Sediment variability affects fish community structure in unconsolidated habitats of a subtropical marine park

Arthur L. Schultz[1,2,*], Hamish A. Malcolm[3], Michelle Linklater[4], Alan R. Jordan[5], Tim Ingleton[4], Stephen D. A. Smith[1,2]

[1]National Marine Science Centre, Southern Cross University, Charlesworth Bay, Coffs Harbour, NSW 2450, Australia
[2]Marine Ecology Research Centre, School of Environment, Science and Engineering, Southern Cross University, Lismore, NSW 2480, Australia
[3]Marine Ecosystem Research, Fisheries NSW, Department of Primary Industries, Coffs Harbour, NSW 2450, Australia
[4]New South Wales Office of Environment and Heritage, 59 Goulburn St, Sydney, NSW 2000, Australia
[5]New South Wales Department of Primary Industries, Locked Bag 1, Port Stephens, NSW 2315, Australia

ABSTRACT: Unconsolidated sediments form extensive seafloor habitats worldwide, yet few studies have examined fish assemblage patterns in relation to specific sediment type or morphology. Baited remote underwater videos (BRUVs) were deployed at 3 sites (3 replicates per site) in the Solitary Islands Marine Park (SIMP), in each of 4 apparent 'habitat types' identified from swath acoustic mapping backscatter imagery and bathymetry. Habitat types ranged in reflected signal backscatter intensity: very dark, dark, light, very light. Additionally, apparent morphological features were associated with each (e.g. very dark = lens-shaped; light = sand waves). Sediments were characterised at each site by conducting granulometric analyses of samples collected using a van Veen grab. Both the darker 'habitat types' were found to be gravels and both lighter types were fine sands. There was a strong pattern in fish assemblage structure in relation to habitat type, and distinct assemblages were seen between 'gravel' and 'fine sand' habitats. Species richness was higher in gravel than in sand habitats. Additionally, 6 species were only recorded in the very dark lens habitat. However, there were no apparent differences in assemblage patterns between the 2 fine sand habitats. Of the different granulometric measures, fish assemblages were most strongly correlated with a combination of median grain size, % gravel and arithmetic sorting. The current habitat classification system for the SIMP includes habitat type (unconsolidated or hard substrata) as criteria for conservation planning. Further division of unconsolidated habitats into 'gravel' and 'fine sand' categories is needed to better represent biotic assemblages.

KEY WORDS: Fish assemblage · Sediment type · Granulometrics · Backscatter intensity · Marine protected area

INTRODUCTION

Seascape-scale ecology is a growing trend in marine ecology (Grober-Dunsmore et al. 2007, Moore et al. 2011, Olds et al. 2012), and is analogous to landscape ecology in terrestrial systems (Turner 2005). However, while investigations at this scale are relatively common in the terrestrial environment (McGarigal & Cushman 2002, Wu & Hobbs 2002, Turner 2005), they are comparatively rare in subtidal marine environments. Nevertheless, many of the principles and methods defining terrestrial landscape ecology are

equally applicable to subtidal systems (Hinchey et al. 2008). As mapping of benthic habitats is generally a key requisite for seascape studies, much of the focus has been on shallow coastal systems for which remote data can be readily accessed through photographic or satellite imagery (Mishra et al. 2006, Moore et al. 2011, Thorner et al. 2013). More recently, developments in high-resolution swath acoustics have allowed cost-effective benthic mapping to extend into depths beyond that suitable for airborne remote-sensing methods (Holmes et al. 2007, Jordan et al. 2010, Brown et al. 2011, Rattray et al. 2013), and this has extended the capacity for seascape-scale studies across larger areas. Principally, this advance has greatly increased the ability to spatially link patterns of biological assemblages and ecological processes with broad geographic features such as seascape composition or orientation (Moore et al. 2009).

Mapping of this type has been recently applied to examine the influence of benthic habitat distribution on demersal fish assemblages (Moore et al. 2009, 2011, Schultz et al. 2012, Rees et al. 2013), and has been found to be an important component for the predictive modelling of biotic communities (Moore et al. 2009). However, to date, the focus has been on evaluating differences in demersal fish assemblages between rocky reef and soft-sediment environments (Anderson et al. 2009, Moore et al. 2009, 2011, Harvey et al. 2013), or examining biotic variation with other environmental parameters such as depth (Anderson et al. 2009, Fitzpatrick et al. 2012, Schultz et al. 2014) or distance from reef (Schultz et al. 2012). Despite the increasing availability of high resolution maps of benthic features, investigations into the effects of fine-scale differences in sedimentary habitats (both spatially and compositionally) on biotic patterns are rare. There are very few studies that explicitly use seabed backscatter of soft-sediments to examine correlations with fish assemblages. Using volume backscatter strength measurements which were also validated using granulometric analysis, D'elia et al. (2009) found a strong association between pelagic fish schools and broad sediment classes. However, to date, we have not found any published accounts that combined fish assemblage surveys, sediment analyses, and acoustic methods to assess the differences between fishes and the fine-scale structure of unconsolidated substrata.

When compared with rocky reef habitats, subtidal soft-sediment environments are considered to be homogenous and physically stressful habitats for biota (Underwood & Chapman 2000). However, these habitats can be highly heterogenous for a range of reasons (Thrush & Dayton 2002) and research on specific fish-habitat associations in unconsolidated environs has lagged behind comparable investigations of reef fish (Connell & Lincoln-Smith 1999, Thrush & Dayton 2002, Owen & Gladstone 2010). This lack of detailed data is out of proportion to the extent of the habitat, with the majority of the seafloor comprising unconsolidated sediments. In the interests of objective management of all habitat types and species in marine ecosystems, further understanding of patterns and processes of fish assemblages in unconsolidated habitats is required. Most sampling of fish in this habitat has been performed using trap or trawl methods (e.g. Gray & Otway 1994, Connell & Lincoln-Smith 1999, Travers et al. 2010). However, the destructive and extractive nature of these methods is often untenable in marine protected areas (MPAs).

As a non-destructive alternative, baited remote underwater video (BRUV) has become increasingly popular for studies of demersal fish assemblages (Ellis & DeMartini 1995, Willis et al. 2000, Willis & Babcock 2000, Watson et al. 2005, Harvey et al. 2007, 2012, Malcolm et al. 2007, 2011). BRUVs can effectively sample species of fish and elasmobranchs which are attracted to the bait, or attracted to the commotion around the bait, as well as species in the vicinity or passing through. As with all fish assemblage sampling methods, BRUV has limitations, such as the inability to effectively sample some very small cryptic species (Harvey et al. 2007), however BRUVs have been shown to be comparable to other methods (Cappo et al. 2004, Harvey et al. 2007, Langlois et al. 2010, Lowry et al. 2012). While most BRUV studies focus on reef fish assemblages, this method also provides an effective approach for assessing fish assemblages of soft-sediment environments (Harvey et al. 2007, 2012, Owen & Gladstone 2010, Schultz et al. 2012, 2014). Cappo et al. (2004) demonstrated that BRUVs, while sampling a different component of the overall assemblage, are as effective as trawling in resolving patterns in fish assemblage structure in unconsolidated habitats.

The lack of comprehensive biotic datasets is a typical problem in the objective planning and management of MPAs (Malcolm et al. 2010a, 2011). One method of overcoming this restriction is to use surrogates, which may include a reduced set of species (Smith 2005, Malcolm & Smith 2010) where such data are available, or environmental categories that effectively represent biotic patterns. In the absence of comprehensive biotic data, a habitat classification scheme (HCS) has been employed as a planning tool

for marine parks in New South Wales (NSW) (Malcolm et al. 2010a, 2011). This system uses hierarchical classification, based primarily on substratum type (unconsolidated sediments and hard substrata) and depth (shallow, intermediate and deep) to identify habitats likely to support different community types. However, if there is a mismatch between these physical categories and patterns of community structure, the effectiveness of planning and management is reduced (Stevens & Connolly 2004, Malcolm et al. 2010a).

Habitat characteristics and their relationship with fish assemblages have been examined in rocky reef environments (Friedlander & Parrish 1998, Malcolm et al. 2010a, Fitzpatrick et al. 2012), for factors such as latitude, distance from shore, depth, dominant benthos or topographic complexity, but fish assemblage data of this nature is comparatively rare for sedimentary environments. While there is considerable regional-scale (100s to 1000s of km) heterogeneity in sediments of the Australian continental shelf (Williams et al. 2010), there is scant information on associated biota. Indeed, the influence of finer-scale habitat heterogeneity has not been explicitly examined for fish assemblages of sedimentary habitats in NSW marine parks. Johnson et al. (2013) argue that studies examining abiotic habitat requirements of demersal fish require a decrease in study scale and an increase in resolution if conservation ecology is to progress in this field.

Seabed mapping in the Solitary Islands Marine Park (SIMP) and Solitary Islands Marine Reserve (SIMR) (Jordan et al. 2010) has revealed distinct differences in sediment characteristics based on backscatter imagery (see Fig. 1). Large areas of relatively darker-shaded, higher-intensity backscatter suggest a more 'reef-like' seafloor, such as pebbles and cobbles, while lighter-shaded, lower-intensity backscatter suggests sandy habitat types (Jordan et al. 2010). In the same way that different fish assemblages have been recorded in different habitat types on hard substrata (Anderson & Millar 2004, Malcolm et al. 2010a, 2012, Fitzpatrick et al. 2012), it is likely that assemblages will differ between different sedimentary habitats. In previous work, Schultz et al. (2014) detected patterns supporting this hypothesis in a study which primarily focused on the effects of depth and distance from shore. They found that fish assemblages were correlated with backscatter intensity, which was potentially confounding the patterns in assemblage structure across the main factors (Schultz et al. 2014). Here, we provide a more robust and targeted test of the relationship between type of unconsolidated sediment and fish assemblages to further inform the refinement of the HCS for the SIMP.

The specific aims of this research were therefore to (1) evaluate the relationship between fish assemblage structure and different types of unconsolidated habitats (defined using high-resolution swath acoustic mapping and validated using sedimentary granulometrics); and (2) evaluate if acoustic backscatter potentially represents an effective physical proxy for demersal fish assemblages on the inner continental shelf of subtropical eastern Australia.

MATERIALS AND METHODS

Study area and backscatter metrics

The SIMP and adjacent SIMR are positioned in the Tweed-Moreton Bioregion on the mid-north coast of NSW, south-eastern Australia, and, combined, cover approximately 860 km^2. Both the SIMP and SIMR are multiple use MPAs that contain sanctuary zones (SZs), habitat protection zones (HPZs) and general use zones (GUZs). This region is known to exhibit high diversity due to a broad overlap between tropical and temperate fauna, with consequently high conservation status (Harriott et al. 1994, Smith et al. 2008, Malcolm et al. 2010b). While there are extensive reef habitats throughout the SIMP and SIMR, the majority (~80%) of mapped benthic habitat is unconsolidated sediments.

An area of approximately 24 km^2 positioned within the GUZ in the SIMR and SIMP was designated as the study area (Fig. 1). The study area had almost complete swath acoustic mapping coverage using a 125 kHz GeoSwath interferometric sidescan sonar. Cleaned backscatter data were gridded at 5 × 5 m grid cell resolution and the layers examined in ArcGIS (ArcGIS v9.3, ESRI Software). Beam and scatter functions were extracted and applied to normalise the data. There are potential problems with visually interpreting sidescan sonar imagery to define between habitats, in part due to artefacts left by the beam footprint. Artefacts are a consequence of each measurement taken from the different grazing angles of the swath not being subject to the same isonification geometry (Hughes-Clarke 1994). Dual-transducer systems also suffer from a paucity of data at nadir, requiring interpolation of backscatter immediately below the vessel. Thus only broad backscatter classes were delineated from the backscatter and used to define the different seabed types, and, where possible, sites were placed away from obvious artefacts.
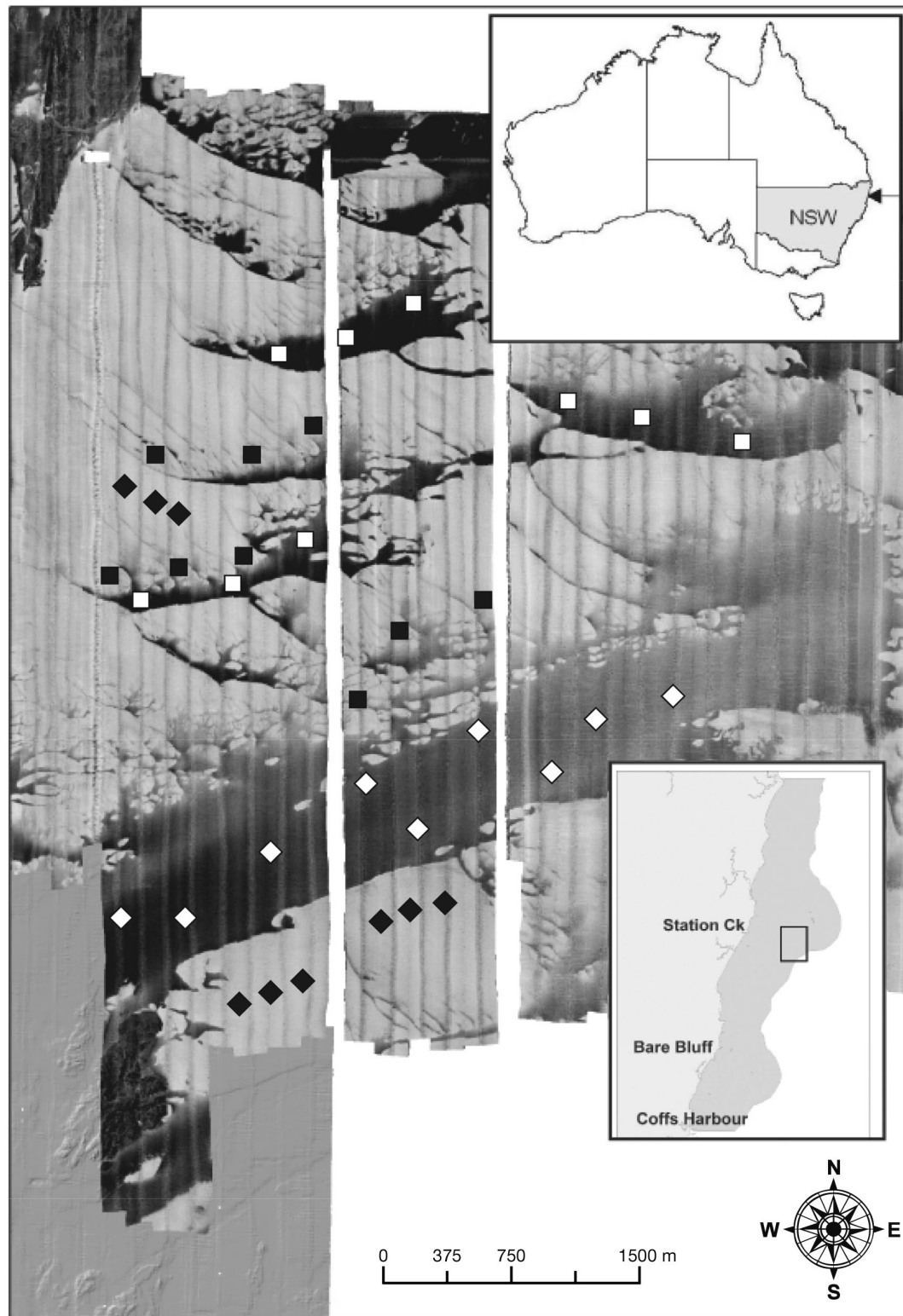
Fig. 1. The location of the 36 individual stereo-BRUVs deployments within the Solitary Islands Marine Reserve and Solitary Islands Marine Park, New South Wales, Australia. White squares = dark lens sites, white diamonds = dark shade sites, black squares = complex sand sites, black diamonds = flat sand sites. Background shading represents reflected signal backscatter intensity, with darker shading representing greater intensity and lighter shading representing less intensity. Top inset shows study area in relation to Australian coastline. Bottom inset shows study area position within the SIMP/SIMR area (shaded)

Initially, 4 apparent 'habitat types' were selected based on a combination of relative backscatter (greyscale) intensity and morphological differences in habitat types. Relative backscatter intensity (very dark = very high intensity, dark = high intensity, light = low intensity, very light = very low intensity), in which darker areas represent coarser sediments comprising gravel and cobbles, while lighter shades represent finer sediments (Jordan et al. 2010), was used to define between areas with different sediment types. Secondly, there were also visually apparent morphological differences in habitat size, shape, and orientation differentiating these habitat types. The very dark areas were narrow, elliptical shaped lenses, the dark areas were more broadly spread, the light areas appeared to have complex bedforms with sand waves, and the very light areas were flat. For the purpose of this study, we named these 4 habitats dark lens (DL), dark shade (DS), complex sand (CS) and flat sand (FS). Three sites were sampled within each of the 4 'habitat types' (e.g. DL1, DL2 and DL3) using BRUVs, with 3 replicate BRUVs per site. All 36 replicates were distributed within a fixed depth range (35 to 50 m), and within 4 km of each other, to negate effects of depth or meso-scale spatial variation on fish assemblage structure (Schultz et al. 2014). Each of the 3 BRUV replicates deployed at a site within a habitat was spatially separated by at least 200 m. The general position of each site and coordinates for each BRUV deployment were selected using ArcGIS. Coordinates were uploaded to a handheld GPS for positioning of BRUVs and collection of sediments in the field.

Ten, 25, 50 and 100 m radius buffers were generated around each BRUV deployment using the Buffer tool in ArcGIS (v9.3). However, when calculating spatial statistics, larger buffer sizes tended to include more values associated with artefacts in the beam footprint than smaller buffer values, and only spatial statistics for the 10 m buffer are discussed hereafter. Zonal statistics (ArcGIS Spatial Analyst) were performed on the backscatter data (5 m cell size) at this buffer radius. Statistics including mean, minimum, maximum, range, standard deviation and sum of cell values were calculated within the buffer zone (10 m radius) around each BRUV sample. These results were output to a table and incorporated into the variable data for subsequent statistical analyses.

Field methods

Field sampling was conducted during a 3 wk period of good weather in October and November 2011 (Austral spring). To avoid potential confounding effects associated with different levels of protection (i.e. fishing pressure) among sites, all sampling sites were within GUZs in the SIMP and SIMR. Fish assemblages in each of the 4 habitat types were assessed using BRUVs deployed for 30 min (Harasti et al. 2015), and sediment granulometry was determined from samples extracted using a van Veen grab (1 sediment sample per site). All sediment grabs were deployed after BRUVs were completed and sediment samples were discarded and repeated if the van Veen grab was not fully closed. The BRUVs unit was the replicate in the study, and 3 replicates were deployed at each site, generally within 5 min of each other. Thus, a total of 36 replicates were completed in the study area. Each BRUV unit comprised a digital camcorder with a wide-angle lens, inside a waterproof housing. Housings were secured within a steel attachment frame, and a rope and float system linked the unit to the surface. We used ~1 kg of pilchards *Sardinops neopilchardus* mashed into a bait bag approximately 1.5 m from the cameras for each 30 min deployment (Hardinge et al. 2013). Deployment methods follow those of Malcolm et al. (2007).

Video interrogation

Video files were converted to avi format, and analysed using the program EventMeasure (SeaGIS). The identity of each species of fish and an index of its relative abundance (MaxN) were recorded. MaxN is the maximum number of each species of fish within the field of view at any one instant during a 30 min recording (Malcolm et al. 2007). This removes the possibility of double counts of individual fish. Very small fish that could not be identified were not recorded.

Sediment analysis

Sediment samples were dried in an oven at 60°C before any subsequent processing. Once dry, three 200 g subsamples were taken from each van Veen grab sample and sieved though a series of nested sieves on a Ro-Tap Sieve Shaker (W. S. Tyler). Sieve sizes were scaled at 1/2 phi intervals according to the Wentworth scale to separate pebbles and cobbles (gravels), from coarse sediments (granules, coarse, medium and fine sand) and the finer sediment fractions (silt and clay) (Wentworth 1922). After sieving, each component of the overall sample was weighed

to the nearest 0.1 g. This dataset was then processed in the grain size distribution and statistics package GRADISTAT (Blott & Pye 2001), which generates mean, mode, sorting, skewness, median and other statistics, both arithmetically and geometrically (in metric units) and logarithmically (in phi units), using both moment (Friedman & Johnson 1982) and Folk and Ward (Folk & Ward 1957) methods.

Statistical methods

A range of multivariate and univariate analyses were performed using the PRIMER + PERMANOVA statistical software package (Clarke & Gorley 2006, Anderson 2001, Anderson et al. 2008). A 2-way hierarchical model was used, with Habitat analysed as a fixed factor, and Site analysed as a random factor nested within Habitat. Non-metric multi-dimensional scaling (nMDS), based on a Bray-Curtis dissimilarity matrix of square root-transformed data, was used to visually depict patterns in the fish assemblage structure across different habitats. Permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001, Anderson et al. 2008), was then used to test the null hypothesis of no significant difference between Habitat, and between Site nested within Habitat.

The relationship between the different granulometric measures and the biotic data was explored in 2 ways. (1) Bubble plots, scaled to represent the value of the factor of interest, were superimposed on the biotic data to visually compare the different granulometric measures with the fish assemblages (Clarke & Gorley 2006). (2) Fish data and different measures of sediment data were quantitatively explored using BIOENV in BEST (Clarke & Ainsworth 1993). In our case, the BIOENV procedure conducted rank correlations between Bray-Curtis dissimilarity matrices of the fish assemblage data and each of the statistical measures of granulometry (mean grain size, median grain size, etc.), and found the combination of factors that gave the highest correlation coefficient. Prior to analysis, granulometric measures were tested for autocorrelation in BIOENV and the eleven initial measures were reduced to 5 (median grain size, % gravel, arithmetic sorting, skewness and kurtosis) as a result.

Where PERMANOVA revealed a significant difference in assemblages between the habitat types, the SIMPER routine (Clarke & Warwick 2001) was applied to the biotic data to determine which species were primarily responsible for differences in assem-

blage structure. Univariate PERMANOVAs (using Euclidean distance as the similarity measure) were performed for species that were consistently found to contribute the most to differences among factor levels. Correlations between metrics generated from swath imagery and granulometrics were evaluated using the RELATE procedure. Correlation between swath metrics was first tested using draftsman's plots, and minimum cell value and range of cell values were retained, as all other variables were closely correlated. The range metric (the difference between the highest and lowest value) was used for subsequent analyses, as it was the best indicator of sediment complexity between minimum cell value and range of cell values. Matrices for swath metrics and granulometrics were constructed using Euclidean distance as the similarity measure. Both datasets were normalised prior to construction of similarity matrices. The RELATE procedure (using 4999 permutations) was then applied to correlate the swath metrics with the granulometrics using Spearman rank correlation.

RESULTS

General

A total of 19 species from 14 families was recorded from the 4 habitat types. Of these, 9 species were recorded in only 1 habitat type, and each habitat type contained at least 1 of these 9 species. The most speciose family was the flatheads (Family Platycephalidae, 3 species) followed by shovelnose rays (1 Rhinobatidae, 2 species) and grubfishes (1 Pinguipedidae, 2 species). When combining all MaxN values, the most numerically abundant species was southern yellowtail scad *Trachurus novaezelandiae* (211 ind.), followed by the longspine flathead *Platycephalus longispinis* (149 ind.), whiting *Sillago* spp. (117 ind.), bluespotted flathead *Platycephalus caeruleopunctatus* (58 ind.) and six-lined trumpeter *Pelates sexlineatus* (54 ind.).

Multivariate analyses

nMDS ordinations demonstrated a clear difference between assemblages found in different habitats (Fig. 2). The nMDS separated assemblages found in the 2 gravel habitats from those found in the 2 fine sand habitats (Fig. 2A). There was some within-habitat separation for DL and DS types, with 1 DS site clustering with 2 DL sites towards
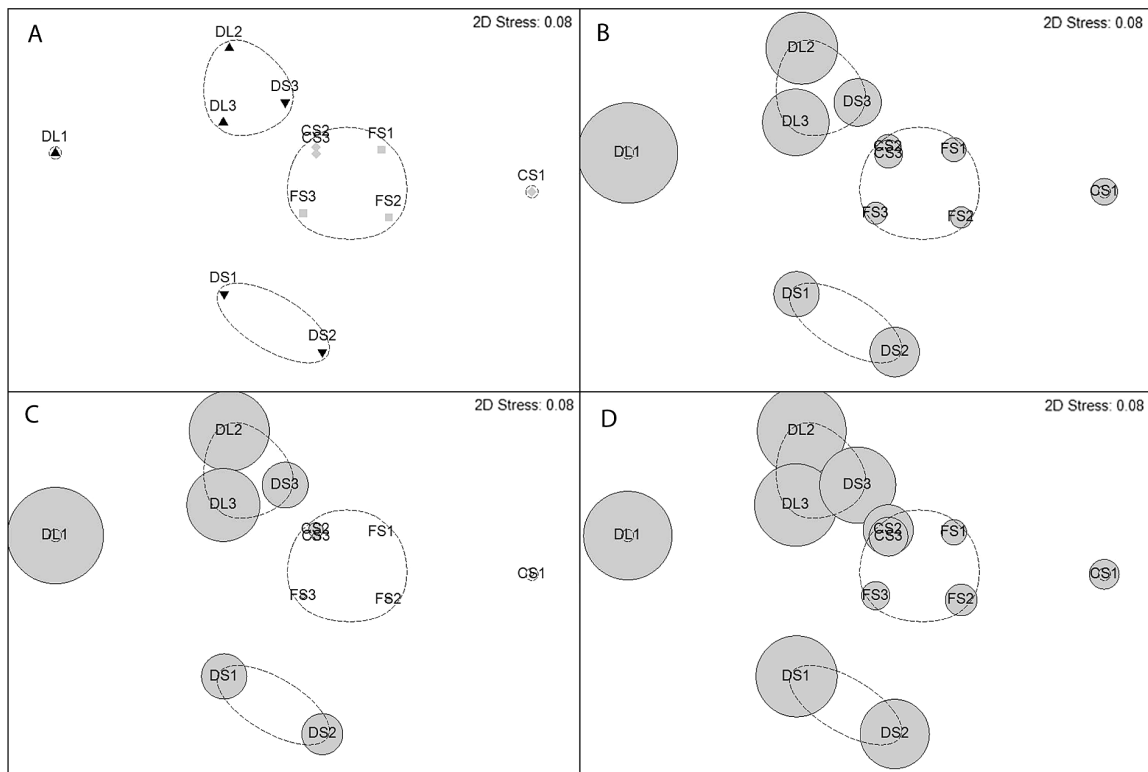
Fig. 2. Non-metric multi-dimensional scaling (nMDS) ordination of the fish assemblage (centroids of the 3 replicates for each site) across the 4 habitat types, and bubble overlays for the 3 factors found to have the best combined correlation coefficient. A smaller bubble = relatively smaller value (lower % gravel, lower arithmetic sorting value, lower median grain size), grading to a larger bubble = relatively larger value (higher % gravel, higher arithmetic sorting value, higher median grain size). Points in the left part of the plot represent assemblages found in the 2 gravel habitats, while points in the right part of the plot represent assemblages in the fine sand habitats. (A) No factors selected; (B) median grain size; (C) % gravel; (D) arithmetic sorting. DL = dark lens; DS = dark shade; FS = flat sand; CS = complex sand. Dashed lines indicate 75 % similarity

the top of the plot, and 2 DS sites clustering together below these. The one DL outlier to the far left of the plot was largely attributed to the high abundance of six-lined trumpeter at that site, as well as 4 other species (*Parapercis nebulosa*, *Parapercis stricticeps*, *Priacanthus blochii*, *Mustelus antarcticus*) that were otherwise not recorded in this study. The FS sites and 2 of the CS sites clustered together to the left of these as a discrete group. The remaining outlier (CS1) included 1 species otherwise not recorded in the study (*Rachycentron canadum*), and one other species only recorded in one other replicate (*Orectolobus maculatus*)—if these 2 species were removed from the analysis, then this site clustered with all other fine sand habitat sites. PERMANOVA supported the trends seen in the nMDS ordination, indicating a significant effect for the factor Habitat (p = 0.004) but not for Site (Habitat) (Table 1).

To visually explore the effects of different granulometric measures on the fish assemblage patterns, dif-

ferent measures were superimposed on the biotic data points (Fig. 2B–D). The strength of these associations was also quantified using BIOENV. A combination of median grain size, % gravel and arithmetic sorting produced the best overall correlation coefficient ($\rho = 0.51$, Table 2), with % gravel having the highest individual correlation coefficient ($\rho = 0.50$, p = 0.014). These 3 environmental factors were therefore superimposed over multivariate ordination plots (Figs. 2B–D). While nMDS ordination also shows

Table 1. PERMANOVA for the analysis of differences in assemblage structure across the different factors. **Bold**: significant at $p \leq 0.05$

Source of variation	df	MS	Pseudo-F	p
Habitat	3	2530.9	3.0397	**0.004**
Site(Habitat)	8	832.61	1.4327	0.102
Residual	24	581.16		

Table 2. Spearman rank correlation coefficients from the BIOENV procedure for 36 sites, for 5 factors (K = number of factors for each combination, only 3 factors which generated strong correlations are shown: D_{50} = median grain size, % Gr = percentage gravel, σ = arithmetic sorting). $ρ_w$ = correlation coefficient for that combination

K	Best	Variable combinations ($ρ_w$) 2nd	3rd
Overall	D_{50}, % Gr, σ 0.51		
Two factors	D_{50}, σ 0.50	D_{50}, % Gr 0.49	
Single factor	% Gr 0.50	D_{50} 0.49	σ 0.37

both median grain size and arithmetic sorting to be visually correlated with the fish assemblage, BIOENV generated lower individual values than for % gravel (median grain size ρ = 0.49, arithmetic sorting ρ = 0.37, Table 2).

The best nMDS visualisation of the 3 measures applied in overlays was % gravel (Fig. 2C). The DL1 site was notably different in both assemblage structure and % gravel (73.2 %), and separated clearly from other sites to the left of the ordination. With slightly lower % gravel values, the DL2 (50.7 %) and DL3 (42.2 %) grouped together in the top right of the plot. Of the DS sites, DS3 had the highest % gravel (16.7 %), and this assemblage grouped with DL2 and DL3. Sites DS1 (16.3 %) and DS2 (13.4 %) grouped as a separate cluster in the lower portion of the plot. All fine sand sites, which had between 0 and 1.7 % gravel, grouped as the main right-hand cluster, except for CS1 which separated to the far right of the plot.

Having established that differences in assemblage structure existed across the different habitats, the SIMPER routine was used to determine which species were primarily responsible for these differences. Four species (*Trachurus novaezelandiae, Pelates sexlineatus, Platycephalus longispinis* and *Sillago* spp.) were found to be important discriminators, accounting for >50 % of assemblage differences; these were therefore explored further with univariate analyses.

Univariate analyses

Overall, species richness was higher at gravel sites, with 14 species recorded in the DL habitat, 11 species in the DS habitat, 8 species recorded in FS habitats,

and 8 species in CS habitats. While some of the more common species were relatively evenly distributed across all habitats, others showed greater association with either fine sand or gravel habitats in general. For example, eastern shovelnose rays *Aptychotrema rostrata* were more than 4 times more abundant in fine sand habitats than in gravel habitats, while another species from the same family, the eastern fiddler ray *Trygonorrhina fasciata*, was almost 3 times more abundant in gravel habitats than in fine sand habitats. Six species recorded in the DL habitat were not found in any other habitat type (*P. sexlineatus, M. antarcticus, P. blochii, P. nebulosa, P. stricticeps, Gymnothorax prionodon*). Most notably, six-lined trumpeter *P. sexlineatus* was abundant at the DL sites but absent from all other habitats.

While mean species richness was slightly higher in the 2 gravel habitats than in the 2 fine sand habitats (Fig. 3), these differences were not significant in the PERMANOVA analyses (Table 3). One site, DL1 (the site with the highest % gravel), had noticeably higher species richness (8) than all others which ranged between 3.33 and 6. Total MaxN values varied between 7.33 and 27 across all sites except for site DL1, which had a total MaxN value of 40.33 (Fig. 3). This difference was mostly due to high abundances of both *P. sexlineatus* and *T. novaezelandiae*. Again, no significant differences were found in the PERMANOVA analysis (Table 3). No obvious trends were evident for *T. novaezelandiae* (Fig. 4). This species was abundant at 3 sites (DL1, DL3 and CS2), but was otherwise uncommon or absent from all other sites. The PERMANOVA revealed significant differences associated with Site(Habitat) (p = 0.016), but not Habitat (Table 3). There was a clear trend for *P. sexlineatus,* which was only recorded at DL sites (Fig. 4). DL1 had high relative abundance, while low abundances were recorded at the other DL sites. The PERMANOVA revealed a significant Habitat effect (p = 0.017) but no Site(Habitat) effect (Table 3). There were slightly higher abundances of *P. longispinis* at fine sand habitats, with the highest relative abundance seen at FS sites, and lowest relative abundances at DS sites (Fig. 4). However, the PERMANOVA recorded no significant differences between Habitat or Sites(Habitat) for *P. longispinis* (Table 3). *Sillago* spp. were recorded at all sites, but were most abundant at FS sites, and least abundant at CS sites, while moderate relative abundances were seen in both gravel habitats (Fig. 4). The PERMANOVA revealed a significant Habitat effect (p = 0.004) but not for the Site(Habitat) factor (Table 3).
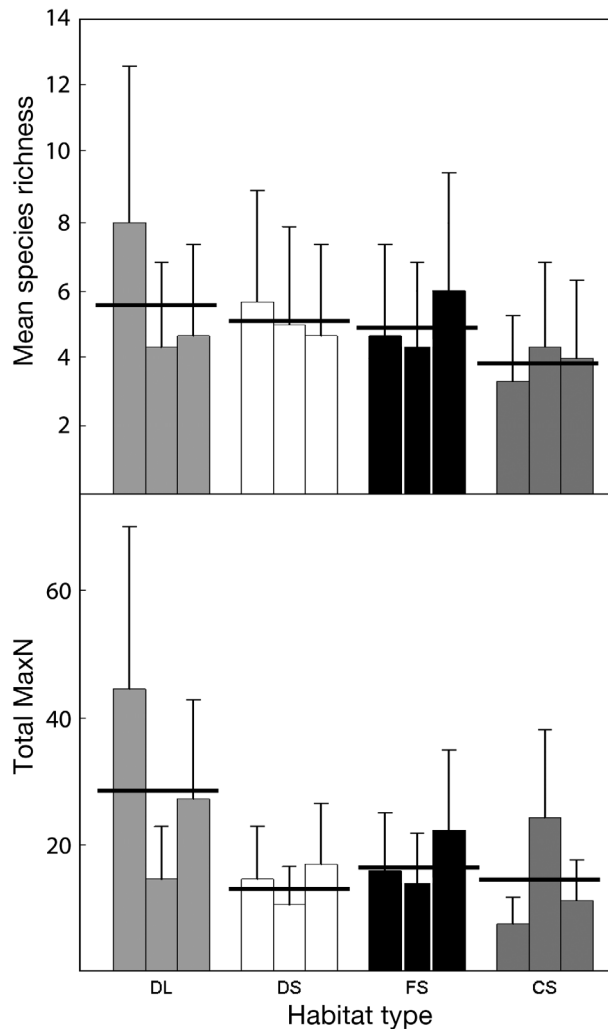
Fig. 3. Mean species richness and total MaxN (±SE) across 4 habitat types (3 replicates per type). Horizontal bars: mean relative abundance for each species within each habitat type. See Fig. 2 for habitat abbreviations

Correlations between swath metrics and granulometrics

Correlations between the similarity matrices for swath metrics and granulometrics indicated a strong and highly significant relationship ($\rho = 0.825$, $p = 0.0002$). This suggests that backscatter intensity from swath acoustics is a reliable proxy for sediment composition at the spatial scale examined here.

DISCUSSION

General

Using a combination of spatially explicit benthic mapping techniques and BRUVs, this study has demonstrated that there are clear differences in fish assemblages associated with unconsolidated habitats with different acoustic backscatter intensity and granulometric characteristics. This is important because unconsolidated sediments are the predominant subtidal habitat in the SIMP but are poorly known because the majority of focus to date has been on reef habitat. To date, acoustic mapping (~25% of the marine park area) has revealed a number of unconsolidated areas with substantially different characteristics, particularly in backscatter intensity (Jordan et al. 2010). Our previous research indicated that fish assemblage patterns are linked to factors such as depth, but also suggested that sediment type may also be an important determinant (Schultz et al. 2014): this study further supports that hypothesis. Thus, in locations where sedimentary characteristics vary extensively over relatively large spatial scales (kilometres to 10s of kilometres), it is possible that the type or complexity of unconsolidated habitats may have a greater influence on patterns of demersal fish assemblage structure than factors such as depth (Schultz et al. 2014). Here we demonstrate the potential value of detailed backscatter maps in assessing spatial patterns of demersal fish in this context. By further ground-truthing the backscatter data, using granulometrics generated from grab samples, we have strengthened the validity of these findings, and provide an explicit measure of sediment composition for planning purposes that links broad-scale backscatter imagery to the fish assemblage.

Different measures of habitat heterogeneity have been recognised as potential predictors of fish assemblage patterns at a seascape scale (Grober-

Table 3. Univariate PERMANOVA for mean species richness (S) and total MaxN, and for the 4 species determined by SIMPER as being the primary drivers of assemblage differences across the study. Data are p-values. **Bold**: significant at p ≤ 0.05

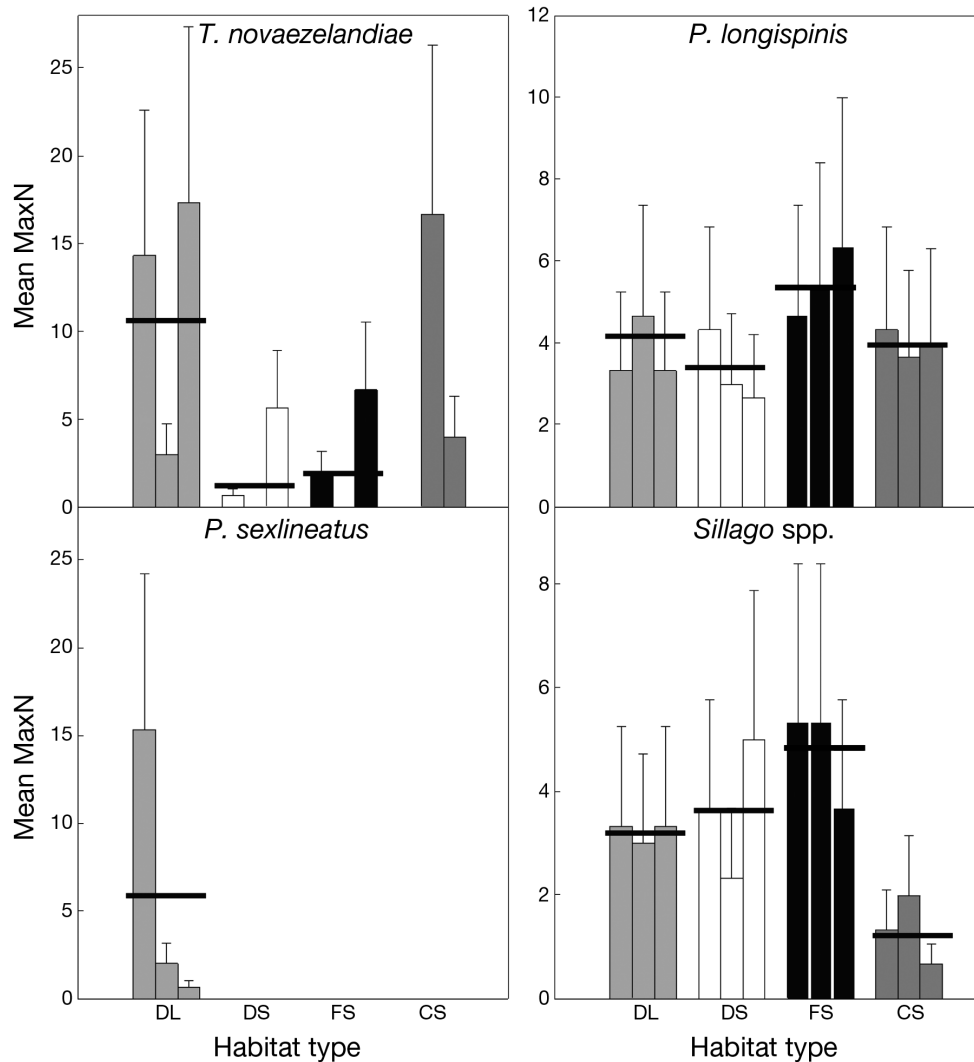| Source	S	Total MaxN	*Trachurus novaezelandiae*	*Pelates sexlineatus*	*Platycephalus longispinis*	*Sillago* spp.
Habitat	0.248	0.214	0.844	**0.017**	0.083	**0.004**
Site(Habitat)	0.384	0.322	**0.016**	0.801	0.45	0.854

Fig. 4. Relative abundances (mean MaxN ± SE) of 4 species determined by SIMPER as being most responsible for discriminating between fish assemblages across the 4 habitat types (3 replicates per type). Horizontal bars: mean relative abundance for each species within each habitat type. Significant Habitat effects were found for *Pelates sexlineatus* and *Sillago* spp., and a significant Site(Habitat) effect was found for *Trachurus novaezelandiae*. See Fig. 2 for habitat abbreviations

Dunsmore et al. 2007, Moore et al. 2011), and BRUVs have been used in conjunction with detailed habitat maps in other studies to assess the spatial ecology of different guilds of demersal fish (Colquhoun et al. 2007, Moore et al. 2009, 2011). Similarly, D'elia et al. (2009) used acoustic backscatter imagery and corroborating granulometric measures to assess pelagic fish schools. However, our study appears to be the first to use acoustic backscatter and granulometric measures, in combination with BRUVs, to assess assemblages of demersal fish in unconsolidated habitats.

A number of different factors may contribute to the disjunct patterns in assemblage structure between gravel and fine sand habitats in this study. Many fish

are epibenthic predators that are highly selective in their prey (Thrush 1999), and may consequently frequent specific habitats or forage in habitats substantial distances from their shelter habitat (Langlois et al. 2005, Grober-Dunsmore et al. 2007). For example, white trevally *Pseudocaranx dentex* was found to travel between 4 and 7 km in one day (Afonso et al. 2009). This species, which was recorded in our study on the DL and DS habitats, but not in either fine sand habitat, is known to feed on epibenthic crustaceans such as *Nebalia* species (Rainer & Unsworth 1991) and molluscs. Whether this species is making feeding excursions from nearby reefs or these gravel-dominated habitats are a residential area for individ-

ual fish is unclear, but it is possible that specific prey items are more common in this habitat type than in finer sands. Similarly, *P. sexlineatus*, which has a preferred diet of crustaceans (Sanchez-Jerez et al. 2002), was present in large numbers in the DL habitat and absent from other habitats. While benthic community ecology is far more complicated than a simple relationship between sediment type and community type (Seiderer & Newell 1999, J. Rowland unpubl.) it is possible that specific prey items for these species are found in higher densities in gravel-rich sediments than in finer sands. Furthermore, it is also possible that gravel-dominated habitats can act as a 'reef surrogate'. Several of the species recorded in our study, such as the 2 mentioned above, are considered 'reef-associated' (Kuiter 1993, Swainston 2011) and were both moderately abundant in the gravel habitats in this study. These gravel-rich habitats may provide refuge from larger predators, and/or foraging opportunities not available on reefs for some species.

Juvenile life stages of some fish are often positively correlated with the complexity of soft-sediment habitat (Auster et al. 1995), and the use of microhabitat features in sedimentary habitats must also be considered in this context, rather than at the seascape scale. It is possible that fine-scale habitat complexity is higher in gravel- and/or cobble-dominated habitats than in sand-dominated habitats in terms of rugosity and available shelter for fish, and this could influence predation and predator avoidance, although this clearly requires further investigation. For example, Thrush et al. (2002) found a positive correlation between numbers of juvenile snapper *Pagrus auratus* and both biogenic features (e.g. sponges, hydroids, suspension-feeding bivalves) and heterogeneity created by physical features (e.g. cobbles, shell hash, sand waves). Enhanced survivorship of juvenile cod *Gadus morhua* was demonstrated (Gotceitas & Brown 1993) in cobble-dominated habitat when compared with sand/gravel habitats in the presence of a predator, with individuals using interstices within the cobble matrix as refuge. While juveniles were not the focus of our study, a number of small epibenthic predators, which may themselves be prey for larger biota, were recorded in the DL habitat, such as *Parapercis stricticeps*, *Parapercis nebulosa*, and *P. sexlineatus*. These species are small enough to potentially use larger cobble matrices as refuge from potential predators.

This study recorded low species diversity relative to that recorded for hard substrata in this marine park (Malcolm et al. 2007, 2010a, 2011, Schultz et al. 2012), which is typical of sedimentary habitats in other studies in eastern Australia (Williams & Bax 2001, Moore et al. 2011). However, the presence of strong differences in sediment type provides a component of habitat heterogeneity in unconsolidated habitats in the SIMP, which will likely increase available niches for a greater variety of organisms. Multivariate analyses demonstrated a significant difference between assemblages, and 11 of the 19 species recorded were found in only 1 of the 2 major habitat types (fine sand or gravel). Further evidence of habitat specificity in some sediment-associated species has been recorded in the SIMP. Schultz et al. (2014) detected 4 species that were only found in locations with higher intensity backscatter. These habitat-specific species, which are not likely to be primarily responsible for driving broad fish assemblage patterns in sedimentary habitats due to their rarity, are nevertheless important contributors to the biodiversity of the SIMP, and should be considered in conservation planning for this habitat type.

Implications for management

This study has implications for management of biodiversity in MPAs, where adequate and comprehensive representation of biodiversity is required (ANZECC TFMPA 1999). It suggests that, where biotic data are lacking, separating unconsolidated sediments into gravel and fine sand classifications, as an abiotic proxy, may improve conservation outcomes for demersal fish assemblages. The present categories used for the HSC, a planning surrogate for biota that is used in the SIMP and more broadly across NSW, only separates sedimentary habitats based on depth (Schultz et al. 2014). This mirrors the approach that has been found to be effective for reefs (Malcolm et al. 2010a, 2011). Fortunately, sediments can be readily separated and mapped across broad areas using backscatter-derived metrics, and these data can be applied in systematic conservation algorithm tools such as Marxan (Malcolm et al. 2012). This is also relevant from the perspective of spatial fisheries management, as many of the species recorded in this study are commercially or recreationally targeted.

Acoustic mapping techniques can be a useful tool for predictive modelling of fish assemblages in sedimentary habitats, both in the SIMP and other areas. Previous studies have demonstrated sediment characteristics such as % sand to be useful predictors for infaunal communities (see Huang et al. 2009); however, these parameters have been typically derived by the removal of a sediment sample. With the tech-

nological advances in acoustic mapping, broad-scale predictive modelling of these sediment characteristics (and thus associated communities) has become viable (Brown et al. 2011). While the link between sediment characteristics and demersal fish assemblages is not widely explored, predictive modelling techniques applied to benthic communities could also be modified to suit fish. An extension of this approach into other depth ranges, and across a broader spatial area, as well as examining the temporal stability of these patterns, would assist in determining if the findings of this study are more broadly applicable. A number of other seascape-scale questions, such as effects of habitat orientation, connectivity or isolation, and proportion or size of individual habitats, still need to be examined, as do specific granulometric questions such as sediment origin and biogenic fraction.

The use of high-resolution acoustic data to reliably predict both infaunal and fish communities is potentially a very valuable tool for planning and management of this dominant marine habitat. Our data suggest that, for the purpose of separating discrete fish assemblages, the division between assembleges associated with 'gravel' and 'fine sand' habitat lies between 13.4% gravel and 1.7% gravel. While our data do not allow an exact value to be set, they nevertheless highlight the importance of recognising these broad habitat types for conservation planning in this marine park. We have demonstrated that metrics generated from mapping in GIS to separate dark and light backscatter areas are suitable to separate gravel and sand habitats in this region, and these data also provide a testable framework for other MPAs, both in this region and more widely.

CONCLUSIONS

Differences in fish assemblage structure were found across most of the unconsolidated habitats examined, with the greatest difference between fine sand and gravel habitats. Nine species that were recorded in gravel habitats were not recorded in fine sand habitats, and conversely 2 species recorded in fine sand habitats were not found in gravel habitats. Thus, our study has clearly demonstrated that sediment complexity in unconsolidated habitats, within a fixed depth range, has an effect on demersal fish assemblage structure. Gravel and fine sand habitats are readily discernible in backscatter layers sourced from swath mapping, and backscatter intensity is strongly correlated with sediment granulometry. This

provides the framework for an extension of the use of biophysical surrogates for objective conservation management of biodiversity in a dominant, though little studied, habitat type.

LITERATURE CITED

Afonso P, Fontes J, Holland KN, Santos RS (2009) Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex,* and their implication for marine reserve design. Mar Ecol Prog Ser 381: 273–286

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Anderson MJ, Millar RB (2004) Spatial variation and effects of habitat on temperate reef fish assemblages in north-eastern New Zealand. J Exp Mar Biol Ecol 305:191–221

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Anderson TJ, Syms C, Roberts DA, Howard DF (2009) Multi-scale fish-habitat associations and the use of habitat surrogates to predict the organisation and abundance of deep-water fish assemblages. J Exp Mar Biol Ecol 379: 34–42

ANZECC TFMPA (1999) Understanding and applying the principles of comprehensiveness, adequacy and representativeness for the NRSMPA, Version 3.1. Marine Group Environment Australia, Canberra

Auster PJ, Malatesta RJ, LaRosa SC (1995) Patterns of micro-habitat utilisation by mobile megafauna on the southern New England (USA) continental shelf and slope. Mar Ecol Prog Ser 127:77–85

Blott SJ, Pye K (2001) GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf Process Landf 26:1237–1248

Brown CJ, Smith SJ, Lawton P, Anderson JT (2011) Benthic habitat mapping: a review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. Estuar Coast Shelf Sci 92:502–520

Cappo M, Speare P, De′ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. J Exp Mar Biol Ecol 302:123–152

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Mar Ecol Prog Ser 92:205–219

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Colquhoun J, Heyward A, Rees M, Twiggs E and others (2007) Ningaloo Reef Marine Park benthic biodiversity survey—annual report. Joint report by the Australian Institute of Marine Science, Curtin University of Technology, The University of Western Australia and the Western Australian Museum, Perth

Connell SD, Lincoln-Smith MP (1999) Depth and the structure of assemblages of demersal fish: experimental trawling along a temperate coast. Estuar Coast Shelf Sci 48: 483–495

D'elia M, Patti B, Sulli A, Tranchida G and others (2009) Distribution and spatial structure of pelagic fish schools in relation to the nature of the seabed in the Sicily Straits (Central Mediterranean). Mar Ecol 30(Suppl 1):151–160

Ellis DM, DeMartini EE (1995) Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, *Pristipomoides filamentosus,* and other Hawaiian insular shelf fishes. Fish Bull 93:67–77

Fitzpatrick BM, Harvey ES, Heyward AJ, Twiggs EJ, Colquhoun J (2012) Habitat specialisation in tropical continental shelf demersal fish assemblages. PLoS ONE 7:e39634

Folk RL, Ward WC (1957) Brazos River bar: a study in the significance of grain size parameters. J Sediment Petrol 27:3–26

Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Biol Ecol 224:1–30

Friedman GM, Johnson KG (1982) Exercises in sedimentology. Wiley, New York, NY

Gotceitas V, Brown JA (1993) Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologica 93:31–37

Gray CA, Otway NM (1994) Spatial and temporal differences in assemblages of demersal fishes on the inner continental shelf off Sydney, south-eastern Australia. Aust J Mar Freshw Res 45:665–676

Grober-Dunsmore R, Frazer TK, Lindberg WJ, Beets J (2007) Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. Coral Reefs 26: 201–216

Harasti D, Malcolm HA, Gallen C, Coleman MA, Jordan A, Knott NA (2015) Appropriate set times to represent patterns of rocky reef fishes using baited video. J Exp Mar Biol Ecol 463:173–180

Hardinge J, Harvey ES, Saunders BJ, Newman SJ (2013) A little bait goes a long way: the influence of bait quantity on a temperate fish assemblage sampled using stereo-BRUVs. J Exp Mar Biol Ecol 449:250–260

Harriott VJ, Smith SDA, Harrison PL (1994) Patterns of coral community structure of the subtropical reefs in the Solitary Islands Marine Reserve, eastern Australia. Mar Ecol Prog Ser 109:67–76

Harvey ES, Cappo M, Butler J, Hall N, Kendrick GA (2007) How does the presence of bait as an attractant affect the performance of remote underwater video stations in assessments of demersal fish community structure? Mar Ecol Prog Ser 350:245–254

Harvey ES, Butler JJ, McLean DL, Shand J (2012) Contrasting habitat use of diurnal and nocturnal fish assemblages in temperate Western Australia. J Exp Mar Biol Ecol 426-427:78–86

Harvey ES, Cappo M, Kendrick GA, McLean DL (2013) Coastal fish assemblages reflect geological and oceanographic gradients within an Australian zootone. PLoS ONE 8:e80955

Hinchey EK, Nicholson MC, Zajac RN, Irlandi EA (2008) Preface: marine and coastal applications in landscape ecology. Landscape Ecol 23:1–5

Holmes KW, Radford B, Van Niel KP, Kendrick GA, Grove SL, Chatfield B (2007) Mapping the benthos in Victoria's Marine National Parks, 1. Cape Howe Marine National Park. Parks Victoria, Melbourne

Huang Z, Nichol S, Daniell J, Siwabessy J, Brooke B (2009) Predictive modelling of seabed sediment parameters using multibeam acoustic data: a case study on the Carnarvon Shelf, Western Australia. In: Lees BG, Laffan SW (eds) Proc 10th Int Conf on GeoComputation. UNSW Press, Sydney, p 114–119

Hughes-Clarke J (1994) Towards remote seafloor classification using the angular response of acoustic backscattering: a case study from multiple overlapping GLORIA data. IEEE J Oceanic Eng 19:112–127

Johnson AF, Jenkins SR, Hiddink JG, Hinz H, (2013) Linking temperate demersal fish species to habitat: scales, patterns and future directions. Fish Fish 14:256–280

Jordan A, Davies P, Ingleton T, Mesley E, Neilson J, Pritchard TR (2010) Seabed habitat mapping of the continental shelf of NSW. NSW Department of Environment, Climate Change and Water Occasional Paper Series 209, Sydney

Kuiter RH (1993) Coastal Fishes of south-eastern Australia. Crawford House Press, Bathurst

Langlois TJ, Andersen MJ, Babcock RC (2005) Reef-associated predators influence adjacent soft-sediment communities. Ecology 86:1508–1519

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. Aquat Biol 9:155–168

Lowry M, Folpp H, Gregson M, Suthers I (2012) Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries. J Exp Mar Biol Ecol 416-417:243–253

Malcolm HA, Smith SDA (2010) Objective selection of surrogate families to describe reef fish assemblages in a subtropical marine park. Biodivers Conserv 19:3611–3618

Malcolm HA, Gladstone W, Lindfield S, Wraith J, Lynch TP (2007) Spatial and temporal variation in reef fish assemblages of marine parks in New South Wales, Australia—baited video observations. Mar Ecol Prog Ser 350:277–290

Malcolm HA, Smith SDA, Jordan A (2010a) Using patterns of reef fish assemblages to refine a Habitat Classification System for marine parks in NSW, Australia. Aquat Conserv Mar Freshw Ecosyst 20:83–92

Malcolm HA, Jordan A, Smith SDA (2010b) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. Mar Biodiv 40:181–193

Malcolm HA, Jordan A, Smith SDA (2011) Testing a depth based Habitat Classification System against reef fish assemblage patterns in a subtropical marine park. Aquat Conserv Mar Freshw Ecosyst 21:173–185

Malcolm HA, Foulsham E, Pressey RL, Jordan A and others (2012) Selecting zones in a marine park: early systematic planning improves cost efficiency, combining habitat and biotic data improves effectiveness. Ocean Coast Manag 59:1–12

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345

Mishra D, Narumalani S, Rundquist D, Lawson M (2006) Benthic habitat mapping in tropical marine environments using quickbird multispectral data. Photogramm Eng Remote Sens 72:1037–1048

Moore CH, Harvey ES, Van Niel KP (2009) Spatial prediction of demersal fish distributions: enhancing our understanding of species-environment relationships. ICES J Mar Sci 66:2068–2075

Moore CH, Van Niel K, Harvey ES (2011) The effect of landscape composition and configuration on the spatial distribution of temperate reef fish. Ecography 34:425–435

Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. Mar Ecol Prog Ser 462:191–203

Owen V, Gladstone W (2010) The effectiveness of an abiotic classification of subtidal unvegetated habitat as a surrogate for the diversity of fish assemblages in a marine protected area. In: Program and abstracts for the 2010 meeting of the Australian Marine Science Association, 4–8 July 2010, Woolongong, p 142

Rainer SF, Unsworth P (1991) Ecology and production of *Nebalia* sp. (Crustacea: Leptostraca) in a shallow water seagrass community. Mar Freshw Res 42:53–68

Rattray A, Ierodiaconou D, Monk J, Versace VL, Laurenson LJB (2013) Detecting patterns of change in benthic habitats by acoustic remote sensing. Mar Ecol Prog Ser 477:1–13

Rees MJ, Jordan A, Price OF, Coleman MA, Davis AR (2013) Abiotic surrogates for temperate rocky reef biodiversity: implications for marine protected areas. Divers Distrib 20:284–296

Sanchez-Jerez P, Gillanders BM, Kingsford MJ (2002) Spatial variation in abundance of prey and diet of trumpeter (*Pelates sexlineatus*: Terapontidae) associated with *Zostera capricorni* seagrass meadows. Austral Ecol 27:200–210

Schultz AL, Malcolm HA, Bucher DJ, Smith SDA (2012) Effects of reef proximity on the structure of fish assemblages of unconsolidated substrata. PLoS ONE 7:e49437

Schultz AL, Malcolm HA, Bucher DJ, Linklater M, Smith SDA (2014) Depth and medium-scale spatial processes influence fish assemblage structure of unconsolidated habitats in a subtropical marine park. PLoS ONE 9:e96798

Seiderer LJ, Newell RC (1999) Analysis of the relationship between sediment composition and benthic community structure in coastal deposits: implications for marine aggregate dredging. ICES J Mar Sci 56:757–765

Smith SDA (2005) Rapid assessment of invertebrate biodiversity on rocky shores: where there's a whelk there's a way. Biodivers Conserv 14:3565–3576

Smith SDA, Rule MJ, Harrison M, Dalton SJ (2008) Monitoring the sea change: preliminary assessment of the conservation value of nearshore reefs, and existing impacts,

in a high-growth, coastal region of subtropical eastern Australia. Mar Pollut Bull 56:525–534

Stevens T, Connolly RM (2004) Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management. Biol Conserv 119:351–362

Swainston R (2011) Fishes of Australia: the complete illustrated guide. Penguin, Camberwell

Thorner J, Kumar L, Smith SDA (2013) Fine-scale three-dimensional habitat mapping as a biodiversity conservation tool for intertidal rocky reefs. J Coast Res 29:1184–1190

Thrush SF (1999) Complex role of predators in structuring soft-sediment macrobenthic communities: implications of changes in spatial scale for experimental studies. Aust J Ecol 24:344–354

Thrush SF, Dayton PK (2002) Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Annu Rev Ecol Syst 33:449–473

Thrush SF, Schultz D, Hewitt JE, Talley D (2002) Habitat structure in soft-sediment environments and abundance of juvenile snapper *Pagrus auratus.* Mar Ecol Prog Ser 245:273–280

Travers MJ, Potter IC, Clarke RK, Newman SJ, Hutchins JB (2010) The inshore fish faunas over soft substrates and reefs on the tropical west coast of Australia differ and change with latitude and bioregion. J Biogeogr 37:148–169

Turner MG (2005) Landscape ecology in North America: past, present and future. Ecology 86:1967–1974

Underwood AJ, Chapman MG (2000) Coastal marine ecology of temperate australia. 2nd edn. University of New South Wales Press, Sydney

Watson DL, Harvey ES, Anderson MJ, Kendrick GA (2005) A comparison of temperate reef fish assemblages recorded by three underwater stereo video techniques. Mar Biol 148:415–425

Wentworth CR (1922) A scale of grade and class terms of clastic sediments. J Geol 30:377–392

Williams A, Bax NJ (2001) Delineating fish-habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. Mar Freshw Res 52:513–536

Williams A, Althaus F, Dunstan PK, Poore GCB, Bax NJ, Kloser RJ, McEnnulty FR (2010) Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100—1100 m depths). Mar Ecol 31:222–236

Willis TJ, Babcock RC (2000) A baited underwater video system for the relative density of carnivorous reef fish. Mar Freshw Res 51:755–763

Willis TJ, Millar RB, Babcock RC (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. Mar Ecol Prog Ser 198:249–260

Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landsc Ecol 17:355–365