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Drawing lines at the sand: Evidence for functional vs. visual reef boundaries in temperate Marine Protected Areas ☆

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ABSTRACT

Marine Protected Areas (MPAs) can either protect all seabed habitats within them or discrete features. If discrete features within the MPA are to be protected humans have to know where the boundaries are. In Lyme Bay, SW England a MPA excluded towed demersal fishing gear from 206 km^2 to protect rocky reef habitats and the associated species. The site comprised a mosaic of sedimentary and reef habitats and so 'non reef' habitat also benefited from the MPA. Following 3 years protection, video data showed that sessile Reef Associated Species (RAS) had colonised sedimentary habitat indicating that 'reef' was present. This suggested that the functional extent of the reef was potentially greater than its visual boundary. Feature based MPA management may not adequately protect targeted features, whereas site based management allows for shifting baselines and will be more effective at delivering ecosystem goods and services.

1. Introduction

Healthy biodiverse seas are vital for future proofing marine ecosystem services such as global food security (Ehrlich et al., 1993; Toledo and Burlingame, 2006; Worm et al., 2006) and climate regulation (Danovaro et al., 2008; Mooney et al., 2009). Natural biodiverse communities have greater functional redundancy than disturbed communities, which increases ecosystem resilience to future climatic changes, such as rising temperatures and ocean acidification (Costanza et al., 1997; Naeem, 1998; Naeem and Li, 1997; Yachi and Loreau, 1999).

Benthic ecosystems play a key role in maintaining prosperous fisheries (Hovey et al., 2012; Walters and Juanes, 1993). Benthic communities include commercial target species, such as flat fishes and shellfish (lobsters and scallops) and non-target, sessile, colonial fauna, such as corals, sponges and bryozoans (Garthe et al., 1996; Hiddink et al., 2008; Saila et al., 2002). The targeted fishes, crustaceans and molluscs live amongst the non-target fauna that give structural complexity to the seabed (Bradshaw et al., 2003). Biogenic structural complexity provides nursery areas for larvae, substrate for spat settlement and cover to hide from predation (Eggleston et al., 1990; Lima and Dill, 1990; Mittelbach, 1984; Pirtle et al., 2012). Sessile species capture and recycle water column nutrients through filter feeding (Beaumont, 2009), and produce planktonic larvae that support higher trophic levels. This bentho-pelagic coupling, through a range of trophic links, provides prey for birds (Grecian et al., 2010), commercially important fishes such as cod (*Gadus morhua*, Heath and Lough, 2007; Lomond et al., 1998) and plaice (*Pleuronectes platessa*, Hiddink et al., 2011) and pelagic species of conservation value such as basking sharks (*Cetorhinus maximus*, Musick et al., 2004).

Globally, fishing fleets harvest benthic target species using towed demersal gear, often digging into sediments and so removing slow growing, long lived, structure forming fauna (Thrush and Dayton, 2002). Recovery of some impacted species from just one passage of fishing gear can take decades (Babcock et al., 1999; Foden et al., 2010; Watling and Norse, 1998).

Marine managers' best tool to protect discrete patches of the seabed from fishing, therefore allowing benthic species to contribute to ecosystem function, is the application of Marine Protected Areas (MPAs) (Agardy, 1994; Auster and Shackell, 2000; Babcock et al., 1999; Gell and Roberts, 2003; Halpern, 2003; Murawski et al., 2000; Roberts et al., 2005). MPAs come in a variety of sizes, shapes and forms (Agardy et al., 2003; Agardy, 1994; Rabaut et al., 2009) depending on the 'features' that they are designated to protect, a feature being a species or specific habitat that has received formal protection from a type of human activity. The size and level of protection from human activity in MPAs ranges from 1 to 1000s km^2; and from 'No-take' to seasonal fishing closures (Lester and Halpern, 2008). Protection of the features can be limited to the features' periphery such as Special Areas of Conservation in Europe

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(European Commission, 2000) or protection can surround features and therefore protect the whole 'site' such as Tortugas Ecological Reserve, Buck Island National Reef Monument and Chagos (Jeffrey et al., 2012; Kendall et al., 2004; Koldewey et al., 2010). The former relies on human ability to adequately draw lines around the features' functional extent, which is generally considered to be the visible, physical extent of the feature (e.g. reef) used as an analogue of the associated species that require protection. Some European and international MPAs, such as La Restinga Marine Reserve (Spain) and the Great Barrier Reef Marine Park (Australia) (Claudet et al., 2008; Day, 2002), have surrounding areas called Buffer Zones to prevent direct and indirect physical interaction and disturbance of fishing gear on the feature(s) of interest.

In 2008, a statutory MPA in south west UK was designated to protect rocky reef habitat (Fig. 1). The management regime involved protecting all of the seabed at the 'site' level. This equated to a 206 km^2 exclusion zone from towed demersal fishing gear across a MPA that contained a mosaic of rocky reef (bedrock, boulders and cobbles), pebbly sand and soft muddy sediments.

To assess the success of the MPA, an annual monitoring program commenced soon after this MPA was instigated. The aim was to determine if and when recovery occurred for epibenthic assemblages on rocky reefs. A flying array with mounted High Definition video (Fig. 2) was flown over the seabed to sample benthic transects within the MPA and in Open Controls. While sites were located to survey hard substratum, pebbly sand habitats that occurred between the reefs were also recorded but not analysed as they were not considered a designated part of the reef feature. During analysis of rocky habitats, observations were made that sessile RAS were occurring on pebbly sand, which therefore must be overlying bedrock that the species could attach to (Keough and Downes, 1982). This observation became of critical importance as fishers were seeking permission to scallop dredge sediments between the reef features within the MPA.

By returning to the video archive we could formally enumerate pebbly sand Reef Associated Species (RAS) assemblages, which had previously been ignored for the reef species recovery analysis, and compare them over time from 2008, when the exclusion was enforced, to 3 years later in 2011. Here we test the hypothesis that, if protected from fishing, inter-reef pebbly sand habitats can support significantly more sessile RAS than similar habitats in areas that remain open to fishing. If pebbly sand habitats were found to support sessile RAS, this would provide evidence to broaden the definition of 'reef' as a feature, with consequences for how lines are drawn around such protected features in MPAs. We measured the following response variables for sessile RAS: Species Richness, Overall Abundance, Assemblage Composition, and a subset of sessile RAS indicator species that were preselected (ross coral *Pentapora fascialis*, sea squirt *Phallusia mammillata*, dead man's fingers *Alcyonium digitatum*, branching sponges, pink sea fans *Eunicella verrucosa* and hydroids (Jackson et al., 2008)).

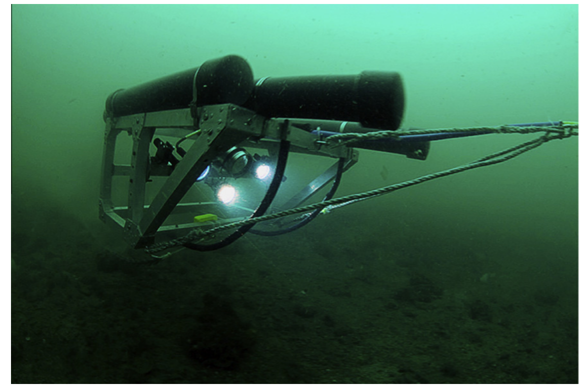

Fig. 2. The towed flying array mounted with high definition video.

2. Methods

The case study site is in Lyme Bay (Fig. 1), located on the south west coast of the UK. Lyme Bay comprises a mosaic of rocky reefs with boulders, cobbles and mixed sediments, known to support some fragile biogenic reef species of national importance (Hiscock and Breckels, 2007; Vanstaen and Eggleston, 2011). This study focused on pebbly sand habitats (particle size ⩽64 mm diameter (Irving, 2009)), which occurred between areas of rock, boulders and cobbles.

All identifiable species were enumerated; however, only the sessile Reef Associated Species (sessile RAS = structure forming species that are attached to the seabed and are associated with hard substratum) were analysed as it was considered that it was

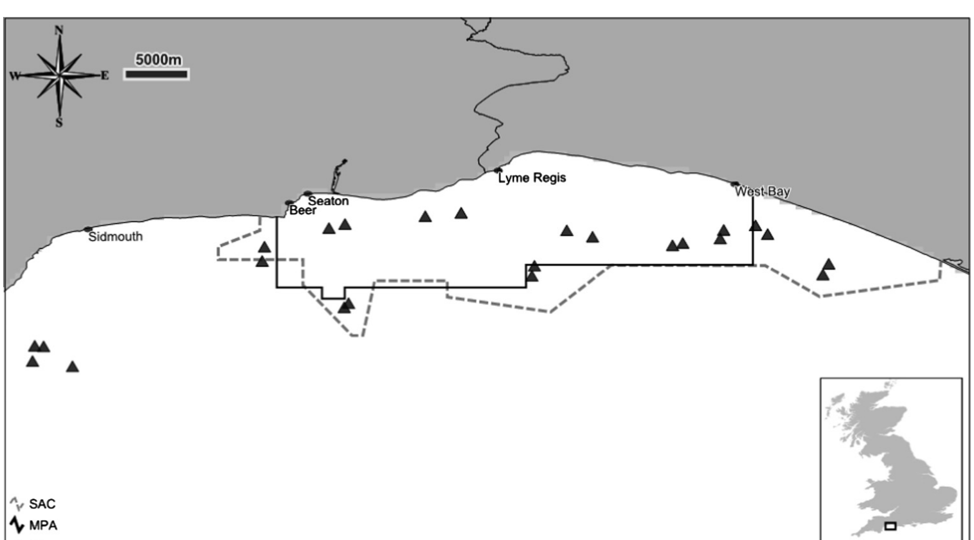

Fig. 1. Lyme Bay in SW UK. Triangles indicate site locations located in pairs (Areas), either inside or outside of the Marine Protected Area (solid line). Candidate Special Area of Conservation indicated by a dashed line.

only the sessile RAS that could truly indicate the 'reef' feature. To determine whether sessile RAS can occur on pebbly sand if fishing pressure is relieved, the seabed was surveyed across Lyme Bay at the point when towed demersal trawling was excluded from the proposed MPA (2008), which is considered here as the 'Before' baseline data. Samples were taken inside the MPA or outside the MPA, which remained open to fishing ('Open Controls; OC'). The survey was then repeated three years later. The design is effectively a Before After Control Impact (BACI) design (Underwood, 1994). While the 'Before' samples were taken six weeks after the MPA was designated, changes in the sessile RAS species assemblage were expected to occur over several years (Glasby, 1997) and so the first sampling time represented 'Before' the effect of fishing pressure relief could be realised. For this reason, fast growing and quick to recover hydroids (Bradshaw et al., 2003; Harris, 1975) were excluded from overall assemblage analyses and were analysed separately.

2.1. Site selection

To account for geographic variation, 12 areas were identified across the bay, which contained reef and pebbly sand habitat. 5 areas were selected in the MPA, and 7 areas in the OC, with 2 replicate sites in each area. All areas were sampled in 2008 and 2011 giving a total of 24 sites for each year. The position of transects were haphazardly selected within each site by starting the video tow at the site GPS and allowing the wind and tide to dictate the direction of the transect.

2.2. Field methods

A towed flying video array with mounted High Definition HD video was used to survey each site, which constituted a 200 m transect over heterogeneous and sensitive benthos (Sheehan et al., 2010). The HD video system included a camera (Surveyor-HD-J12 colour zoom titanium, 720p), LED lights (Bowtech Products limited, LED-1600-13), two green laser pointers (Z-bolt Scuba-1) and a mini CTD profiler (Valeport Ltd.). An umbilical connected the video system topside to a Bowtech System power supply/control unit allowing control of light intensity and camera focus, zoom and aperture. The camera was positioned at a 45° angle to the seabed, with the three lights fixed in front and below the camera to provide improved image definition and colour. The lasers were used to quantify field of view (Freese et al., 1999) and were positioned parallel to each other.

2.3. Video analysis

Species counts were determined by viewing each video transect 'site' at normal speed, recording every identifiable organism that occurred on pebbly sand habitat if it passed through the 'gate' formed by the 2 laser dots. All organisms present were identified to the highest taxonomic level possible and their abundance recorded. Taxonomically similar species, which could not be distinguished with confidence, were grouped, such as branching sponges and hydroids.

To calculate the area of pebbly sand per video transect, the occurrence of observable pebbly sand was timed regardless of whether species were present or not. The area of each transect was calculated by multiplying the length of the tow by the distance between the laser gate, which was set according to water visibility (good visibility = 45 cms; bad visibility 30 cms). The transect area was then divided by the total time of each transect and multiplied by the amount of pebbly sand time, giving the area of pebbly sand per tow. Species counts could then be calibrated per tow to estimate density (individuals m^{-2}).

2.4. Data analysis – indicator species

Permutational Multivariate Analysis of Variance (PERMANOVA+) in the software package PRIMER v6 (Anderson, 2001; Clarke and Warwick, 2001) was used to test for differences between sessile RAS response variables: Species Richness, Abundance, Assemblage Composition and Population Abundances of six preselected indicator taxa (ross coral *P. fascialis*, sea squirt *P. mammillata*, dead man's fingers *A. digitatum*, branching sponges, pink sea fans *E. verrucosa* and hydroids (Jackson et al., 2008)).

The factors Time and Treatment were fixed and had two levels (Time: Before and After; Treatment: MPA and Open Control). Area was random and nested in Treatment (MPA = 5 areas, OC = 7 areas). All Areas were sampled in both Times and comprised two replicate sites.

Prior to calculation of the Bray–Curtis (Bray and Curtis, 1957) similarity index, multivariate data (Assemblage Composition) were dispersion weighted and square root transformed to down weight taxa with erratic abundances and/or high abundances (Clarke et al., 2006). As joint species absences were important to consider between treatments, data were 'zero-adjusted by adding a dummy value of 1 (Clarke et al., 2006). Without the dummy value, Bray-Curtis would not consider samples similarly devoid of species as similar, such as those in the Before and/or Open Controls.

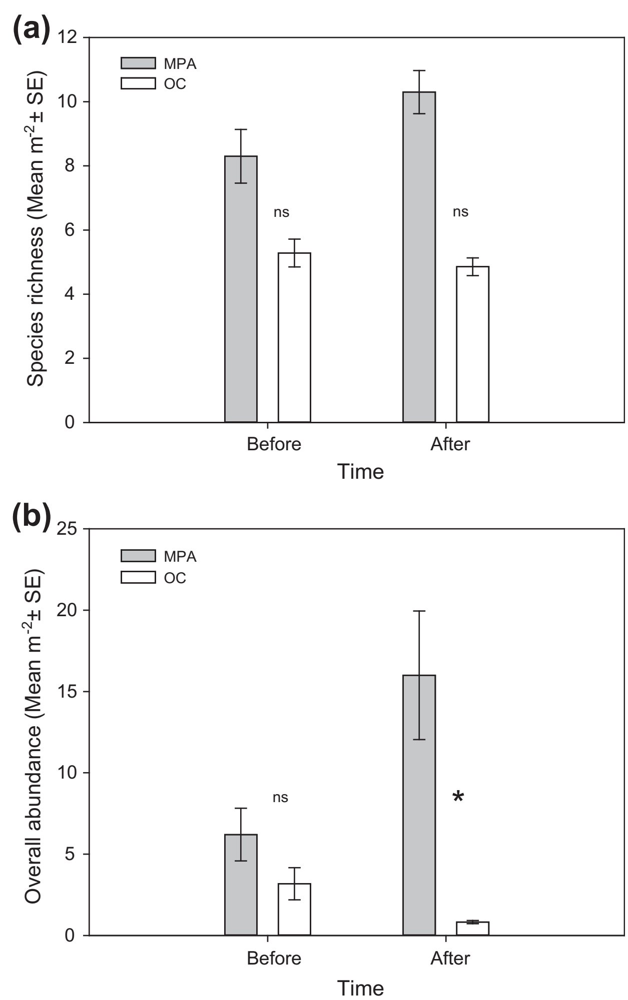

Fig. 3. Differences between (a) Species Richness and (b) Overall Abundance of sessile Reef Associated Species recorded on pebbly-sand habitat between Times 'Before' and 'After' 3 years of protection and between Treatments (MPA = Marine Protected Area; OC = Open Control).

Euclidean distance indices were calculated for univariate data (Species Richness, Abundance and Abundances of indicator species) that were Log $(x + 1)$ transformed (Anderson and Millar, 2004). Each term in the analyses used 9999 permutations of the appropriate units (Anderson and Ter Braak, 2003). Significant interactions of fixed terms were tested using PERMANOVA pairwise tests. Assemblage Composition was visualised using non-metric Multi-Dimensional Scaling (nMDS).

3. Results

A total of 2448 m^2 of pebbly sand habitat was observed between rocky reef habitats over the two years. 71 taxa were recorded from pebbly sand habitats. Species included those commonly associated with sedimentary habitats, such as: queen scallop (*Aequipecten opercularis*), anemone *Cerianthus* spp. and the common hermit crab (*Pagurus bernhardus*); mobile taxa that are associated with reefs such as cuckoo wrasse (*Labrus mixtus*) and ballan wrasse (*Labrus bergylta*) and 24 sessile Reef Associated Species such as dead man's fingers (*A. digitatum*), branching sponges and ross coral (*P. fascialis*).

3.1. Species Richness/Abundance/Assemblage Composition

While the sessile RAS Species Richness did not change significantly in the MPA relative to controls despite a clear increasing trend (Fig. 3), three years after towed demersal fishing was excluded from the MPA, the overall sessile RAS Abundance was significantly greater in the MPA compared to the 'Before' and Open Controls 'OC' (all $P < 0.05$, PERMANOVA and Pairwise tests see Table 1). Mean Abundance of sessile RAS in the MPA increased 158% from 6.2 m^{-2} 'Before' to 15.99 m^{-2} 'After' (Fig. 3). The overall Assemblage Composition change was clearly demonstrated by the nMDS (Fig. 4). The 'Before' OC and MPA sites and the 'After' OC were spread between treatments and showed no clear grouping in the nMDS plot, while the 'After' MPA sites were separated from the other sites, suggesting that they were different to the control sites. The overall Time × Treatment interaction was not significant ($P = 0.06$, Table 1). However, OC sites and MPA sites were similar to each other 'Before' towed demersal fishing was excluded and were significantly different to each other 'After' ($P = 0.002$, Table 1).

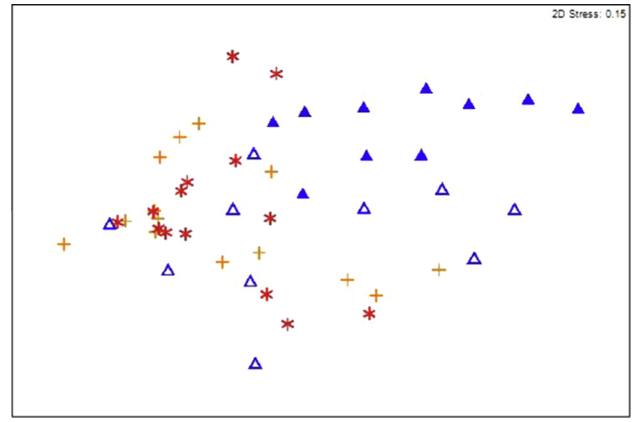

Fig. 4. nMDS ordination illustrating similarities in pebbly-sand Assemblage Composition between Times 'Before' and 'After' three years of protection and Treatment 'MPA' and 'Open Controls' (MPA Before = open triangles, MPA After = blue filled triangles, OC Before = orange crosses, OC After = red stars). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Indicator species

Four of the six indicator sessile RAS (Ross coral *P. fascialis*, sea squirt *P. mammillata*, Dead man's fingers *A. digitatum* and branching sponges) significantly increased in Abundance from the 'Before' MPA to the 'After' MPA relative to Open Controls ($P < 0.05$; Fig. 6, Table 2). While pink sea fans (*E. verrucosa*) and hydroids showed an increasing trend over time, there was no significant Time × Treatment interaction (Fig. 5, Table 2).

4. Discussion

If protected from towed demersal fishing activity, sedimentary habitats between rocky reefs contribute to the reef ecosystem by supporting diverse epibenthic Assemblages. While some of the species observed here were characteristic of sediment habitats (mobile: sole *Solea solea*, common starfish *Asterias rubens*, common hermit crab *P. bernhardus*; sessile: parchment Worm, *Chaetopterus variopedatus*), some mobile or sessile species observed on the pebbly sand are typically found on hard substratum (Reef Associated Species). Mobile RAS included brown crab (*Cancer pagurus*), that

Table 1
PERMANOVA to test the differences in sessile RAS on pebbly sand for the response metrics: Species Richness, Abundance and Assemblage Composition between Times ('Before' and 'After', Treatments (MPA and Open Control OC)) and Areas within treatments (MPA = 5 areas, OC = 7 areas). Pairwise tests are used to examine significant interactions between fixed factors. Bold values indicate significant differences.

		Species Richness				Abundance				Assemblage			
Source	*Df*	SS	MS	*F*	P	SS	MS	*F*	P	SS	MS	*F*	P
Time Ti	1	0.26	0.26	1.21	0.30	0.37	0.37	0.81	0.39	2845	2845	2.39	0.06
Treatment Tr	1	2.34	2.33	3.8	0.09	10.56	10.56	4.32	0.06	10,266	10,266	4.81	**0.014**
Area Ar (Tr)	10	6.15	0.62	3.64	**0.02**	24.41	24.41	3.99	**0.004**	21,333	2133.3	2.89	**0.0001**
Ti x Tr	1	0.56	0.56	2.59	0.14	2.85	2.85	6.31	**0.03**	2967.6	2967.6	2.49	0.062
Ti x Ar (Ar)	10	2.15	0.22	0.92	0.54	4.52	0.45	0.74	0.69	14,831	1483.1	1.60	**0.022**
Residual	24	5.59	0.23			14.69	0.61			22,223	925.96		
Total	47	17.05				57.4				81,669			
						Pair-wise for term Time × Treatment between MPA and OC				Pair-wise for term Time × Treatment between MPA and OC			
						Time	*t*	*P*		Time	*t*	*P*	
						Before	0.82	0.44		Before	1.19	0.22	
						After	3.39	**0.005**		After	2.68	**0.002**	

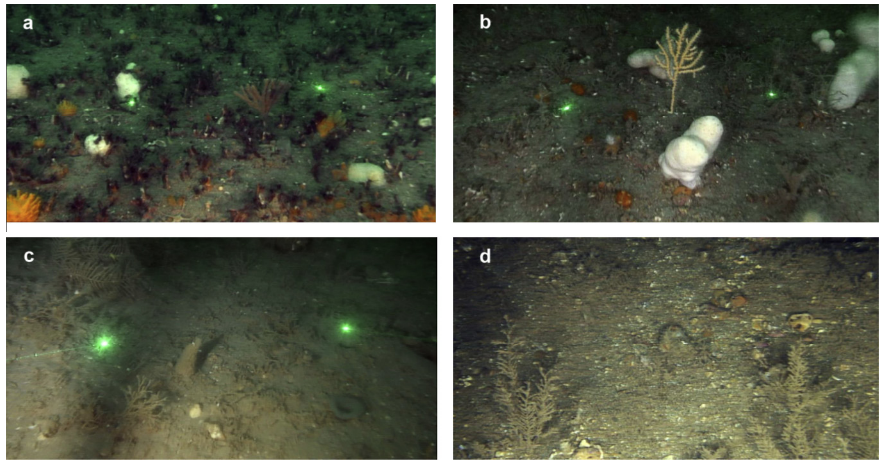

Fig. 5. Examples of species observed on pebbly-sand habitat within Lyme Bay; (a) image from within the MPA including species *Alcyonium digitatum,* sponge *Polymastia boletiformis,* sea cucumber *Cucumaria frondosa* and branching sponge; (b) image from within the MPA including species *A. digitatum, Pecten maximus, Cellepora pumicosa,* branching sponges, *Eunicella verrucosa* and hydroids; (c) image from the OC including species *Sycon ciliatum, Pagurus bernhardus* and hydroids; (d) image from the OC including hydroids.

lives in rocky crevices, ballan wrasse (*L. bergylta*), cuckoo wrasse (*L. mixtus*) and goldsinny wrasse (*Ctenolabrus rupestris*) that are territorial around rocky habitats. Of particular relevance for this study, however, were the 24 observed sessile RAS, such as ross coral (*P. fascialis*), sea squirt (*P. mammillata)* and dead man's fingers (*A. digitatum*). These ecosystem engineers give structural complexity to the sea bed, providing habitats that act as nurseries, protection from predation and safe settlement opportunities for larvae (Bradshaw et al., 2003; Eggleston et al., 1990; Lima and Dill, 1990; Mittelbach, 1984; Pirtle et al., 2012).

P. fascialis, which plays a key role in the formation of biogenic reef nursery areas (Cocito and Ferdeghini, 2001; McKinney and Jackson, 1989), increased by an average of 385% in the MPA over the three years following protection from towed demersal fishing. Branching sponges, which provide structural complexity for larval settlement and shelter from predators (Auster, 1998; Auster et al., 1997; Auster et al., 1996; Bradshaw et al., 2003), increased in Abundance by an average of 414% in the MPA. Hydroids also provide structure for larval settlement (Bradshaw et al., 2001), and had a mean increase of 229% inside the MPA over time, though this was not statistically different to the controls due to high variability.

Phallusia mammillata and *A. digitatum*, which also add structural complexity to benthic habitats, both significantly increased in Abundance over three years in the MPA (467% and 2541% respectively). Similarly, *E. verrucosa* showed an increase in mean Abundance of 636%. Gorgonians such as *E. verrucosa* create complex elevated structures (Jones et al., 1994), which provide settlement sites for larvae (Howarth et al., 2011) and create habitats for associated organisms such as the whip fan nudibranch (*Tritonia nilsodhneri*) (Hall-Spencer et al., 2007).

The sessile RAS indicator species, and their associated biodiversity, produce planktonic larvae that support higher trophic levels. This bentho-pelagic coupling through a range of trophic links provides prey for birds (Grecian et al., 2010), and commercially important fishes such as cod (*G. morhua*, Heath and Lough, 2007; Lomond et al., 1998). For these reasons, sessile RAS are recognised by governments for their importance to ecosystem functionality, and receive protection under environmental legislation from destructive human activities. This includes species such as *E. verrucosa* in the UK, which is protected by the UK Biodiversity Action Plan. By their very nature, sessile RAS need to attach to hard substratum and therefore, indicate 'reef', which is often a protected feature of environmental legislation. Reef substratum can be observed by humans as rock, boulders or cobbles, and protected to allow recovery of RAS. However, where sediment overlies rock, reef cannot be identified through habitat assessment, but could be identified by the presence of sessile RAS. Our results indicate that sessile RAS can only indicate such additional reef habitat if the area is protected from fishing, thereby giving sensitive species a chance to recover. This however, presents a difficult situation for marine managers.

Site based protection which encompasses features, such Tortugas Ecological Reserve, and Buck Island Reef National Monument in the USA (Jeffrey et al., 2012; Kendall et al., 2004), allows sessile RAS to colonise not only areas of visual reef but also areas that are functionally reef to these species i.e. they can find attachment to hard substratum through overlying sediments. It is clear that by 'Drawing lines at the sand' where the visible rocky reef feature ends, managers limit the reef area, but by alternatively protecting sites that encompass features, the functional reef extent can expand and be fully protected. This effect observed here could occur with other protected features in MPAs such as seagrass beds.

Our findings are currently of particular importance as improving, low cost GPS technology is allowing what some GIS experts may think is a 'more intelligent' detailed design of MPA boundaries rather than a simple box. However, in practice for ecosystem function, simplicity of enforcement and clarity to users (Great Barrier Reef Marine Park Authority 2002) would be the more intelligent design. For example, in Europe, Special Areas of Conservation management focuses on the features within designated sites (European Commission 2000), such as the physical reef habitat. A SAC now envelopes the Lyme Bay statutory instrument (MPA), extending the MPA to the east, south and west. While this study has shown the rocky reef feature in the SAC is greater in scale than the actual visually observed reef, only the rocky habitats benefit if management is feature based. Unfortunately, the full extent of a functional reef is often larger than its legal protection (Rees et al., in press) and results here show that the full extent can only be visually recognised once recovery has started to take place. The presented results will hopefully inform discussions among managers and governmental authorities to include other substrata and associated species in order to appropriately maintain and restore the full extent of the functional reef (Rees et al., in press). Furthermore, based on our findings we recommend that reef features of conservation interest are protected at the scale of the MPA site (e.g. SAC boundary for EU Habitats Directive) at least until species have

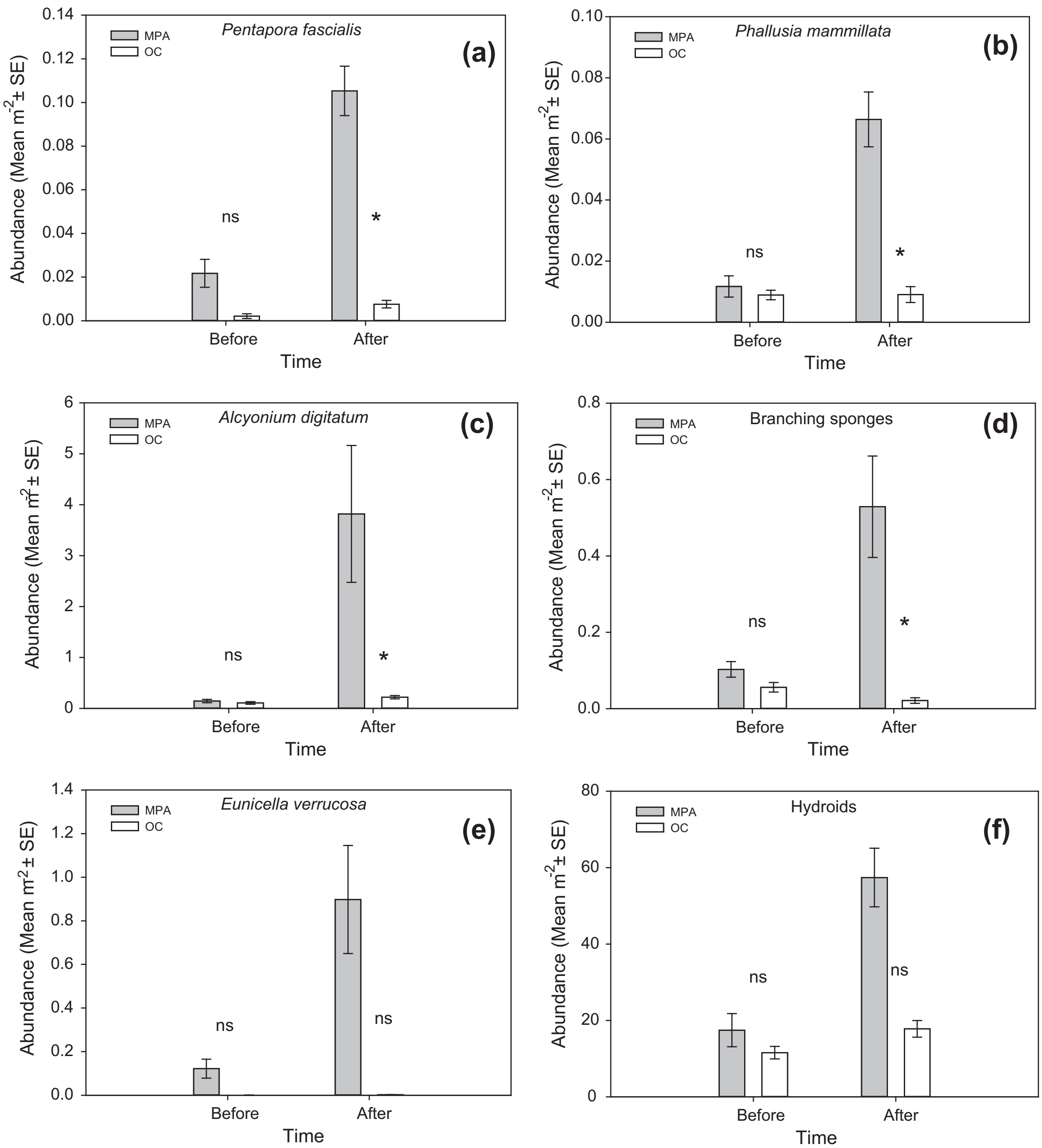

Fig. 6. Differences between Abundances of sessile Reef Associated Species on pebbly sand between Times 'Before' and 'After' three years of protection and between Treatments (MPA = Marine Protected Area; OC = Open Control). (a) *Pentapora fascialis*, (b) *Phallusia mammillata*, (c) *Alcyonium digitatum*, (d) Branching sponges, (e) *Eunicella verrucosa* and (f) Hydroids. Scales on the *y*-axes vary.

begun to recover and indicate where features extend to. Only then should detailed lines be drawn and buffer zones introduced (Halpern et al., 2010). No comparison is made here between the sessile RAS on sediment to sessile RAS on observable hard reef. However, even if they were considered substandard assemblages, this reef expansion, and increase in biogenic structure in these areas connecting rocky habitats would increase overall ecosystem health and resilience of benthic systems to environmental change, such as ocean acidification, temperature rise, and invasive species (Carpenter et al., 2008; Hoegh-Guldberg et al., 2007; Stachowicz et al., 2002; Veron et al., 2009).

The Convention on Biological Diversity (CBD COP 10 2011-2020) requests that by 2020 ecosystem based management approaches are applied in marine systems to avoid overfishing. This is in accordance with the site rather than feature based approach. A mosaic of habitat types is essential for the success of any marine ecosystem, as different life stages or foraging techniques often require different substratum types (Christensen et al., 2003). Functional boundaries should also consider not only extent of adult RAS but their entire benthic life history. Only considering adult stages limits our interpretation of functional habitat use by reef organisms. It has been documented that some reef organisms such as lobsters use neighbouring sediments for cburying juvenile stages or foraging (Howard and Bennett, 1979), and this should be taken into account when proposing MPA boundaries.

Differing life history traits demonstrate the importance of managers being able to employ adaptive management strategies that

Table 2
PERMANOVA to test differences for indicator sessile RAS on pebbly sand between Times (Before and After) and Treatments (MPA and OC). For details see Table 1 legend. Bold values indicate significant differences.

		Pentapora fascialis				*Phallusia mammillata*				*Alcyonium digitatum*			
Source	*df*	SS	MS	*F*	P	SS	MS	*F*	P	SS	MS	*F*	P
Time Ti	1	0.02	0.02	6.51	**0.03**	0.01	0.01	9.71	**0.01**	1.66	1.66	9.22	**0.009**
Treatment Tr	1	0.04	0.04	74.35	**0.001**	0.01	0.01	19.24	**0.0008**	1.58	1.58	5.72	**0.02**
Area Ar (Tr)	10	0.005	0.0005	0.48	0.9	0.01	0.001	0.47	0.91	2.76	0.28	1.14	0.37
Ti x Tr	1	0.02	0.02	6.55	**0.03**	0.01	0.01	13.6	**0.01**	1.32	1.32	7.33	**0.01**
Ti x Ar (Ar)	10	0.02	0.002	2.36	**0.05**	0.01	0.001	0.55	0.85	1.8	0.18	0.75	0.72
Residual	24	0.02	0.001			0.03	0.001			5.79	0.24		
Total	47	0.12				0.06				14.89			
		Pair-wise for term Time × Treatment between MPA and OC				Pair-wise for term Time × Treatment between MPA and OC				Pair-wise for term Time × Treatment between MPA and OC			
		Time	*t*	*P*		Time	*t*	*P*		Time	*t*	*P*	
		Before	1.46	0.09		Before	0.33	0.79		Before	0.44	0.66	
		After	5.14	**0.001**		After	4.97	**0.002**		After	2.61	**0.01**	

		Branching sponges				*Eunicella verrucosa*				Hydroids			
Source	*df*	SS	MS	*F*	P	SS	MS	*F*	P	SS	MS	*F*	P
Time Ti	1	0.07	0.07	3.65	0.08	0.22	0.22	3.12	0.11	6.95	6.95	3.6	0.09
Treatment Tr	1	0.34	0.34	4.55	0.05	0.75	0.75	3.16	**0.05**	4.55	4.55	1.2	0.3
Area Ar (Tr)	10	0.75	0.08	1.68	0.12	2.36	0.24	5.04	**0.002**	37.97	3.80	11.94	**0.0001**
Ti × Tr	1	0.2	0.2	10.07	**0.01**	0.3	0.3	4.28	0.07	3.39	3.39	1.75	0.22
Ti × Ar (Ar)	10	0.2	0.02	0.44	0.92	0.7	0.07	1.49	0.16	19.33	1.93	6.08	**0.0001**
Residual	24	1.07	0.05			1.12	0.05			7.63	0.32		
Total	47	2.64				5.45				79.82			
		Pair-wise for term Time × Treatment between MPA and OC											
		Time	*t*	*P*									
		Before	0.71	0.47									
		After	2.65	**0.03**									

could result in the expansion of conservation features and recovery of benthic systems (Folke et al., 2004).

5. Conclusions

This study highlights a fundamental management predicament known as shifting baselines. Without knowing the natural state of the benthos without human disturbance is it illogical to assume that feature boundaries can be drawn? We have argued that it is only species rather than visually observed habitats, e.g. drawing lines between rock and sand, which can inform the functional extent of features, such as a reef. Before feature boundaries and buffer zones can be established, the MPA should be protected at the scale of the site around observable features to allow species to recover and therefore demonstrate functional feature extent. The Lyme Bay case study has shown that by protecting a reef system, the extent of reef feature increased: an unexpected positive result for marine conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.marpolbul.2013.09.004.

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