonar (GeoAcoustics, UK) with three-dimensional motion solution using a POSMV (Applanix, USA). The seabed at each site was ensonified on a total of four passes of the vessel (100% overlap at 30 m transect lines) in two directions (N–S and E–W transects) at a rate of 3–4 pings m^{-1} in the along-track direction. A smoothed best estimate of trajectory (SBET) solution was calculated to provide an improved horizontal and vertical accuracy for soundings, achieving better than x = 0.04, y = 0.03 and z = 0.07 m.

The SBET was applied to the acoustic data files before initial filtering in GS+ (GeoAcoustics, UK) using group, water column, amplitude, box, along-track and across-track filters. Processed data files (GSF format) were merged into a sounding cloud surface in Fledermaus (QPS, the Netherlands) and a cube-model of depth soundings were created for further editing. The cube model resulted in the removal of soundings outside that of the International Hydrographic Office Order 1 standard (IHO1). The filtering and cubing process provided approximately 150–300 soundings per m^{-2} within each of the survey areas.

Cleaned soundings were gridded using Fledermaus (QPS, the Netherlands) with weighted averaging to produce digital elevation models (DEM) at 0.5, 1, 2 and 5 m horizontal grid scales for each transect. All spatial derivatives (see Table S1 for definitions) were then calculated from the DEM on a 3 × 3 cell basis at each of the grid resolution scales. The derivatives aspect and slope were calculated in ArcMap10 (ESRI, USA), rugosity in Fledermaus, and then plan curvature, profile curvature and mean curvature in Landserf (City University, UK). Data along each of the dive transects was extracted from each layer and used to calculate a transect mean. Mean and standard deviation (depth only) values were also calculated for each transect at each grid scale. Both dive surveys and the multibeam data indicated that sites were almost 100% reef. Thus a backscatter layer, that indicates variability in bottom hardness over unconsolidated habitats, was not included in analyses.

Statistical analyses

To include the spatial structure of the data (transects within sites), mixed models were used to quantify the strength of association between habitat variables and fish assemblage. Initially, flexible mixed-effects penalized cubic splines were fitted using the gamm package in the R language. However, the second-order quadratic and third-order cubic terms were never required for any of the trait variables at any spatial scale, with the exception of a quadratic term for the aspect habitat variable. The preferred model was a second-order linear mixed model using both linear and quadratic terms for aspect, and linear terms for all other habitat variables, and was fitted using the lme4 package in R. Given that aspect represented the compass direction that a topographic slope faced, it was a cyclic variable (in the sense that adding 360 degrees to aspect corresponds to no change). To account for this, a quadratic term was added to the model to account for any nonlinear effect of aspect over its range of measured values (i.e., 92–213 degrees). This quadratic variable is referred to as QAspect throughout.

For analysis, data from the 12 times of sampling were pooled to capture integrated variation in fish assemblages as a whole, rather than among times, to better inform conservation planning. Consistent with other long-term sampling in the study area (Gray & Otway 1994), *a priori* analyses also revealed that there were no consistent patterns in fish abundance with season that warranted its inclusion as a factor (Kelaher 2010). Prior to analysis, predictor variables were evaluated for collinearity, and variables with |r| > 0.7 were combined

Table 2 R^2 values from linear mixed models evaluated using the marginal R^2 formula of Nakagawa & Schielzeth ([2013](#)) for each spatial scale averaged across the entire suite of habitat variables and each variable averaged across all spatial scales. Values significant at $p < 0.05$ are shown in italics. ∗Marginally non-significant ($p < 0.07$). MC = Mean curvature; PC = Plan curvature; SD = Standard deviation.

	Across all habitat variables				Across all spatial scales					
	0.5 m	*1 m*	*2 m*	*5 m*	*Depth*	*MC*	*PC*	*Rugosity*	*Aspect*	*QAspect*
Species richness	*0.404*	0.553∗	0.432∗	*0.596*	0.040	0.005	0.060	*0.205*	*0.149*	0.038
Total abundance	0.285	*0.412*	0.313	0.303	0.060	0.011	0.038	0.136	0.051	0.032
SD of species richness	0.150	0.142	0.296	0.326	0.056	0.008	0.018	0.013	0.053	0.025
SD of abundance	0.174	0.255	0.181	0.254	0.019	0.038	0.026	0.010	0.030	0.037
Maximum length	0.195	0.203	0.164	0.127	0.040	0.020	0.011	0.000	0.020	0.023
Trophic level	0.161	0.243	0.101	0.137	0.004	0.078	0.033	0.061	0.012	0.040
Gregariousness	0.115	0.104	0.120	0.118	0.015	0.021	0.050	0.014	0.109	0.006
Functional richness	0.123	*0.425*	0.234	0.096	0.069	0.009	0.053	0.027	0.013	0.048
Functional dispersion	0.108	0.195	0.109	0.086	0.003	0.034	0.040	0.016	0.019	0.012

(Dormann *et al.* 2013). The R^2 from the linear mixed model was evaluated using the marginal R^2 formula (Nakagawa & Schielzeth 2013). This marginal R^2 quantifies the proportion of total variability that is explained by the fixed effects terms in the model, which here are the habitat variables. The statistical significance of R^2 was determined using bootstrapping techniques, whereby the model was refitted to each of 1000 randomizations of each trait variable.

RESULTS

The extent of multicollinearity among habitat structural variables increased as the spatial resolution of mapping decreased with 1, 3, 3 and 4 highly correlated pairs of habitat variables at 0.5, 1, 2 and 5 m spatial resolution of mapping respectively. Rugosity and slope were correlated at all spatial scales. Similarly, rugosity and standard deviation in depth were correlated at 1, 2 and 5 m resolution. Given that rugosity incorporates both standard deviation in depth and slope, we omitted standard deviation in depth and slope from all analyses. Similarly, we omitted profile curvature from all resolutions leaving in alternate habitat variables with which this variable was correlated.

A total of 38 species of fish were observed on videos over the 12 sampling times and 30 transects. A total of 40–59% of variation in species richness was described by the suite of habitat complexity variables at most spatial scales ([Table 2](#)). When variables were analysed individually, rugosity and aspect contributed most to this pattern across all spatial scales ([Table 2](#)) and when each scale was analysed separately ([Table 3](#) and [Figure 2](#)).

Similarly, the suite of habitat complexity variables explained a large proportion of variation (41%) in the total abundance of fish at the 1 m scale but no single habitat variable explained this pattern across all scales ([Table 2](#)). Instead, different variables were important in explaining variation in total abundance at different scales. Depth and aspect were important at the scale of 1 m and rugosity at 0.5 and 2 m

([Table 3](#)). Interestingly, different species likely explained the above relationships between habitat variables and fish total abundance. Abundances of the schooling species (*Trachinops taeniatus* and *Atypicthys strigatus*) were strongly correlated with depth at the scale of 1 m. Similarly, abundances of wrasses (*Coris sandageri* and *Opthalmolepis lineolata*) were correlated with aspect at the scale of 1 m ($p < 0.05$ for correlations between abundance and each habitat variable at the 1 m scale). Abundances of *Parma microlepis* and *Chromis hypsilepis* (schooling) were correlated with rugosity at most other spatial scales.

The entire suite of habitat variables were significantly correlated with functional richness only at the 1 m scale (explaining 43% of variation; [Table 2](#)) and when variables were analysed individually, depth explained this pattern ([Table 3](#)). Individual functional traits (L_{Max}, TL and gregariousness) and functional dispersion were not significantly explained by the suite of habitat variables ([Table 2](#)) or any individual habitat variable at any scale ([Table 3](#)). The exception was TL for which mean curvature explained ~11% of variation but only at the scale of 1 m ([Table 3](#)).

DISCUSSION

Functional metrics of fish assemblages are useful indicators for measuring change associated with conservation initiatives (Bates *et al.* 2014; Coleman *et al.* 2015) and elucidating new hotspots of fish diversity (Stuart-Smith *et al.* 2013). Despite this, and in contrast to traditional taxonomic metrics of species richness and abundance, we found that habitat structural variables from remotely sensed mapping were generally not useful predictors of functional richness or key functional traits of fish assemblages. This has important implications for conservation planning that often relies heavily on mapped surrogates of biodiversity when detailed biological information is lacking.

Table 3 R^2 values from linear mixed models evaluated using the marginal R^2 formula of Nakagawa & Schielzeth (2013) for each individual habitat variable at each spatial scale with significant values shown in italics.

	Depth				Mean curvature			
	0.5 m	*1 m*	*2 m*	*5 m*	*0.5 m*	*1 m*	*2 m*	*5 m*
Species richness	0.041	0.041	0.073	0.003	0.001	0.016	0.003	0.001
Total abundance	0.012	*0.172*	0.006	0.050	0.010	0.001	0.032	0.000
Maximum length	0.052	0.049	0.052	0.070	0.009	0.020	0.000	0.003
Trophic level	0.010	0.009	0.012	0.044	0.003	*0.114*	0.027	0.010
Gregariousness	0.061	0.000	0.044	0.055	0.002	0.029	0.035	0.016
SD richness	0.000	0.008	0.006	0.000	0.058	0.044	0.079	0.132
SD abundance	0.015	0.038	0.006	0.002	0.002	0.018	0.065	0.001
Functional diversity	0.002	*0.243*	0.001	0.031	0.002	0.011	0.024	0.000
Functional dispersion	0.002	0.003	0.000	0.005	0.017	0.082	0.009	0.030
	Plan curvature				Rugosity			
Species richness	0.065	0.001	0.117	0.054	*0.124*	*0.418*	0.056	*0.222*
Total abundance	0.036	0.003	0.062	0.063	*0.221*	0.010	*0.203*	0.112
Maximum length	0.000	0.048	0.015	0.009	0.020	0.005	0.024	0.004
Trophic level	0.053	0.049	0.002	0.001	0.040	0.000	0.001	0.000
Gregariousness	0.004	0.020	0.018	0.002	0.001	0.000	0.000	0.000
SD richness	0.044	0.071	0.017	0.000	0.032	0.015	0.043	0.153
SD abundance	0.067	0.027	0.060	0.047	0.006	0.015	0.002	0.034
Functional diversity	0.046	0.003	*0.161*	0.001	0.018	0.021	0.007	0.061
Functional dispersion	0.004	0.055	0.091	0.009	0.005	0.054	0.006	0.000
	Aspect				QAspect			
Species richness	*0.158*	0.056	*0.151*	*0.231*	0.015	0.021	0.031	0.084
Total abundance	0.002	*0.195*	0.004	0.001	0.005	0.031	0.005	0.087
Maximum length	0.101	0.001	0.069	0.040	0.013	0.081	0.004	0.000
Trophic level	0.041	0.057	0.005	0.018	0.015	0.014	0.053	0.064
Gregariousness	0.019	0.037	0.006	0.017	0.028	0.019	0.017	0.027
SD richness	0.008	0.000	0.028	0.014	0.007	0.004	0.123	0.027
SD abundance	0.082	*0.138*	0.048	0.166	0.002	0.020	0.000	0.003
Functional diversity	0.009	0.002	0.041	0.002	0.046	0.145	0.000	0.001
Functional dispersion	0.048	0.000	0.002	0.025	0.032	0.000	0.000	0.017
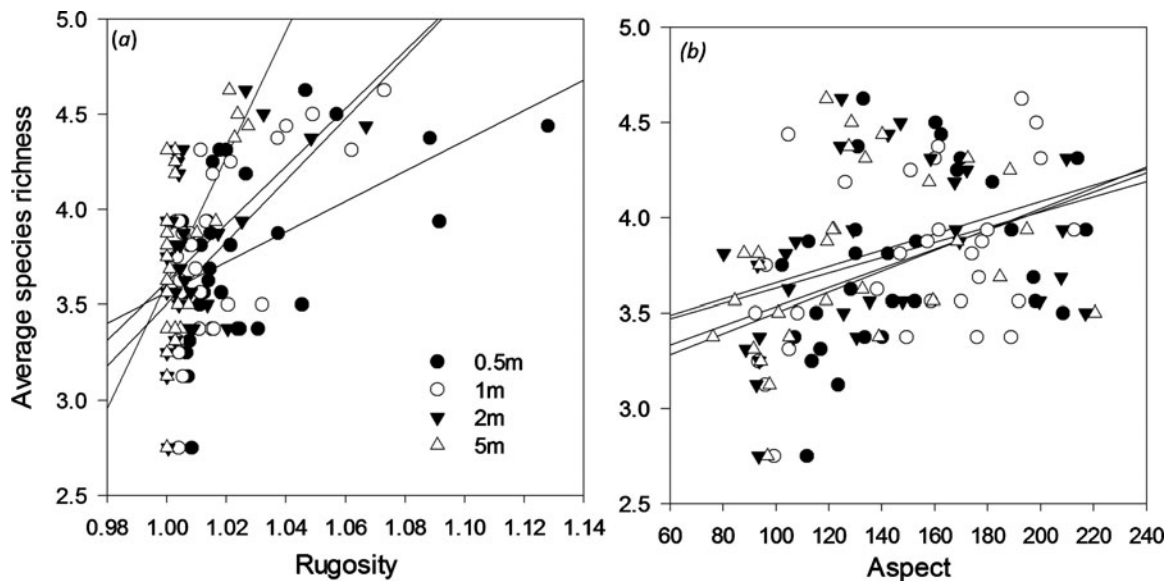
Figure 2 Relationships between average species richness per transect and habitat variables with which it was significantly correlated with (*a*) rugosity and (*b*) aspect, over the four scales of habitat mapping.

Remotely sensed habitat predictor variables proved to be strong surrogates for the traditional taxonomic metrics of fish species richness and abundance. Species richness of fish was best described by aspect and rugosity at all spatial scales. Reefs with different aspects may differ with respect to the strength and nature of prevailing currents, water flow, wave action and associated sessile invertebrate (Palardy & Whitman 2014) and pelagic assemblages. Thus, reefs with certain aspects may provide fish such as planktivores with greater food supplies or shelter from predators or harsh conditions (Coleman & Connell 2001). Similarly, reefs with greater rugosity and thus, more variation in depth, light regimes, water motion and sedimentation (Toohey 2007) are likely to be inhabited by a greater diversity of other species (e.g., sessile invertebrates; Rattray *et al.* 2009; Rees *et al.* 2013). In turn, these may provide a broader range of food sources for fish or a greater range of places for fish to shelter from predators, and thus support a more diverse fish assemblage. Regardless, remotely sensed habitat predictor variables such as aspect and rugosity appear to be strong surrogates for fish richness and abundance, and thus are useful for selecting areas in conservation planning when maximizing species richness and abundance are primary goals.

For traditional taxonomic metrics, the spatial scale of bathymetric mapping generally did not matter and strong correlations between habitat structure and species richness and abundance were seen even at coarser scales (5 m). Consequently, in conservation planning situations with limited resources (e.g., funding or time), bathymetric data may not need to be collected or processed at spatial scales <5 m to be relevant for estimating fish species richness and abundance. Nevertheless, habitat mapping at the scale of 1 m was correlated with the greatest range of fish metrics, including functional richness. The reasons for this pattern are not known but may be due to the matching of mapping at the 1 m scale with the spatial scales of sampling fish (1 m wide video transects). Even though most species encountered were generally wider-ranging species, some cryptic, site attached species that may respond to habitat variation on the 1 m scale were enumerated in videos. Furthermore, knowledge of which variables (traditional, functional etc) are the best correlates of habitat structure will also allow prioritization of the most appropriate biotic variables to be measured during field sampling. Certainly, identification of the most appropriate variables and scales to use will help ensure cost-effective conservation planning.

Functional traits are correlated to habitat variables in a range of marine environments (Angel & Ojeda 2001; Hewitt *et al.* 2008) but did not correlate with measures of remotely sensed habitat in this study. That is, in contrast to traditional taxonomic metrics, remotely sensed habitat structure was a poor surrogate for fish functional multimetrics and traits because there were no significant correlations between trophic, size, behavioural or overarching functional multimetrics and habitat predictor variables at any spatial scale. The exception to this was fish functional richness, which was positively associated with habitat structural variables (mostly depth) at 1 m only. This lack of a general relationship between remotely sensed habitat structure and fish functional richness, but strong correlation between fish species richness and habitat predictor variables, is surprising given the often strong relationships between functional and species richness (Pauly *et al.* 2001). However, we found no such associations between species richness and functional richness for the fish assemblages here (r = 0.142, *p* > 0.05), and nor did Coleman *et al.* (2015). The lack of relationship between habitat structure and fish functional richness and traits may, in part, be due to the fine spatial scale used to calculate the spatial metrics for this study (5 m), which may not fully capture habitat characteristics important to functional suites of fish species over greater spatial scales. For example, certain trophic groups of species such as predators may respond to habitat features, such as larger topographic changes (boulders, walls, drop-offs) than those captured here. Analysis of habitat variables over areas >5 m may be required to elucidate the value of remotely sensed habitat structure in predicting functional aspects of fish assemblages. Alternatively, the lack of relationship between fish functional traits and multimetrics and remotely sensed habitat mapping could be due to the method of sampling used (diver held video) and the component of the fish assemblage it sampled. We generally did not enumerate cryptic species in our survey method and these species are known to be highly associated with complexity of habitats (Willis & Anderson 2003). It is possible, therefore, that sampling cryptic fish assemblages using alternative methods may provide more power to detect subtle links to remotely sensed habitat mapping data.

The lack of correlation between fish assemblages and functional richness found here and elsewhere (Bates *et al.* 2014; Coleman *et al.* 2015), brings into question the validity of some of the common overarching aims of conservation. These aims often strive to preserve species richness under the assumption that protecting a broad range of species will also result in broad changes in or protection of ecological functions. For example, in New South Wales, Australia, the goal of marine reserves is to protect not only biological diversity but also ecological processes (NSW Marine Parks Authority 2001; Coleman *et al.* 2013; Kelaher *et al.* 2015). Thus, where conserving ecological processes and functions is a priority for conservation strategies, perhaps species richness is not the most desirable measure to maximize *a priori* in conservation planning. Instead, maximizing functional richness may be a better conservation target than species richness *per se* and thus, alternative planning surrogates must be sought for predicting functional richness.

Conservation planning has traditionally relied on measures such as species richness, diversity and abundance to prioritize areas for protection. Nonetheless, alternative measures such as functional traits and multimetrics may be useful for detecting biological change in conservation settings (Bates *et al.* 2014; Coleman *et al.* 2015), and may also be appropriate conservation targets where conserving ecological processes

and functions is a goal. However, while we show that high resolution remotely sensed measures of habitat structure predicted traditional taxonomic metrics of species richness and abundance, these useful relationships did not exist for functional traits and multimetrics, although the generality of this pattern needs to be determined by sampling alternative components of fish assemblages (e.g., cryptic species). In conclusion, the measures derived from marine remotely sensed habitat mapping may be appropriate and cost-effective surrogates for conservation planning where conserving species richness is the primary goal, but alternative surrogates may need to be sought to adequately describe functional aspects of fish assemblages. Coupling conservation planning to specific goals related to components of biodiversity to be protected will help ensure resilient marine communities into the future.

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Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0376892916000205

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