

Predicting biodiversity changes due to loss of bioengineers from an intertidal landscape, a case study from Sydney Harbour

V.J. Cole^{*1}, P.A. Hutchings² and P.M. Ross^{1,3}

¹ School of Science and Health, Western Sydney University, NSW, Australia

² Australian Museum Research Institute, Australian Museum, NSW, Australia

³ Faculty of Science, University of Sydney.

* Corresponding author: Victoria J. Cole v.cole@westernsydney.edu.au

ABSTRACT

Loss of habitat is considered to be one of the major threats to biodiversity. This is of concern because habitats created by bioengineering species support and enhance local biodiversity. The present study investigated the abundance and distribution of polychaetes among distinct patches of the biogenic habitats created by the tubeworm *Galeolaria caespitosa*, the Sydney rock oyster *Saccostrea glomerata* and the turfing red alga *Corallina officinalis* on natural rocky shores within Sydney Harbour, NSW, Australia. Assemblages of polychaetes were compared among the habitats, species of polychaetes restricted to single habitats were identified (1 species was unique to oysters or *Galeolaria*, and 7 species were unique to coralline turf), estimates of their contribution to diversity at the patch and landscape scale, and unique species were made. The relative cover of each of the habitats throughout Sydney Harbour is patchy but within the marine dominated sections of natural rocky shores, they are widespread. All habitats supported unique species of polychaetes and overall assemblages differed among the habitats. Loss of biogenic habitats due to climate change, harvesting or other anthropogenic activities, will result in loss of many species of polychaetes and will have larger scale implications. Future management of marine biodiversity, including the potential for a marine park network in Sydney Harbour, needs to take into account the importance of biogenic habitats in supporting these diverse assemblages of invertebrates.

Key words: Diversity; Ecosystem engineer; Habitat loss; Polychaetes; Marine Parks; Rocky shore

DOI: <http://dx.doi.org/10.7882/AZ.2015.034>

Introduction

Loss of habitat has been identified as one of the major threats to Australia's biodiversity (Butler *et al.* 2010; McNeely *et al.* 1990), and is being driven by the increase in urban areas (McKinney 2002). Many of these natural habitats are being replaced by anthropogenic structures to make way for cities and urban sprawl (Bulleri and Chapman 2010). This has resulted in marina development, construction of coastal defences, and land reclamation replacing natural rocky shores and mangrove forests (Goodsell *et al.* 2007). Sydney Harbour is an example of a highly urbanised estuary, where more than 50% of the natural shoreline has been modified (Chapman 2003; Hedge *et al.* 2014; Mayer-Pinto *et al.* 2015).

Many of these coastal habitats are not just physical structures of the landscape, but are created by living organisms which provide biogenic habitats for other taxa. For example, intertidal rocky shores are comprised of mosaics of many different sessile organisms (Sousa 1984; Underwood 1981) which support diverse assemblages of macrofauna (Castilla *et al.* 2004; Cole and McQuaid 2010; Seed 1996). These organisms that create biogenic habitat facilitate the presence of smaller taxa (Bruno *et al.* 2003) and enhance

local biodiversity are referred to as "structural species" (Huston 1994), "foundation species" (Dayton 1972), and "physical ecosystem engineers" (Jones *et al.* 1994; 1997).

Protection of bioengineers therefore should be a key priority (Crain and Bertness 2006), because loss of those species that alter the environment have ecosystem-level consequences (Coleman and Williams 2002). For example, loss of kelp forests (*Ecklonia radiata* and *Phyllospora comosa*) due to the range expansion of the urchin, *Centrostephanus rodgersii*, led to an overall change in faunal composition and reduction in the abundance of limpets (Ling 2008).

Loss of ecosystem engineers within a landscape has been proposed to lead to wide spread loss of biodiversity (Wright and Jones 2006). In addition to the threat of losing biodiverse habitats, the unique attributes of each type of bioengineer mean that loss of only one type will lead to loss of a unique assemblage of species. Throughout the world, examples of loss of key bioengineering habitats have been observed. In terrestrial systems, loss of important foundation tree species resulted in changes to rates of decomposition, nutrient fluxes,

carbon sequestration, and energy flow (Ellison *et al.* 2005). In the marine environment, destruction and mass removal of shellfish beds and seagrass due to fishing activities result in loss of biodiversity (Coleman and Williams 2002). For example, due to intense artisanal harvesting in South Africa, mussels are absent from all areas outside of marine reserves (Lasiak 1998; Ludford *et al.* 2012), and there has been a subsequent change in diversity and composition of these assemblages (Cole *et al.* 2011; Lasiak and Field 1995). Associated with the change in the composition of habitats, there was a change in the overall biodiversity. Similarly, in the US, due to habitat destruction, loss of oyster reefs has led to fisheries and water quality declines (Beck *et al.* 2011; Coen *et al.* 1998).

In Sydney Harbour, natural rocky shores consist of mosaics of interspersed bioengineers, often separated by only tens of centimetres or less. Conspicuous habitat patches are formed by the calcareous tubeworm *Galeolaria caespitosa* (which cannot be morphologically distinguished from *G. gemineoa*, Halt *et al.* 2009), the Sydney rock oyster *Saccostrea glomerata* and the turfing red alga *Corallina officinalis*. Locally, many different organisms have been found to be associated with such habitats (Kelaher and Cole 2005; Minchinton 1997; Otway 1995). Despite these habitats being common, few comparisons in the literature have been made among them in terms of associated organisms (but see Blockley *et al.* 2007; Chapman *et al.* 2005). By comparing assemblages associated with different habitat-forming organisms, a greater insight into what would happen if there were changes to biogenic habitats on intertidal rocky shores can be gained.

Polychaetes are an abundant and speciose taxon in marine habitats (Fauchald and Jumars 1979), and have often been proposed as indicators (Giangrande *et al.* 2005; Olgard and Somerfield 2000; Olgard *et al.* 2003) because they represent the patterns of distribution and abundance of other taxa (Gobin and Warwick 2006; Olgard *et al.* 2003). There are currently 81 recognised families and 13,000 species, of which, 67 and 1,140, respectively, are found in Australian waters (Hutchings 2000), although this has increased since then (Hutchings, Pers. Comm. 2015). Within a species, many polychaetes have multiple modes of reproduction and are able to reproduce both sexually and asexually (Bentley & Pacey 1992; Hutchings 1998). They cover a range of trophic groups (Fauchald and Jumars 1979; Jumars *et al.* 2015), many are detritivores and herbivores and others are carnivores, of which some are predatory (Ambrose 1984; 1984; Ockelmann and Vahl 1970). By using polychaetes as a model group, a diverse taxocene can be investigated and many different trophic groups can be studied (Hutchings 1998).

This study aimed to: (1) describe the assemblages of polychaetes associated with common habitat forming species on rocky shores in Sydney Harbour; (2) determine the ecological significance of each biogenic habitat in

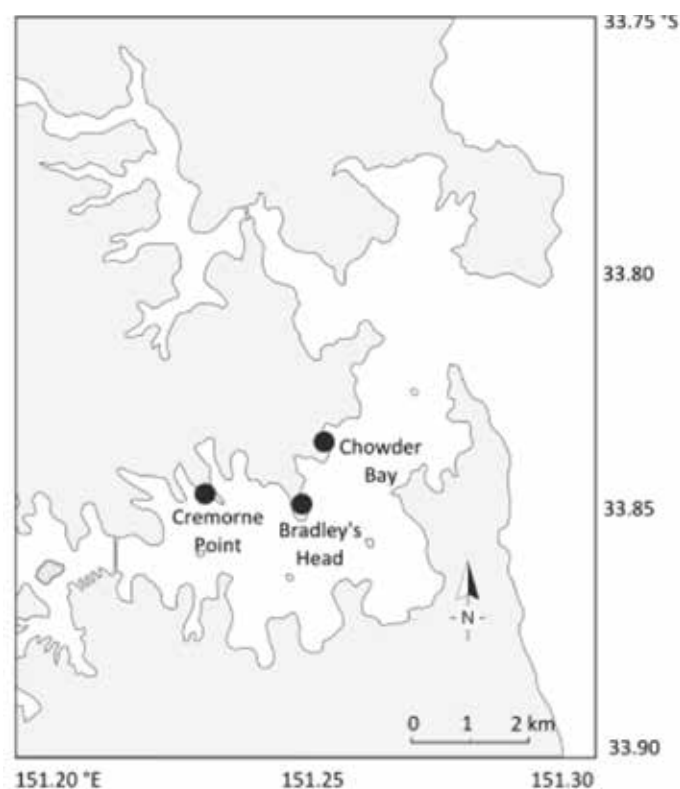


Figure 1: Sydney Harbour, Australia, with sampling locations at Cremorne Point, Bradley's Head, and Chowder Bay.

the landscape; and (3) predict the consequences in terms of loss of species if biogenic habitats were to be lost from the landscape.

Methods

Study Area

This study was carried out on intertidal rocky shores on the north side of Sydney Harbour, New South Wales, Australia (Figure 1). All places are east of the Harbour Bridge (Figure 1), with a strong marine tidal influence. These shores were randomly chosen examples of natural rocky shores within Sydney Harbour (Figure 2). The shores that were sampled are gently sloping Hawkesbury sandstone platforms, backed by native bushland. They have relatively little exposure to waves because they are protected in the harbour but sometimes they experienced waves created by ferry and boat wake. The average local tidal range is 1.6 m, and the tides are semi-diurnal.

The habitats sampled were beds of the Sydney rock oyster *Saccostrea glomerata*, dense aggregations of the serpulid tubeworm *Galeolaria caespitosa*, and mats of the turfing coralline alga *Corallina officinalis* (Figure 3). Habitats will hereafter be referred to as oysters, *Galeolaria* or coralline turf, respectively. Habitats were defined as being continuous patches, covering 100% of primary space. Patches of these habitats varied from

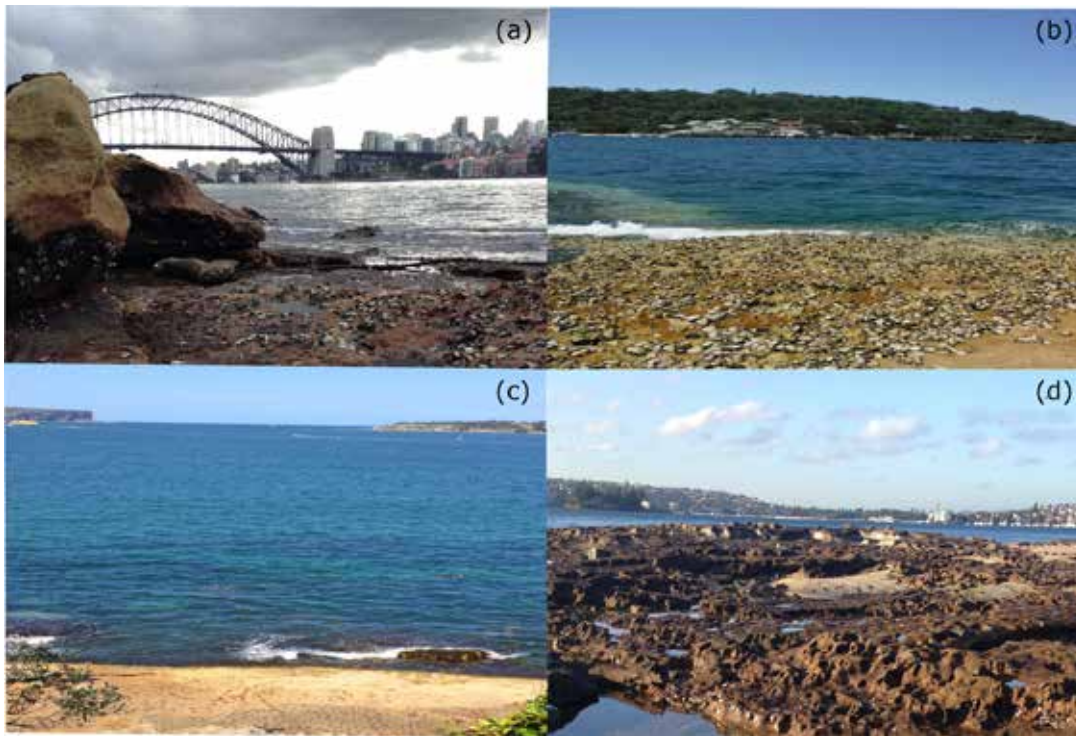


Figure 2: Examples of intertidal rocky shores in Sydney Harbour (a) looking west towards the Sydney Harbour Bridge, (b) at Chowder Bay opposite the Sydney Institute of Marine Science, (c) looking east out of the heads, and (d) surrounded by urban development.

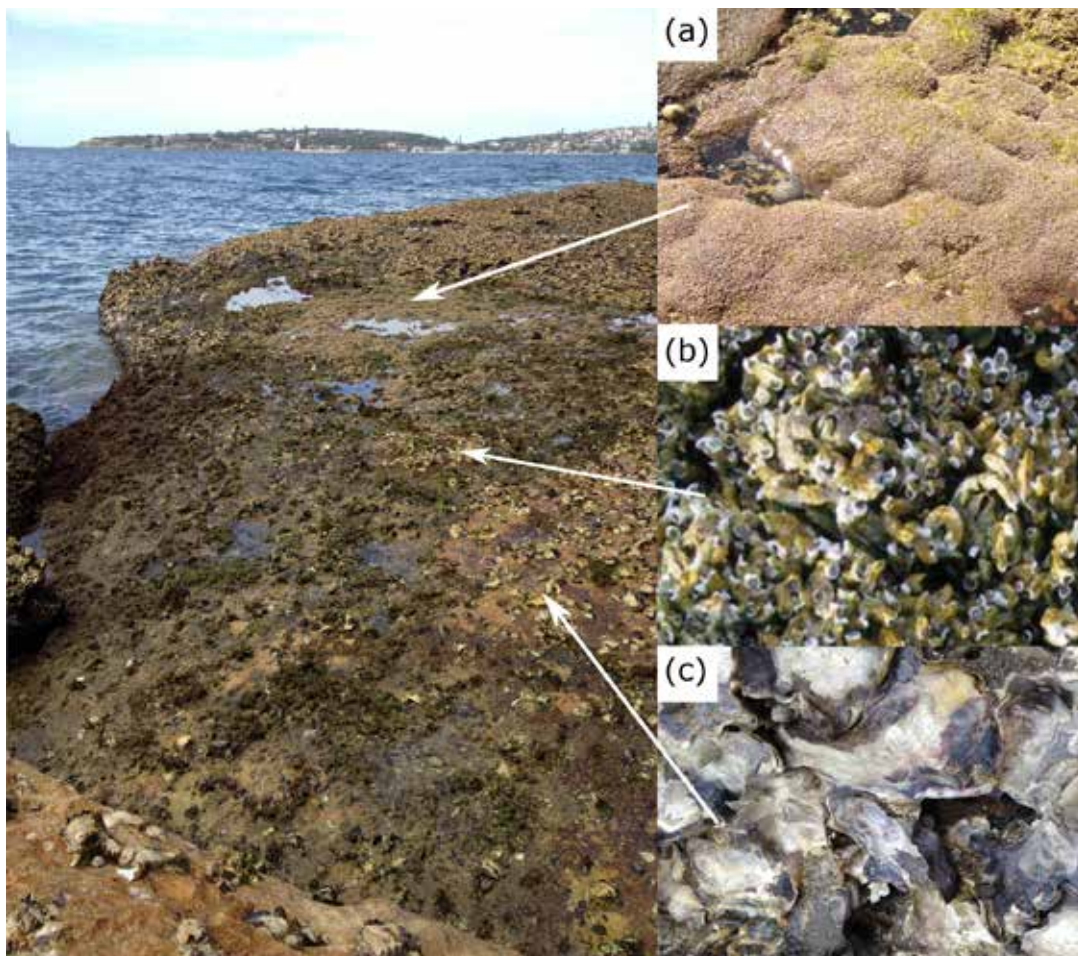


Figure 3: (a) A natural intertidal rocky shore in Sydney Harbour showing extensive urban development in the background, and in the foreground, a mosaic of mid-shore habitats of (a) turfing *Corallina officinalis*, (b) the tubeworm *Galeolaria caespitosa*, and (c) the oyster *Saccostrea glomerata*.

tens of centimetres to metres in diameter. They were interspersed with each other on the rock platform and separated by centimetres to tens of centimetres. All habitats co-occurred on the mid-low shore.

Estimation of the cover of habitats on rocky shores in Sydney Harbour

The percentage cover of oysters, *Galeolaria*, mussels, and coralline turf was estimated at Bradley's Head, Cremorne Point, and Chowder Bay (Figure 1). Independent estimates of cover for each type of bioengineered habitat were made. At each location, six, 50 x 50 cm quadrats in each habitat were haphazardly selected on the mid-low shore.

Comparison of the assemblages associated with bioengineers

Oysters, *Galeolaria*, mussels, and coralline turf (Figure 3) on intertidal rocky shores at Cremorne Point and Bradley's Head were sampled (Figure 1). Two independent, randomly-chosen sites (separated by tens of metres) at each location were sampled. Sampling was done by scraping the habitat, down to the rocky substratum, into a 10 cm diameter PVC core. Three replicate cores of each habitat were sampled at each of two sites. Although the depth of samples within habitats varied, abundances of polychaetes were not correlated with the amount of habitat in each core and therefore did not require standardising (Cole 2006).

Samples were fixed in 7% formalin buffered with filtered seawater and subsequently rinsed with freshwater through a 500 μm sieve. Polychaetes greater than 500 μm (i.e. macrofauna) were retained and identified to species or family under a dissecting microscope (often aided with use of a compound microscope for identification to species)

and preserved in 70% ethanol. Polychaetes were identified to species at the Australian Museum, with a reference collection being deposited.

Polychaetes were grouped into feeding guilds based on the dominant mode for each Family (Fauchald & Jumars 1979; Jumars *et al.* 2015). Polychaetes were separated into omnivores (including Chrysopetalidae, Nereididae, Syllidae), suspension feeders or surface deposit feeders (including Cirratulidae, Spionidae, Terebellidae), subsurface deposit feeders (including Capitellidae, Opheliidae, Orbiniidae, Maldanidae), and carnivores (including: Eunicidae, Lumbrineridae, Oeonidae, Phyllodocidae, Polynoidae).

Statistical analyses

Assemblages of polychaetes were compared among the three bioengineered habitats. Data for multivariate analyses were untransformed to test for differences in the composition and abundance of species. Non-multidimensional scaling (nMDS) ordinations (Field *et al.* 1982) based on Bray-Curtis similarity matrices (Bray and Curtis 1957) were plotted in PRIMER 6.1.11 (Clarke and Gorley 2006) to visualise patterns of difference.

Multivariate data were analysed using permutational analysis of variance (PERMANOVA+, PRIMER 6 add on, Anderson *et al.* 2009), with 9999 permutations, based on Bray-Curtis dissimilarity measures (Bray and Curtis 1957). Habitat was a fixed factor and orthogonal (3 levels). Location (2 levels) and Site (2 levels) were random, and Site was nested within Location. There were $n = 3$ replicates of each habitat in each site, in each location. Pairwise *a posteriori* comparisons were done for significant sources of variation to determine patterns of difference relative to the hypotheses of interest. Furthermore, comparisons of

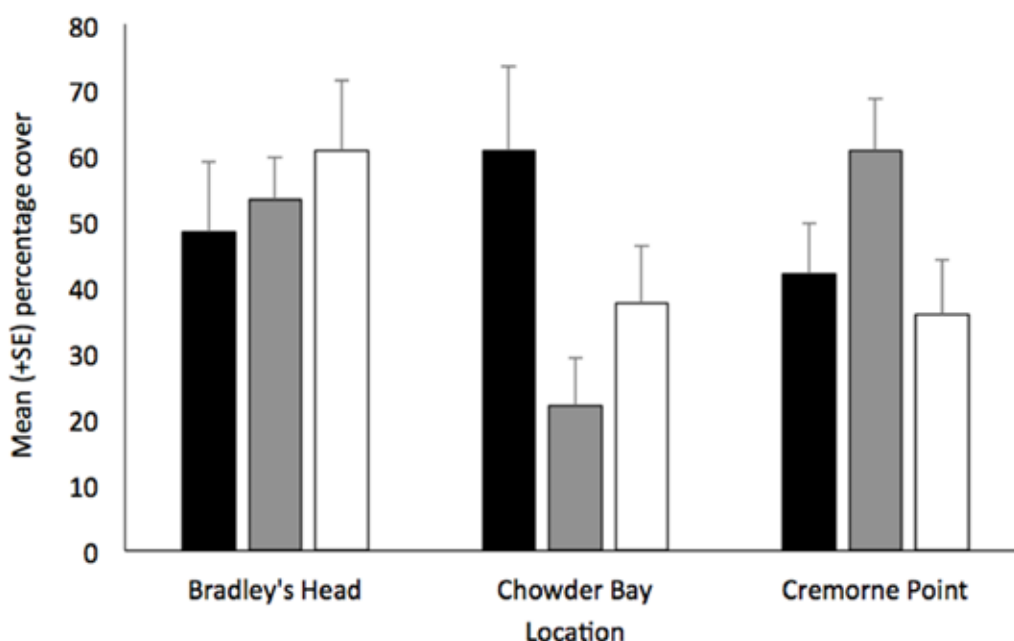


Figure 4: Mean (+SE; $n = 6$) percentage cover of bioengineered habitats created by *Galeolaria* (black bars), Oysters (grey bars) and Coralline turf (white bars) at Bradley's Head, Chowder Bay and Cremorne Point.

numbers of species of polychaetes were calculated for each site and for each type of bioengineered habitat.

Univariate data were analysed with analysis of variance (ANOVA), based on the same experimental design as for the multivariate analyses, with 3 habitats, 2 locations, 2 sites and $n = 3$ replicates. The analysis for the comparison of the cover of habitats was slightly different, with 3 habitats, 3 locations and $n = 6$ replicates. Prior to analyses, data were tested for homogeneity of variances, with Cochran's test. Data for the majority of analyses did not require transformation, and to make simple comparisons among taxa, none of the data were transformed. The violation of homogeneity of variances was considered to be acceptable because ANOVA is relatively robust to heterogeneous variances for large designs such as this (Underwood 1997). When sources of variation were shown to be significant, Student–Newman–Keuls (SNK) tests were used to compare means.

Results

Estimation of the cover of habitats on rocky shores in Sydney Harbour

The cover of bioengineered habitats varied among locations within Sydney Harbour (Figure 4, ANOVA: Location \times Habitat $MS = 1688$, $F_{4,45} = 3.4$, $P = 0.016$). Furthermore, there were spatial differences in the relative amounts of habitat (Figure 4). For example, at Bradley's Head the mean percentage covers of coralline turf, *Galeolaria* and oysters were similar (Figure 4). At Chowder Bay, coralline turf was, however, the most abundant, and at Cremorne

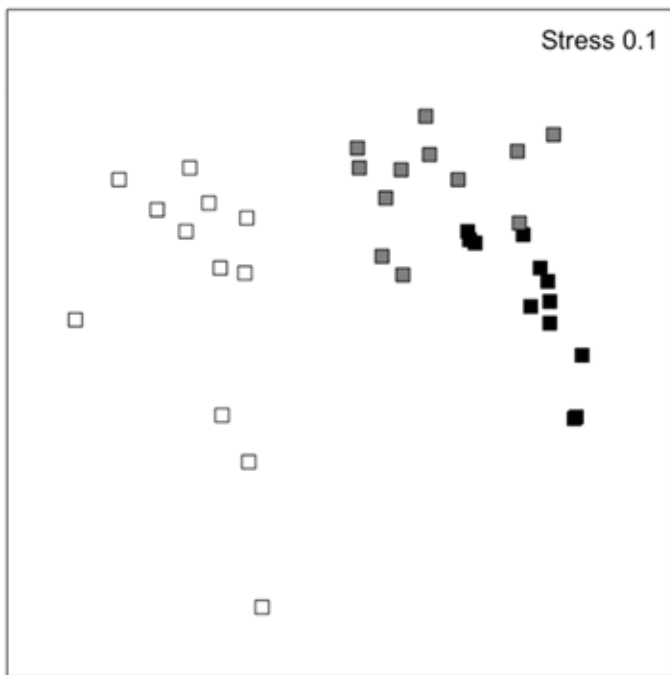


Figure 5: nMDS ordination of assemblages of polychaetes from habitats bioengineered by *Galeolaria* (black shapes), Oysters (grey shapes), Coralline turf (white shapes).

Table 1: PERMANOVA of assemblages of polychaetes from Bradley's Head and Cremorne Point. Location (Bradley's Head and Cremorne Point) and Site (2 sites) were random factors, with Site nested in Location. Habitat (oysters, *Galeolaria*, and coralline turf) was a fixed factor and was orthogonal to Location and Site, $n = 3$. Pair-wise tests compared habitats within each site.

Source	df	MS	Pseudo-F	P(perm)
Habitat	2	19982.0	5.16	0.0816
Location	1	3600.2	2.55	0.3375
Site (Location)	2	1411.9	1.27	0.2132
Location \times Habitat	2	3870.2	2.09	0.0706
Site (Location) \times Habitat	4	1854.2	1.67	0.0146
Residual	24	1110.2		
TOTAL	35			
Pair-wise	Cremorne Point Sites 1 and 2: Oys = Gal \neq Cor			
	Bradley's Head Sites 1 and 2: Oys \neq Gal \neq Cor			

Table 2: Diversity of polychaetes at two sites at each of Cremorne Point and Bradley's Head. The total number of species per site, and mean number of species per site (\pm SE; $n = 3$), and the total number of species in each habitat at each site were calculated.

	Total species	Mean (\pm SE) species	Total species
Cremorne Site 1	19	8.3 \pm 1.76	
Oysters			9
<i>Galeolaria</i>			11
Coralline turf			5
Cremorne Site 2	21	10.3 \pm 0.67	
Oysters			11
<i>Galeolaria</i>			9
Coralline turf			11
Bradley's Site 1	22	10.7 \pm 2.85	
Oysters			5
<i>Galeolaria</i>			13
Coralline turf			14
Bradley's Site 2	24	8.3 \pm 1.2	
Oysters			6
<i>Galeolaria</i>			9
Coralline turf			10

Table 3: Diversity of polychaetes across both sites at Cremorne Point and Bradley's Head. The total number of species, mean (\pm SE; $n = 6$) number of species, and unique species per habitat were calculated.

	Total species	Mean (\pm SE) species	Unique species
Oysters	16	7.75 \pm 1.38	1
<i>Galeolaria</i>	20	10.5 \pm 0.96	1
Coralline turf	23	10 \pm 1.87	7

Table 4: List of species (families) that are unique to oysters, *Galeolaria* and coralline turf, and species that are common to all three habitats.

Species unique to Oysters	Species unique to <i>Galeolaria</i>	Species unique to Coralline turf	Species common to all habitats
<i>Perinereis vallata</i> (Nereididae)	<i>Polydora woodwicksi</i> (Spionidae)	<i>Chrysopetalum debile</i> (Chrysopetalidae)	<i>Perinereis amblyodonta</i> (Nereididae)
		<i>Arichlidon hanneloreae</i> (Chrysopetalidae)	<i>Dipolydora giardia</i> (Spionidae)
		<i>Nereis maxilloidentata</i> (Nereididae)	<i>Syllis prolifera</i> (Syllidae)
		<i>Lumbrineris</i> sp. (Lumbrineridae)	<i>Lepidonotus melanogrammus</i> (Polynoidae)
		<i>Micromaldane nutricula</i> (Maldanidae)	<i>Polycirrus rosea</i> (Polycirridae)
		<i>Scoloplos</i> sp. (Orbiniidae)	<i>Polyophthalmus pictus</i> (Opheliidae)
		<i>Oenone</i> sp. (Oeononidae)	

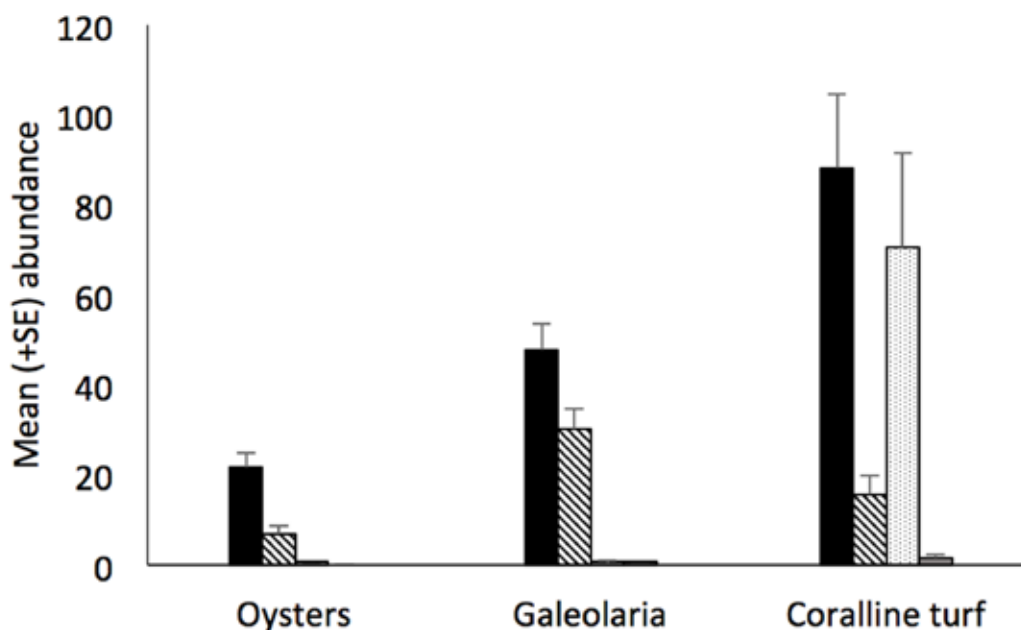


Figure 6: Mean (+SE; $n = 12$) abundance of omnivorous (black bars), suspension and surface deposit feeding (striped bars), subsurface deposit feeding (spotted bars), and carnivorous (grey bars) polychaetes in oysters, *Galeolaria*, and coralline turf.

Table 5: Analysis of variance comparing abundances of polychaetes that are (a) omnivores, (b) suspension/surface deposit feeders, and (c) subsurface deposit feeders from Bradley's Head and Cremorne Point. Location (Bradley's Head and Cremorne Point) and Site (2 sites) were random factors, with Site nested in Location. Habitat (oysters, *Galeolaria*, and coralline turf) was a fixed factor and was orthogonal to Location and Site, $n = 3$. SNK tests were done for significant sources of variation relative to the hypotheses of interest.

Source	df	(a) Omnivores $C = 0.39 (P > 0.05)$			(b) Suspension/Surface deposit $C = 0.31 (P > 0.05)$			(c) Subsurface deposit $C = 0.64 (P < 0.01)$		
		MS	F	P	MS	F	P	MS	F	P
Habitat	2	13472.19	114.14	0.009	1665.44	1.93	0.341	19647.03	7.71	0.022
Location	1	684.69	0.38	0.598	0.11	0.00	0.981	2791.36	1.28	0.376
Site (Lo)	2	1778.81	1.43	0.259	156.50	1.31	0.285	2184.14	1.43	0.260
Ha × Lo	2	118.03	0.07	0.935	863.44	7.25	0.003	2952.86		
Ha × Si(Lo)	4	1724.06	1.38	0.269	×147.67			×2344.22		
Residual	24	1244.92			×114.36			×1532.39		
Total	35									
Pooled	28				119.07			2547.10	1.66	0.17
SNK		Oys < Gal < Cor			Cremorne Point: Oys = Gal = Cor Bradley's Head: Oys = Cor < Gal			Oys = Gal < Cor		

× Denotes post hoc pooling, $P > 0.25$. New F -ratios are given for those tested against the pooled term.

Point, oysters were more abundant (Figure 4). Although oysters were most abundant at Cremorne Point, they were least abundant at Chowder Bay (Figure 4).

Assemblages associated with bioengineers

Each habitat supported a unique assemblage of polychaetes (Figure 5), but differences were location specific (Table 1). Subsequent analysis indicated that assemblages of polychaetes significantly differed between coralline turf and the other two habitats at Cremorne Point (Table 1). Assemblages of polychaetes were similar in habitat bioengineered by oysters and *Galeolaria* at Cremorne Point (Table 1). At Bradley's Head, assemblages of polychaetes significantly differed among all three habitats (Table 1).

At each site, there were a total of 19–24 species of polychaete representing 16 families (Table 2). The mean abundance of polychaetes per site was also similar (Table 2). The total number of species within each habitat differed with each site. At both sites at Cremorne Point, coralline turf had the most species, whereas at one site at Bradley's Head, coralline turf had the fewest species (Table 2).

Overall, coralline turf had the greatest number of species of polychaetes (Table 3). Furthermore, seven species were unique to coralline turf, and one species was unique to either oysters or *Galeolaria* (Table 3 & 4). Six species were common to all three habitats (Table 3 & 4).

Omnivorous polychaetes were the most abundant feeding guild, and they were most abundant in coralline turf (Table 5, Figure 6). Suspension feeding or surface deposit feeding polychaetes were most abundant in *Galeolaria* (Figure 6), but this was significant for one of the two locations (Table 5). Subsurface deposit feeding polychaetes were most abundant in coralline turf (Table 5, Figure 6). The relative abundances of different feeding guilds of polychaetes differed among habitats (Figure 6). In oysters and *Galeolaria*, omnivores and suspension feeding or surface deposit feeding polychaetes were the dominant feeding guilds (Figure 6). Abundances of carnivores were too few for analyses but they were most abundant in coralline turf and completely absent from oysters (Figure 6).

Discussion

The biogenic habitats under investigation were patchily distributed but present on all shores that were sampled. Within the marine dominated section of Sydney Harbour, these species are common on natural rocky shores (Bulleri *et al.* 2005). For example, Moreira *et al.* (2007) found seawalls to be dominated by *S. glomerata* and *G. caespitosa*, and Chapman *et al.* (2005) measured covers of *C. officinalis* up to 95% on seawalls in Sydney Harbour. Further upstream, oysters dominate hard substrata (Scanes *et al.* submitted). In the present study, although independent estimates of the percentage cover were done,

all habitats co-occurred on the mid-low shore, generally either directly adjacent or only centimetres to tens of centimetres away from each other. Similarly, patches of the biogenic habitats ranged in size at the scale of tens of centimetres to metres (Cole, pers. obs). Underwood and Chapman (1996) proposed that patchiness at these spatial scales is generally as a result of biological processes such as predation or competition. In addition to competition for space with other taxa (Menge and Sutherland 1976), and predation and/or grazing (Petraitis 1987; Connolly and Roughgarden 1999), storms (Connell *et al.* 1997; Underwood 1999), and trampling (Brosnan and Crumine 1994; Brown and Taylor 1999; Povey and Keough 1991) may result in loss of biogenic habitat.

Anthropogenic activities will transform landscapes resulting in a loss of species (Lindborg and Eriksson 2004). The loss of a single bioengineer would not just have consequences for unique species that inhabit it, but there will also be overall landscape consequences. Loss of a single habitat within a matrix has shown that there are landscape implications (Fahrig and Merriam 1994). The size of habitat patches and the ability of dispersal of a species inhabiting habitat patches influences colonisation (Cole *et al.* 2012; Fahrig 2003; Thrush *et al.* 1996), and recolonisation may occur from neighbouring patches (Hanski 1998). Highly mobile polychaetes can colonise newly created biogenic habitat patches by moving from adjacent habitat but those that are sessile or sedentary rely entirely on larval settlement (Cole *et al.* 2007). Loss of a single habitat type may alter the current proportions of different trophic groups and lead to ecosystem decline (see Dobson *et al.* 2006, for review). The present study indicates that there are a number of common species and individuals may move among the different habitats. Furthermore, there were distinct patterns of abundance of different feeding guilds of polychaetes among the different habitats. Previous studies have shown that polychaetes move between different biogenic habitats and colonise newly available habitat (Cole *et al.* 2007). Increases in the proportion of predatory polychaetes such as those from the families Polynoidae and Eunicidae, or even omnivorous Nereididae (Fauchald and Jumars 1979, Jumars *et al.* 2015) may have effects on the rest of the assemblage. Studies have shown strong influences of predators on the existing and newly colonised assemblages in benthic habitats (Commito 1982, Desroy *et al.* 1998). Specifically, omnivorous polychaetes from within biogenic habitats show strong selective choices in types of prey (Cole *et al.* 2012), and can consume and reduce other polychaete abundances in biogenic habitats (e.g. *Perinereis amblyodonta*, Cole 2009).

Under future climate change scenarios of increased storm events, sea level rise, ocean acidification and rising temperature (IPCC 2014), all habitats on rocky shores will be affected (Hawkins *et al.* 2008; Helmuth *et al.* 2006). With ocean warming, the distributional ranges of marine invertebrates are predicted to continue

(Cheung *et al.* 2009). Furthermore, changes to salinity and coastal runoff due to rainfall can have negative impacts on marine invertebrates (Pedersen and Perkins 1986). With rising sea levels, the entire intertidal rocky shore systems will be reduced (Thompson *et al.* 2002). All the bioengineering species in the present study are calcified so will therefore be threatened by ocean acidification (Orr *et al.* 2005). Ocean acidification affects a range of physiological processes (Pörtner 2008), and growth, reproduction, and survival (Doney *et al.* 2009; Kurihara 2008), which also lead to ecosystem-scale effects (Hall–Spencer *et al.* 2008; Pörtner and Farrell 2008). Of the three habitat forming species in the present study, oysters may be most at risk because molluscs rank among the most affected (Gazeau *et al.* 2013; Kroeker *et al.* 2010; Ries *et al.* 2009; Ross *et al.* 2011). In addition to negative effects of ocean acidification on *S. glomerata* (Parker *et al.* 2009; 2010), declines in survival of coralline algae (Kuffner *et al.* 2008; Martin and Gattuso 2009), and tubeworms (Lane *et al.* 2013; San Chan *et al.* 2012) have also been observed.

Many of these climate related threats will be unavoidable in the future. It is therefore imperative that immediate non-climate related threats are mitigated. Replacement of rocky shores with seawalls will reduce the amount of available intertidal space for these habitat-forming species (Chapman 2003). In urban areas, such as in Sydney Harbour, run-off introduces contaminants into biological systems (Pedersen and Perkins 1986; Stark 1998), which has extensive impacts on species associated with biogenic habitats (Roberts *et al.* 2008), and on ecological functioning (Johnston *et al.* 2014). There is also extensive boating activity within the harbour (Widmer and Underwood 2004), and increases in wave-action will affect the structure of these habitats (McQuaid and Lindsay 2002). Increases in artificial structures within Sydney Harbour may also aid the arrival or spread of marine nonindigenous species (Glasby *et al.* 2007).

Many intertidal rocky shores throughout the world are over-exploited for food and bait, including Portugal (Jacinto *et al.* 2009; Rius and Cabral 2004), Chile (Duran and Castilla 1989; Bustamante and Castilla 1990), and South Africa (Kyle *et al.* 1997; Lasiak and Field 1995).

References

Ambrose, W.G.J. 1984. Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. *Journal of Experimental Marine Biology and Ecology* 80: 67–75. [http://dx.doi.org/10.1016/0022-0981\(84\)90094-7](http://dx.doi.org/10.1016/0022-0981(84)90094-7)

Ambrose, W.G.J. 1984. Influences of predatory polychaetes and epibenthic predators on the structure of a soft-bottom community in a Maine estuary. *Journal of Experimental Marine Biology and Ecology* 81: 115–145. [http://dx.doi.org/10.1016/0022-0981\(84\)90002-9](http://dx.doi.org/10.1016/0022-0981(84)90002-9)

Underwood (1993) investigated overexploitation of rocky shores in Sydney. Although oysters have been historically exploited in Sydney and throughout the world, it is unlikely tubeworms and coralline turf will also be harvested. In South Africa, there is a negative relationship between mussels that are overharvested and coralline turf. Similarly, in Sydney Harbour, removal of mussels on seawalls increased the cover of coralline algae (Chapman *et al.* 2005). Although coralline algae had a greater diversity of polychaetes than the other two habitats, their loss will lead to the loss of unique species. Specifically loss of oysters in Sydney Harbour will mean loss of a number of unique species. If harvesting goes unchecked it can create a scenario of overharvesting and rarity of intertidal species in other countries (Coen 1995, Moreno 2001; Roy *et al.* 2003).

Marine protected areas have been shown to be important and effective in protecting target species (Halpern 2003; Halpern and Warner 2003; Roberts *et al.* 2001), but the effects on associated species may not be so clear (Cole *et al.* 2011). Although marine parks can be useful, in the absence of other management strategies, they may not be the best solution for protection of biodiversity (Boersma and Parrish 1999). Any management strategies to protect parts of the Hawkesbury Manning Shelf Bioregion through the creation of a marine park in Sydney Harbour need to recognise the importance of biogenic habitats in enhancing local biodiversity (Creese and Breen 2003). As threats to intertidal habitats continue with increasing human populations, this may become increasingly important (Helmuth *et al.* 2006; Thompson *et al.* 2002). Similarly, any decisions and attempts at restoring oyster reefs within Sydney Harbour have implications for not just the oysters but also the neighbouring biogenic habitats and associated fauna. This study highlights the importance of biogenic habitats within Sydney Harbour and the need to consider the diverse assemblages associated with bioengineers when making management decisions.

Acknowledgements

The authors are grateful to G. San Martín, K. Atkinson, and A. Murray for assistance with identifications of polychaetes, and E. Scanes for help in the field.

Anderson, M.J., Gorley, R.N. and Clarke, K.R. 2009. PERMANOVA+ for PRIMER: *Guide to Software and Statistical Methods*. PRIMER-E, Plymouth, UK.

Beck, M.W., Brumbaugh, R.D., Airoidi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G. and Guo, X. 2011. Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management. *Bioscience* 61: 107–116. <http://dx.doi.org/10.1525/bio.2011.61.2.5>

- Blockley, D.J., Cole, V.J., People, J. and Palomo, M.G. 2007. Effects of short-term rain events on mobile macrofauna living on seawalls. *Journal of the Marine Biological Association of the United Kingdom* 87: 1069–1074. <http://dx.doi.org/10.1017/S0025315407055117>
- Boersma, P.D. and Parrish, J.K. 1999. Limiting abuse: marine protected areas, a limited solution. *Ecological Economics* 31: 287–304. [http://dx.doi.org/10.1016/S0921-8009\(99\)00085-3](http://dx.doi.org/10.1016/S0921-8009(99)00085-3)
- Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27: 326–349. <http://dx.doi.org/10.2307/1942268>
- Brosnan, D.M. and Crumrine, L.L. 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology* 177: 79–97. [http://dx.doi.org/10.1016/0022-0981\(94\)90145-7](http://dx.doi.org/10.1016/0022-0981(94)90145-7)
- Brown, P.J. and Taylor, R.B. 1999. Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal. *Journal of Experimental Marine Biology and Ecology* 235: 45–53. [http://dx.doi.org/10.1016/S0022-0981\(98\)00186-5](http://dx.doi.org/10.1016/S0022-0981(98)00186-5)
- Bruno, J.F., Stachowicz, J.J. and Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119–125. [http://dx.doi.org/10.1016/S0169-5347\(02\)00045-9](http://dx.doi.org/10.1016/S0169-5347(02)00045-9)
- Bulleri, F., Champan, M.G. and Underwood, A.J. 2005. Intertidal assemblages on seawalls and vertical rocky shores in Sydney Harbour, Australia. *Austral Ecology* 30: 655–667. <http://dx.doi.org/10.1111/j.1442-9993.2005.01507.x>
- Bulleri, F. and Chapman, M.G. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* 47: 26–35. <http://dx.doi.org/10.1111/j.1365-2664.2009.01751.x>
- Bustamante, R.H. and Castilla, J.C. 1990. Impact of human exploitation on populations of the intertidal Southern Bull-kelp *Durvillaea antarctica* (Phaeophyta, Durvilliales) in central Chile. *Biological Conservation* 52: 205–220. [http://dx.doi.org/10.1016/0006-3207\(90\)90126-A](http://dx.doi.org/10.1016/0006-3207(90)90126-A)
- Butler, A.J., Rees, T., Beesley, P. and Bax, N.J. 2010. Marine biodiversity in the Australian region. *PloS One* 5: e11831. <http://dx.doi.org/10.1371/journal.pone.0011831>
- Castilla, J.C., Lagos, N.A. and Cerda, M. 2004. Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky-shore. *Marine Ecology Progress Series* 268: 119–130. <http://dx.doi.org/10.3354/meps268119>
- Chapman, M.G., People, J. and Blockley, D. 2005. Intertidal assemblages associated with natural *Corallina* turf and invasive mussel beds. *Biodiversity and Conservation* 14: 1761–1773. <http://dx.doi.org/10.1007/s10531-004-0698-8>
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10: 235–251. <http://dx.doi.org/10.1111/j.1467-2979.2008.00315.x>
- Clarke, K.R. and Gorley, R.N. 2006. PRIMER v6. PRIMER-E: Plymouth Marine Laboratory, Plymouth.
- Coen, L.D. 1995. *A review of the potential impacts of mechanical harvesting on subtidal and intertidal shellfish resources*. South Carolina Department of Natural Resources, Marine Resources Research Institute Charleston, SC.
- Coen, L.D., Luckenbach, M.W. and Breitburg, D.L. 1998. The role of oyster reefs as essential fish habitat: A review of current knowledge and some new perspectives. In: Benaka, L.R. (eds) *Fish Habitat: Essential Fish Habitat and Rehabilitation*. pp 438–454
- Cole, V.J. 2006. *The ecology of polychaetes in biogenic habitats on intertidal rocky shores*. PhD. The University of Sydney.
- Cole, V.J. 2009. Densities of polychaetes in habitat fragments depend on the surrounding matrix but not the complexity of the remaining fragment. *Austral Ecology* 34: 469–477. <http://dx.doi.org/10.1111/j.1442-9993.2009.01947.x>
- Cole, V.J., Chapman, M.G. and Underwood, A.J. 2007. Landscape and life-histories influence colonisation of polychaetes to intertidal biogenic habitats. *Journal of Experimental Marine Biology and Ecology* 348: 191–199. <http://dx.doi.org/10.1016/j.jembe.2007.05.001>
- Cole, V.J., Johnson, L.G. and McQuaid, C.D. 2012. Effects of patch-size on populations of intertidal limpets, *Siphonaria* spp., in a linear landscape. *PloS One* 7: e52076. <http://dx.doi.org/10.1371/journal.pone.0052076>
- Cole, V.J. and McQuaid, C.D. 2010. Bioengineers and their associated fauna respond differently to the effects of biogeography and upwelling. *Ecology* 91: 3549–3562. <http://dx.doi.org/10.1890/09-2152.1>
- Cole, V.J., McQuaid, C.D. and Nakin, M.D.V. 2011. Marine protected areas export larvae of infauna, but not of bioengineering mussels to adjacent areas. *Biological Conservation* 144: 2088–2096. <http://dx.doi.org/10.1016/j.biocon.2011.04.030>
- Cole, V.J., McQuaid, K.A. and McQuaid, C.D. 2012. Examination of small- and large-scale influences on the diet of an omnivorous polychaete indicates weak effects of upwelling. *Journal of Experimental Marine Biology and Ecology* 436: 28–35. <http://dx.doi.org/10.1016/j.jembe.2012.08.013>
- Coleman, F.C. and Williams, S.L. 2002. Overexploiting marine ecosystem engineers: Potential consequences for biodiversity. *Trends in Ecology and Evolution* 17: 40–43. [http://dx.doi.org/10.1016/S0169-5347\(01\)02330-8](http://dx.doi.org/10.1016/S0169-5347(01)02330-8)

- Commito, J.A.** 1982. Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. *Marine Biology* 68: 77–81. <http://dx.doi.org/10.1007/BF00393144>
- Connell, J.H., Hughes, T.P. and Wallace, C.C.** 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* 67: 461–488. [http://dx.doi.org/10.1890/0012-9615\(1997\)067\[0461:AYSOCA\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(1997)067[0461:AYSOCA]2.0.CO;2)
- Crain, C.M. and Bertness, M.D.** 2006. Ecosystem engineering across environmental gradients: Implications for conservation and management. *Bioscience* 56: 211–218. [http://dx.doi.org/10.1641/0006-3568\(2006\)056\[0211:EE](http://dx.doi.org/10.1641/0006-3568(2006)056[0211:EE)
- Creese, R.G. and Breen, D.A.** 2003. Marine protected areas in New South Wales, Australia: challenges for research. In: Hutchings, P.A., and Lunney, D. *Conserving Marine Environments. Out of Sight Out of Mind*. Royal Zoological Society of New South Wales, Mosman, NSW, Australia, pp. 120–128. <http://dx.doi.org/10.7882/9780958608565>
- Dayton, P.K.** 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. *Colloquium on Conservation Problems in Antarctica 1971*. Allen Press, Lawrence, pp 81–96
- Desroy, N., Retière, C. and Thiébaud, E.** 1998. Infaunal predation regulates benthic recruitment: an experimental study of the influence of the predator *Nephtys hombergii* (Savigny) on recruits of *Nereis diversicolor* (O.F. Müller). *Journal of Experimental Marine Biology and Ecology* 228: 257–272. [http://dx.doi.org/10.1016/S0022-0981\(98\)00033-1](http://dx.doi.org/10.1016/S0022-0981(98)00033-1)
- Dobson, A., Lodge, D., Alder, J., Cumming, G.S., Keymer, J., McGlade, J., Mooney, H., Rusak, J.A., Sala, O. and Wolters, V.** 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* 87: 1915–1924. [http://dx.doi.org/10.1890/0012-9658\(2006\)87\[1915:HLTCAT\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87[1915:HLTCAT]2.0.CO;2)
- Doney, S.C., Fabry, V.J., Feely, R.A. and Kleypas, J.A.** 2009. Ocean acidification: The other CO₂ problem. *Annual Review of Marine Science* 1: 169–192. <http://dx.doi.org/10.1146/annurev.marine.010908.163834>
- Duran, L. and Castilla, J.C.** 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Marine Biology* 103: 555–562. <http://dx.doi.org/10.1007/BF00399588>
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Forester, D.R. and Webster, J.R.** 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3: 479–486. [http://dx.doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Fahrig, L.** 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*. 34: 487–515. <http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- Fahrig, L. and Merriam, G.** 1994. Conservation of fragmented populations. *Conservation Biology* 8: 50–59. <http://dx.doi.org/10.1046/j.1523-1739.1994.08010050.x>
- Fauchald, K. and Jumars, P.A.** 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17: 193–284.
- Field, J.G., Clarke, K.R. and Warwick, R.M.** 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37–52.
- Gazeau, F., Parker, L.M., Comeau, S., Gattuso, J.-P., O'Connor, W.A., Martin, S., Pörtner, H.-O. and Ross, P.M.** 2013. Impacts of ocean acidification on marine shelled molluscs. *Marine Biology* 160: 2207–2245. <http://dx.doi.org/10.1007/s00227-013-2219-3>
- Giangrande, A., Licciano, M. and Musco, L.** 2005. Polychaetes as environmental indicators revisited. *Marine Pollution Bulletin* 50: 1153–1162. <http://dx.doi.org/10.1016/j.marpolbul.2005.08.003>
- Glasby, T.M., Connell, S.D., Holloway, M.G., and Hewitt, C.L.** 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Marine Biology* 151: 887–895. <http://dx.doi.org/10.1007/s00227-006-0552-5>
- Gobin, J.F. and Warwick, R.M.** 2006. Geographical variation in species diversity: A comparison of marine polychaetes and nematodes. *Journal of Experimental Marine Biology and Ecology* 330: 234–244. <http://dx.doi.org/10.1016/j.jembe.2005.12.030>
- Goodsell, P.J., Chapman, M.G. and Underwood, A.J.** 2007. Differences between biota in anthropogenically fragmented habitats and in naturally patchy habitats. *Marine Ecology–Progress Series* 351: 15–23. <http://dx.doi.org/10.3354/meps07144>
- Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D. and Buia, M.-C.** 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454: 96–99. <http://dx.doi.org/10.1038/nature07051>
- Halpern, B.S.** 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13: S117–S137. [http://dx.doi.org/10.1890/1051-0761\(2003\)013\[0117:TOMRD\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2003)013[0117:TOMRD]2.0.CO;2)
- Halpern, B.S. and Warner, R.R.** 2003. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London Series B–Biological Sciences* 270: 1871–1878. <http://dx.doi.org/10.1098/rspb.2003.2405>

- Halt, M.N., Kupriyanova, E.K., Cooper, S.J. and Rouse, G.W. 2009. Naming species with no morphological indicators: species status of *Galeolaria caespitosa* (Annelida: Serpulidae) inferred from nuclear and mitochondrial gene sequences and morphology. *Invertebrate Systematics* 23: 205–222. <http://dx.doi.org/10.1071/IS09003>
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396: 41–49. <http://dx.doi.org/10.1038/23876>
- Hawkins, S.J., Moore, P., Burrows, M.T., Poloczanska, E., Mieszkowska, N., Herbert, R.J., Jenkins, S.R., Thompson, R.C., Genner, M.J. and Southward, A.J. 2008. Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. *Climate Research* 37: 123–133. <http://dx.doi.org/10.3354/cr00768>
- Hedge L.H., Johnston E.L., Ayhong S.T., Birch G.F., Booth D.J., Creese R.G., Doblin M.A., Figueira W.F., Gribben P.E., Hutchings P.A., Mayer Pinto M., Marzinelli E.M., Pritchard T.R., Roughan M., Steinberg P.D., 2013. *Sydney Harbour: A systematic review of the science*, Sydney Institute of Marine Science, Sydney, Australia
- Helmuth, B., Mieszkowska, N., Moore, P. and Hawkins, S.J. 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution, and Systematics*: 373–404. <http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110149>
- Huston, M.A. 1994. *Biological Diversity: The coexistence of species in changing landscapes*. Cambridge University Press, Cambridge.
- Hutchings, P. 1998. Biodiversity and functioning of polychaete in benthic sediments. *Biodiversity and Conservation* 7: 1133–1145. <http://dx.doi.org/10.1023/A:1008871430178>
- Hutchings, P.A. 2000. Natural History. In: Beesley, P.L., Ross, G.J.B. and Glasby, C.J. (ed) *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia*. CSIRO Publishing, Melbourne, pp 32–38.
- IPCC 2014. Summary for Policymakers. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R. and White, L.L. (eds) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA, pp 1–32.
- Jacinto, D., Cruz, T., Silva, T. and Castro, J.J. 2009. Stalked barnacle (*Pollicipes pollicipes*) harvesting in the Berlengas Nature Reserve, Portugal: temporal variation and validation of logbook data. *ICES Journal of Marine Science: Journal du Conseil*: fsp226. <http://dx.doi.org/10.1093/icesjms/fsp226>
- Johnston, E.J., Mayer-Pinto, M. and Crowe, T.P. 2014. Chemical contaminant effects on marine ecosystem functioning. *Journal of Applied Ecology* 52: 1365–2664. <http://dx.doi.org/10.1111/1365-2664.12355>
- Jones, C.G., Lawton, H. and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386. http://dx.doi.org/10.1007/978-1-4612-4018-1_14
- Jones, C.G., Lawton, J.H. and Shachak, M. 1997. Ecosystem engineering by organisms: why semantics matters. *Trends in Ecology and Evolution* 12: 275. [http://dx.doi.org/10.1016/S0169-5347\(97\)81019-1](http://dx.doi.org/10.1016/S0169-5347(97)81019-1)
- Jones, C.G., Lawton, J.H. and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957. [http://dx.doi.org/10.1890/0012-9658\(1997\)078\[1946:PANEOO\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2)
- Jumars, P. A., Dorgan, K. M. and Lindsay, S. M. 2015. Diet of worms emended: an update of polychaete feeding guilds. *Marine Science*, 7: 497–520. <http://dx.doi.org/10.1146/annurev-marine-010814-020007>
- Kelagher, B.P. and Cole, V.J. 2005. Variation in abundance and size-structure of populations of the small chiton, *Acanthochitona retrojecta*. *Journal of Molluscan Studies* 71: 145–151. <http://dx.doi.org/10.1093/mollus/eyi017>
- Kroeker, K.J., Kordas, R.L., Crim, R.N. and Singh, G.G. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* 13: 1419–1434. <http://dx.doi.org/10.1111/j.1461-0248.2010.01518.x>
- Kuffner, I.B., Andersson, A.J., Jokiel, P.L., Ku'ulei, S.R. and Mackenzie, F.T. 2008. Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geoscience* 1: 114–117. <http://dx.doi.org/10.1038/ngeo100>
- Kurihara, H. 2008. Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373: 275–284. <http://dx.doi.org/10.3354/meps07802>
- Kyle, R., Pearson, B., Fielding, P.J., Robertson, W.D. and Birnie, S.L. 1997. Subsistence shellfish harvesting in the Maputaland Marine Reserve in northern KwaZulu-Natal, South Africa: Rocky shore organisms. *Biological Conservation* 82: 183–192. <http://dx.doi.org/10.1038/ngeo100>
- Lane, A.C., Mukherjee, J., Chan, V.B. and Thiyagarajan, V. 2013. Decreased pH does not alter metamorphosis but compromises juvenile calcification of the tube worm *Hydroides elegans*. *Marine Biology* 160: 1983–1993. <http://dx.doi.org/10.1007/s00227-012-2056-9>
- Lasiak, T. 1998. Multivariate comparisons of rocky infratidal macrofaunal assemblages from replicate exploited and non-exploited localities on the Transkei coast of South Africa.

- Marine Ecology Progress Series* 167: 15–23. <http://dx.doi.org/10.3354/meps167015>
- Lasiak, T. and Field, J.G.** 1995. Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages. *Journal of Experimental Marine Biology and Ecology* 185: 33–53. [http://dx.doi.org/10.1016/0022-0981\(94\)00130-6](http://dx.doi.org/10.1016/0022-0981(94)00130-6)
- Lindborg, R. and Eriksson, O.** 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85: 1840–1845. <http://dx.doi.org/10.1890/04-0367>
- Ling, S.D.** 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 156: 883–894. <http://dx.doi.org/10.1007/s00442-008-1043-9>
- Ludford, A., Cole, V.J., Porri, E., McQuaid, C.D., Nakin, M.D. and Erlandsson, J.** 2012. Testing source-sink theory: the spill-over of mussel recruits beyond marine protected areas. *Landscape Ecology* 27: 859–868. <http://dx.doi.org/10.1007/s10980-012-9739-y>
- Mayer-Pinto, M., Johnston, E.L., Hutchings, P., Marzinelli, E.M., Birch, G., Booth, D., Creese, R.G., Doblin, M.A., Figueira, W., Gribben, P.E., Pritchard, T., Roughan, M., Ah Yong, S., Steinberg, P.D., and Hedge, L.H.** 2015. Sydney Harbour: A review of anthropogenic impacts on the biodiversity and ecosystem function of one of the world's largest natural harbours *Marine and Freshwater Research* 66: in press.
- Martin, S. and Gattuso, J.P.** 2009. Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Global Change Biology* 15: 2089–2100. <http://dx.doi.org/10.1111/j.1365-2486.2009.01874.x>
- McKinney, M.L.** 2002. Urbanization, Biodiversity, and Conservation The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience* 52: 883–890. [http://dx.doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC](http://dx.doi.org/10.1641/0006-3568(2002)052[0883:UBAC)
- McNeely, J.A., Miller, K.R., Reid, W.V., Mittermeier, R.A. and Werner, T.B.** 1990. *Conserving the world's biological diversity*. International Union for Conservation of Nature and Natural Resources.
- McQuaid, C.D., & Lindsay, T.L.** 2000. Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations. *Marine Ecology Progress Series* 206: 147–154. <http://dx.doi.org/10.3354/meps206147>
- Menge, B.A. and Sutherland, J.P.** 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *The American Naturalist*: 351–369.
- Minchinton, T.E.** 1997. Life on the edge: conspecific attraction and recruitment of populations to disturbed habitats. *Oecologia* 111: 45–52. <http://dx.doi.org/10.1007/s004420050206>
- Moreira, J., Chapman, M. and Underwood, A.** 2007. Maintenance of chitons on seawalls using crevices on sandstone blocks as habitat in Sydney Harbour, Australia. *Journal of Experimental Marine Biology and Ecology* 347: 134–143. <http://dx.doi.org/10.1016/j.jembe.2007.04.001>
- Moreno, C.A.** 2001. Community patterns generated by human harvesting on Chilean shores: a review. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11: 19–30. <http://dx.doi.org/10.1002/aqc.430>
- Oeckelmann, K.W. and Vahl, O.** 1970. On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. *Ophelia* 8: 275–294. <http://dx.doi.org/10.1080/00785326.1970.10429564>
- Olsgard, F. and Somerfield, P.J.** 2000. Surrogates in marine benthic investigations – which taxonomic unit to target? *Journal of Aquatic Ecosystem Stress and Recovery* 7: 25–42. <http://dx.doi.org/10.1023/A:1009967313147>
- Olsgard, F., T. B. and Holthe, T.** 2003. Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups. *Biodiversity and Conservation* 12: 1033–1049. <http://dx.doi.org/10.1023/A:1022800405253>
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G.K., Rodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M.F., Yamanaka, Y. and Yool, A.** 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437: 681–686. <http://dx.doi.org/10.1038/nature04095>
- Otway, N.M.** 1995. Population ecology of the low-shore chitons *Onithochiton querinus* and *Plaxiphora albida*. *Marine Biology* 121: 105–116. <http://dx.doi.org/10.1007/BF00349479>
- Parker, L., Ross, P. and O'Connor, W.** 2009. The effect of ocean acidification and temperature on the fertilisation and embryonic development of the Sydney rock oyster *Saccostrea glomerata* (Gould 1850). *Global Change Biology* 15: 2123–2136. <http://dx.doi.org/10.1111/j.1365-2486.2009.01895.x>
- Parker, L., Ross, P. and O'Connor, W.** 2010. Comparing the effect of elevated pCO₂ and temperature on the fertilization and early development of two species of oysters. *Marine Biology* 157: 2435–2452. <http://dx.doi.org/10.1007/s00227-010-1508-3>
- Pedersen, E. and Perkins, M.** 1986. The use of benthic invertebrate data for evaluating impacts of urban runoff. *Hydrobiologia* 139: 13–22. <http://dx.doi.org/10.1007/BF00770238>

- Pörtner, H.-O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Marine Ecology Progress Series* 373: 203–217. <http://dx.doi.org/10.3354/meps07768>
- Pörtner, H.-O. and Farrell, A.P. 2008. ECOLOGY Physiology and Climate Change. *Science* 322: 690–692. <http://dx.doi.org/10.1126/science.1163156>
- Povey, A. and Keough, M.J. 1991. Effects of trampling on plant and animal populations on rocky shores. *Oikos*: 355–368. <http://dx.doi.org/10.1111/j.1439-0485.2011.00467.x>
- Ries, J.B., Cohen, A.L. and McCorkle, D.C. 2009. Marine calcifiers exhibit mixed responses to CO₂-induced ocean acidification. *Geology* 37: 1131–1134. <http://dx.doi.org/10.1130/g30210a.1>
- Rius, M. and Cabral, H.N. 2004. Human harvesting of *Mytilus galloprovincialis* Lamarck, 1819, on the central coast of Portugal. *Scientia Marina* 68: 545–551. <http://dx.doi.org/10.3989/scimar.2004.68n4545>
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. and Goodridge, R. 2001. Effects of marine reserves on adjacent fisheries. *Science* 294: 1920–1923. <http://dx.doi.org/10.1126/science.294.5548.1920>
- Roberts, D.A., Johnston, E.L. and Poore, A.G.B. 2008. Contamination of marine biogenic habitats and effects upon associated epifauna. *Marine Pollution Bulletin* 56: 1057–1065. <http://dx.doi.org/10.1016/j.marpolbul.2008.03.003>
- Ross, P.M., Parker, L., O'Connor, W.A. and Bailey, E.A. 2011. The impact of ocean acidification on reproduction, early development and settlement of marine organisms. *Water* 3: 1005–1030. <http://dx.doi.org/10.3390/w3041005>
- Roy, K., Collins, A.G., Becker, B.J., Begovic, E. and Engle, J.M. 2003. Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecology Letters* 6: 205–211. <http://dx.doi.org/10.1046/j.1461-0248.2003.00419.x>
- San Chan, V.B., Li, C., Lane, A.C., Wang, Y., Lu, X., Shih, K., Zhang, T. and Thiyagarajan, V. 2012. CO₂-driven ocean acidification alters and weakens integrity of the calcareous tubes produced by the serpulid tubeworm, *Hydroides elegans*. *PloS One* 7: e42718. <http://dx.doi.org/10.1371/journal.pone.0042718>
- Scanes E., Johnston E.L., Cole V.J., O'Connor W.A., Parker L.M., Ross P.R. Submitted. Quantifying native and invasive oyster distribution in an iconic urbanised estuary. *Aquatic Invasions*.
- Seed, R. 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the United Kingdom* 76: 203–210. <http://dx.doi.org/10.1017/S0025315400029131>
- Sousa, W.P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65: 1918–1935. <http://dx.doi.org/10.2307/1937789>
- Stark, J.S. 1998. Heavy metal pollution and macrobenthic assemblages in soft sediments in two Sydney estuaries, Australia. *Marine and Freshwater Research* 49: 533–540. <http://dx.doi.org/10.1071/MF97188>
- Thompson, R.C., Crowe, T.P. and Hawkins, S.J. 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation* 29: 168–191. <http://dx.doi.org/10.1017/S0376892902000115>
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* 25: 1–45. <http://dx.doi.org/10.1111/j.1469-185X.1950.tb00585.x>
- Thrush, S.F., Whitlatch, R.B., Pridmore, R.D., Hewitt, J.E., Cummings, V.J. and Wilkinson, M.R. 1996. Scale-dependent recolonisation: the role of sediment stability in a dynamic sandflat habitat. *Ecology* 77: 2472–2487. <http://dx.doi.org/10.2307/2265747>
- Underwood, A. 1993. Exploitation of species on the rocky coast of New South Wales (Australia) and options for its management. *Ocean & Coastal Management* 20: 41–62. [http://dx.doi.org/10.1016/0964-5691\(93\)90012-N](http://dx.doi.org/10.1016/0964-5691(93)90012-N)
- Underwood, A.J. 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and season changes. *Journal of Experimental Marine Biology and Ecology* 51: 57–85. [http://dx.doi.org/10.1016/0022-0981\(81\)90154-4](http://dx.doi.org/10.1016/0022-0981(81)90154-4)
- Underwood, A.J. 1999. Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *Journal of Experimental Marine Biology and Ecology* 232: 125–140. [http://dx.doi.org/10.1016/S0022-0981\(98\)00105-1](http://dx.doi.org/10.1016/S0022-0981(98)00105-1)
- Underwood, A.J. and Chapman, M.G. 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107: 212–224. <http://dx.doi.org/10.1007/BF00327905>
- Widmer, W.M., and Underwood, A.J. 2004. Factors affecting traffic and anchoring patterns of recreational boats in Sydney Harbour, Australia. *Landscape and Urban Planning* 66: 173–183. [http://dx.doi.org/10.1016/S0169-2046\(03\)00099-9](http://dx.doi.org/10.1016/S0169-2046(03)00099-9)
- Wright, J.P. and Jones, C.G. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *Bioscience* 56: 203–209. [http://dx.doi.org/10.1641/0006-3568\(2006\)056\[0203:TC](http://dx.doi.org/10.1641/0006-3568(2006)056[0203:TC)