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Latitudinal gradients in ecosystem engineering by oysters vary across habitats

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Abstract. Ecological theory predicts that positive interactions among organisms will increase across gradients of increasing abiotic stress or consumer pressure. This theory has been supported by empirical studies examining the magnitude of ecosystem engineering across environmental gradients and between habitat settings at local scale. Predictions that habitat setting, by modifying both biotic and abiotic factors, will determine large-scale gradients in ecosystem engineering have not been tested, however. A combination of manipulative experiments and field surveys assessed whether along the east Australian coastline: (1) facilitation of invertebrates by the oyster *Saccostrea glomerata* increased across a latitudinal gradient in temperature; and (2) the magnitude of this effect varied between intertidal rocky shores and mangrove forests. It was expected that on rocky shores, where oysters are the primary ecosystem engineer, they would play a greater role in ameliorating latitudinal gradients in temperature than in mangroves, where they are a secondary ecosystem engineer living under the mangrove canopy. On rocky shores, the enhancement of invertebrate abundance in oysters as compared to bare microhabitat decreased with latitude, as the maximum temperatures experienced by intertidal organisms diminished. By contrast, in mangrove forests, where the mangrove canopy resulted in maximum temperatures that were cooler and of greater humidity than on rocky shores, we found no evidence of latitudinal gradients of oyster effects on invertebrate abundance. Contrary to predictions, the magnitude by which oysters enhanced biodiversity was in many instances similar between mangroves and rocky shores. Whether habitat-context modifies patterns of spatial variation in the effects of ecosystem engineers on community structure will depend, in part, on the extent to which the environmental amelioration provided by an ecosystem engineer replicates that of other co-occurring ecosystem engineers.

Key words: ecosystem engineer; facilitation; habitat complexity; intertidal; invertebrates; latitudinal gradient; mangrove; positive interactions; rocky shore; stress amelioration; stress-gradient hypothesis; Sydney rock oyster.

INTRODUCTION

Ecosystem engineers exhibit strong influences on biodiversity by modifying abiotic conditions and/or altering the strength of biotic interactions such as competition and predation (Jones et al. 1994, 1997). Although in some instances the alteration of the environment by ecosystem engineers is so complete that the entire habitat changes from one type to another (e.g., beaver dams), in most situations engineering is less extreme and the effects are likely to be highly context-dependent (Jones et al. 1994, 1997). The extent to which ecosystem engineers influence associated communities is predicted to increase with the extent to which they modify physical and biological conditions (Crain and Bertness 2006). Similarly, their impact is predicted to shift from negative to positive with increasing levels of abiotic or biotic stress (Bertness and Callaway 1994).

Support for the context-dependency of ecosystem engineering has been provided by studies comparing the effect of ecosystem engineers across environmental gradients, for example, in salinity, temperature, desiccation, or sedimentation (Broitman et al. 2001, Badano and Cavieres 2006, Wright et al. 2006, Silliman et al. 2011, Kimbro et al. 2014). Several studies have also compared the effect of ecosystem engineers across habitat-settings (Grabowski et al. 2005, Bishop et al. 2009, Romero et al. 2014). It is unclear, however, how spatial patterns in ecosystem engineering vary between instances where the ecosystem engineer is a primary habitat modifier, with no biotic dependency, or a secondary habitat modifier, obligately or facultatively dependent on another (Angelini et al. 2011). Where ecosystem engineers co-occur in nested assemblages with others, their interaction strength and spatial variation may be functionally redundant if they provide similar types of environmental amelioration as the primary habitat modifier.

Oysters are important and widespread ecosystem engineers that may persist as primary habitat modifiers

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directly attached to rock or other abiotic structures, or as secondary habitat modifiers attached to saltmarsh or mangrove roots (Bishop et al. 2009, 2012, Aquino-Thomas and Proffitt 2014, Lomovasky et al. 2014). Oysters facilitate benthic communities by enhancing habitat heterogeneity and complexity (Wells 1961, Coen et al. 1999, Lenihan et al. 2001, Gutiérrez et al. 2003). Their habitat matrix provides interstices for infauna and juvenile fish to shelter against predation and physical stressors, and enhances the surface area available for attachment by fouling organisms (Grabowski et al. 2005, Padilla 2010). In addition, their filter feeding improves water quality by removing suspended solids from water and produces pseudofaeces that may be inhabited by infaunal invertebrates (Newell 2004).

In intertidal environments in which oysters are primary habitat modifiers, a key mechanism by which they engineer their environment might be the retention of moisture and shading of the adjacent substratum at low tide. Without amelioration of abiotic conditions by ecosystem engineers, few, if any, species may persist on the mid to high elevations of intertidal rocky shores where the thermal and desiccation stress experienced by organisms at low tide can be extreme (Somero 2002, Helmuth et al. 2006, Silliman et al. 2011). In mangrove forests, where the canopy of the trees shades the substratum and pneumatophores can reduce the foraging efficiency of predators (Primavera 1997), oysters may be functionally redundant to the mangrove canopy in their provision of refuge. Hence, it may be expected that on otherwise bare rocky shores, lacking other ecosystem engineers such as canopy-forming algae, oysters have positive effects on intertidal biota following latitudinal gradients of temperature and desiccation stress. By contrast, in mangrove forests the relationship between engineering and climate may be weak.

Here we assess how latitudinal gradients in ecosystem engineering by the Sydney rock oyster *Saccostrea glomerata* (Gould 1850) vary between intertidal rocky shores and mangrove forests. *S. glomerata* is broadly distributed along the east coast of Australia, from the cool temperate waters of Victoria (38°09' S) to tropical Queensland (25°17' S). We hypothesize that: (1) on rocky shores but not in mangroves, there will be a strong latitudinal gradient in temperature and humidity; (2) oysters will play a greater role in ameliorating temperature and desiccation stress on rocky shores than in mangroves; and consequently (3) the interaction strength of oysters on associated invertebrate communities will be greater on rocky shores than in mangroves; and (4) a latitudinal gradient of increasing interaction strength with decreasing latitude will be apparent on rocky shores but not in mangroves.

MATERIALS AND METHODS

Study sites

Sampling and experiments were conducted in eight estuaries of New South Wales, Australia between 29.674°

and 36.214° south (Fig. 1). Within each estuary, two rocky shore and two mangrove sites with abundant Sydney rock oysters were sampled within 5 km of the estuary mouth. The sites had salinities of 30–35 and oyster populations that were 99–100% *Saccostrea glomerata*, with few, if any, non-native Pacific oysters, *Crassostrea gigas*. The rocky shores were each exposed to full sun and were predominantly mafic rock in the north and sedimentary rock in the south. Mangrove sites were dominated by the grey mangrove, *Avicennia marina*, and had muddy substratum that was shaded by the mangrove canopy.

At a mid-intertidal elevation (i.e., 0.6–0.9 m above Indian Spring Low Water) of mangroves and rocky shores (hereafter referred to as habitats) we conducted surveys and experiments in two microhabitats: oyster and bare. On rocky shores, oyster microhabitat was defined as a 25 × 25 cm area in which the cover of oysters exceeded 90%. In mangrove forests, oyster microhabitat was a 50 × 50 cm area in which at least three pneumatophores had oyster clumps attached. Within each habitat, the bare microhabitat was similar to the oyster microhabitat except for the presence of oysters. That is, in mangrove forest the bare microhabitat comprised

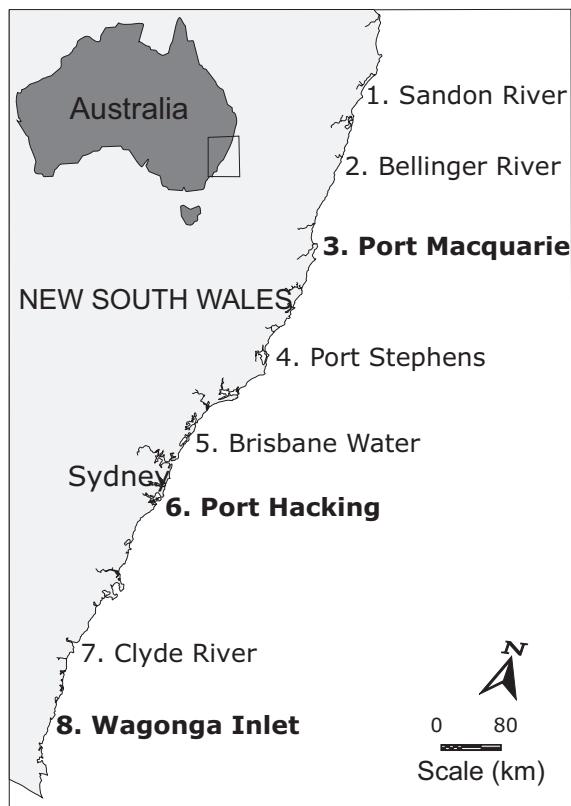


FIG. 1. Locations, between 29.674° and 36.214° south, of the eight estuaries sampled along the coastline of New South Wales, Australia. Manipulative experiments were conducted at estuaries marked in bold.

sediments and *A. marina* pneumatophores, while on the rocky shore it was bare rock.

Temperature and humidity

Measurements of temperature and humidity tested the hypotheses that: (1) temperature ranges would be greater and humidity lower in bare than oyster microhabitat; (2) these differences in temperature and humidity between bare and oyster microhabitat would be greater on rocky shores than in mangrove forests; and (3) latitudinal variation in temperature and humidity would be greater in bare than oyster microhabitat on rocky shores than in mangroves.

At one randomly selected rocky shore and one randomly selected mangrove site per estuary, we deployed six DS1921G Thermochron iButton data loggers (Thermodata Pty. Ltd., Warrnambool, Australia), three in bare microhabitat and three in oyster microhabitat, for 3 weeks in February 2014. Deployments corresponded with the peak of the Austral summer, when temperature stress is at its greatest. Longer-term measurements were not possible due to loss of loggers. The loggers, waterproofed with Plastidip rubber coating (Plasti Dip International, Blaine, Minnesota, USA), were programmed to record temperatures at 20 min intervals, with 0.5°C accuracy. In the bare microhabitat of the rocky shore, iButtons were glued (with Sikaflex Marine Adhesive; Sika Australia, Wetherill Park, Australia) into 5 mm deep depressions in the rock surface, such they sat flush with the substratum. In the bare microhabitat of mangrove forests, where epifauna are primarily found on pneumatophores, iButtons were glued (with Sikaflex) to pneumatophore mimics – 20.5 cm-long wooden chopsticks – that protruded ~10 cm above the sediment. For both rocky shores and mangroves, iButtons were deployed in the oyster microhabitat by gluing them to the middle of oyster clumps using Sikaflex. At the end of the 3 weeks, iButton loggers were collected and the maximum, minimum, and range of temperatures recorded by each were extracted from the data.

At the same sites at which we measured temperature, measurements of humidity were made with DS1923 Hygrochron iButtons (Thermodata Pty. Ltd.). As these iButtons could not be waterproofed, measurements were made only at low tide, in April 2012. Within each site, measurements of humidity were taken from three positions on the bare substratum and three places within the oyster microhabitat every 2 min for a 30-min period. Humidity was averaged across the 15 readings per sampling position to give a single value that was used in analyses. Logistical reasons prevented measurement of humidity in the three southern-most estuaries.

Invertebrate communities

Latitudinal survey—A latitudinal survey of invertebrate communities across the eight estuaries was conducted in April 2012. This tested the hypotheses that: (1) differences

in invertebrate assemblages between patches of microhabitat with and without oysters would be greater on rocky shores than in mangroves; (2) on rocky shores the magnitude by which oysters enhance invertebrate abundance and richness as compared to bare microhabitat would increase with decreasing latitude, as temperature increases and humidity decreases; but (3) in mangrove forests, a latitudinal gradient in the interaction strength of oysters in invertebrates would not be apparent.

At each of the two rocky shore and mangrove sites per estuary, six samples were collected from habitat patches with oysters and six from otherwise similar bare microhabitat without oysters. The differing spatial arrangement of oysters in mangroves, where oysters attach to the biogenic structure of mangrove roots and trunks, and on rocky shores, where they attach to rock, necessitated use of differing sampling units in each habitat. On rocky shores, sampling was done within randomly positioned 25 × 25 cm quadrats (as per Summerhayes et al. 2009). Within mangrove forests, sampling of invertebrates and oysters was within randomly positioned 50 × 50 cm quadrats (Summerhayes et al. 2009). These quadrat sizes resulted in similar numbers of oysters falling within each sampling unit in the oyster microhabitat of each habitat type (mean ± 1 SE, rocky shore: 129 ± 9 oysters; mangrove: 129 ± 8 oysters; $n = 96$).

Oysters and associated fauna were collected from the oyster microhabitat (see Study sites) for laboratory analysis by chiselling (on the rocky shore) or cutting pneumatophores below oyster clumps using secateurs (in mangroves). All other invertebrates >500 µm in diameter and within the bounds of the quadrat, either on rock or on pneumatophores, or the sediment surface were identified in situ. In bare microhabitat (see Study sites), assemblages of invertebrates (>500 µm) on rock or on sediments and pneumatophores were identified in situ.

Upon return to the lab, the contents of each sample from the oyster microhabitat was washed, separately, through a 500 µm sieve with invertebrate fauna >500 µm separated from the oysters for preservation in 70% ethanol. Associate fauna were identified to mixed taxonomic levels: gastropods and bivalves to species; polychaetes to family; crustaceans to family and genera (as per Chapman 1998). The abundance per taxon was recorded for each sample, as well as total abundance and taxon richness. Live and dead oysters were separately enumerated, their shell height and length measured at the widest point (to the nearest mm) using vernier callipers, and their surface area calculated from measurements, using the approximation that valves are oval.

Manipulative experiment—Previous studies have demonstrated causative effects of oysters on invertebrate communities on rocky shores and in mangrove forests (Underwood and Barrett 1990, Summerhayes et al. 2009, Bishop et al. 2012). A manipulative experiment was done to: (1) confirm that across the latitudinal gradient differences in invertebrate communities between oyster and

bare microhabitats could be attributed to an effect of oysters; and (2) test the hypothesis that positive effects of oysters on biodiversity would increase with decreasing latitude.

The experiment was replicated at two rocky shore sites within each of three estuaries: Port Macquarie in the north; Port Hacking in the centre; and Wagonga Inlet in the south (Fig. 1). At each site, we tested for effects of oysters on invertebrate communities by comparing the recolonization of invertebrates between defaunated 25×25 cm quadrats in mid-shore (MLWS + 0.4–0.6 m) oyster microhabitat from which: (1) associate mobile invertebrates (>3 mm in diameter) had been removed; and (2) oysters and associate mobile invertebrates (>3 mm) were removed. Due to difficulties of removing sessile organisms from the interstices of oysters without destroying the oysters themselves, the manipulations were limited to mobile invertebrates >3 mm in diameter. As these mobile organisms are able to rapidly move between habitats, recolonization was assessed after 3 weeks. In the event that ecosystem engineering by oysters was driving differences in invertebrate communities between oyster and bare microhabitats, we expected: (1) greater abundances of invertebrates, or more taxa, would recolonize plots in which oysters remained than in plots in which they were cleared; and (2) the abundance and richness of communities recolonizing defaunated oyster plots would match those of unmanipulated oyster microhabitat and those recolonizing patches cleared of oysters would match those in unmanipulated bare microhabitat.

Six replicate plots were established for each of the two experimental and two control treatments. Among the experimental plots, oysters were removed from designated plots by chiseling, and mobile invertebrates >3 mm in diameter were removed by hand. Numbers, by species, of invertebrates (>3 mm in diameter) in experimental and control plots was assessed at the end of the experiment by thoroughly searching plots in situ.

Statistical analyses

We used univariate PERMANOVAs (Anderson et al. 2008) on Euclidean distance matrices calculated from untransformed data to assess the effect of categorical predictor variables on our response variables of interest. Unlike ANOVAs, PERMANOVAs do not assume that residuals are normally distributed (Anderson et al. 2008). Three-way orthogonal PERMANOVAs, with the factors habitat (rocky shore vs. mangrove), microhabitat (oyster vs. bare), and estuary tested for sources of spatial variability in (1) maximum temperature, (2) minimum temperature, (3) temperature range and (4) mean humidity. Three-way analyses with the factors estuary (8 levels), site nested in estuary (2 levels) and microhabitat (oyster vs. bare) assessed sources of variability in invertebrate abundance, richness, and the abundance of key faunal groups (bivalves, gastropods, barnacles, mobile arthropods, and

polychaetes/soft-bodied invertebrates) in spatial surveys. Separate tests were done for each habitat due to the use of differing sampling units within each. PERMANOVAs with the factors estuary (3 levels), site nested in estuary (2 levels) and treatment (4 levels: oyster and invertebrate removal; invertebrate removal; oyster control; bare control) compared the (a) abundance and (b) richness of invertebrates in plots at the end of the manipulative experiment. Where PERMANOVAs detected significant treatment effects, they were followed by pairwise post-hoc PERMANOVAs to identify sources of differences.

To test hypotheses about whether on rocky shores, and in mangroves the effect of oysters on total invertebrate abundance and richness, and the abundance of key faunal groups would decrease with latitude, we ran linear regressions on log-response ratios, calculated between oyster and bare microhabitats. Ratios were calculated at the scale of estuary using the average abundance or richness of invertebrates across the 12 quadrats sampled within each estuary. Sites were pooled for these analyses because PERMANOVAs indicated similar patterns of difference in invertebrate abundances and richness between microhabitats in each. Separate sets of regressions were run for each of the rocky shore and mangrove habitats.

To test for a relationship between invertebrate community structure and temperature, we ran Spearman's rank correlations between the Bray Curtis dissimilarity matrix of pairwise differences in invertebrate communities between estuaries, and each of the Euclidean distance matrices for pairwise differences in maximum temperature and temperature range among estuaries. A separate correlation was run for each microhabitat in rocky shores and mangroves. These analyses were run using the RELATE procedure of PRIMER 6 (Clarke and Gorley 2006). To determine the influence of oyster morphology on invertebrate abundance and taxon richness, separate multiple-regressions were run for rocky shores and mangrove forests. The predictor variables were quadrat averages of: number of live oysters; number of dead oysters; average oyster surface area; maximum oyster surface area and total surface area per quadrat.

RESULTS

Temperature and humidity

PERMANOVAs on maximum temperature and on temperature range did not reveal any three-way interactions between habitat, microhabitat, and estuary allowing interpretation of two-way interactions (Appendix S1: Table S1). Instead, analyses revealed differences in maximum temperature and temperature range between oyster and bare microhabitats that were dependent on habitat context (PERMANOVA, sig. Habitat \times Microhabitat interaction; Appendix S1: Table S1). On rocky shores, maximum temperatures were significantly greater by $4.5 \pm 0.7^\circ\text{C}$ (mean \pm SE), and

temperature ranges by 4.1 ± 0.7 °C, in bare than oyster microhabitat (post-hoc tests, sig. Habitat \times Microhabitat interaction; Fig. 2A). In mangrove forests, where maximum temperatures were on average 6°C cooler than on rocky shores, there was no significant difference in maximum or temperature range between microhabitats (post-hoc tests, sig. Habitat \times Microhabitat interaction; Fig. 2A).

Patterns of variation among estuaries in maximum temperature and in temperature range were dependent on habitat (PERMANOVA, sig. Estuary \times Habitat interaction; Appendix S1: Table S1). Each of these variables was generally greater on lower latitude than higher latitude rocky shores, but the relationship between temperature and latitude was not linear (post-hoc tests, sig. Estuary \times Habitat interaction; Fig. 2B). Among mangrove forests, there were idiosyncratic differences in maximum temperature and temperature ranges among

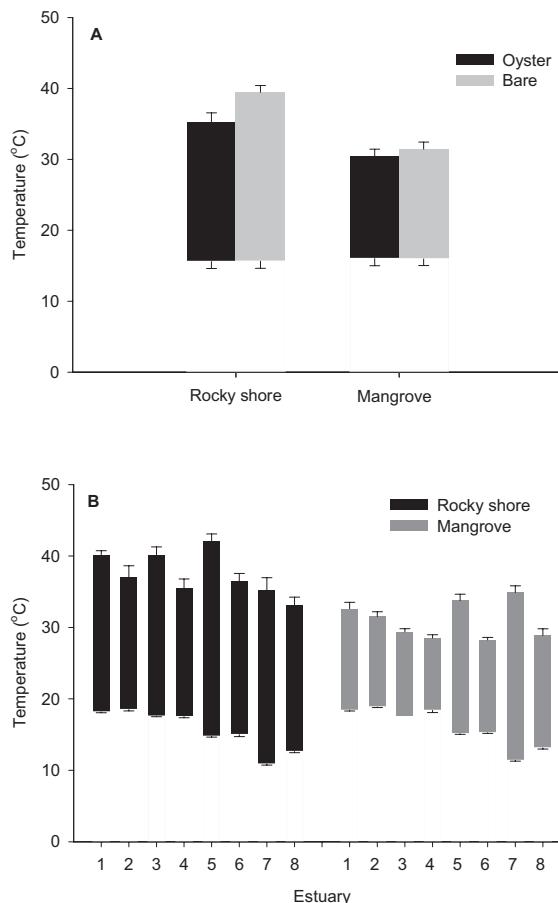


FIG. 2. Comparison of temperature ranges (A) between oyster and bare microhabitats and (B) among estuaries, within rocky shore or mangrove habitat. The upper extent of each bar corresponds to the mean (± 1 SE) maximum temperature recorded by loggers while the lower extent corresponds to the mean (± 1 SE) minimum temperature. Estuaries are numbered from north (1) to south (8), according to Fig. 1. $n = 3$ loggers per microhabitat, per estuary.

estuaries (post-hoc tests, sig. Estuary \times Habitat interaction) that did not correspond to latitude (Fig. 2B).

Minimum temperatures differed less among habitats, microhabitats, and estuaries than maximum temperatures or temperature range, but there was a significant three-way interaction among these factors (PERMANOVA, sig. Estuary \times Habitat \times Microhabitat interaction; Appendix S1: Table S1). On rocky shores, no significant differences between microhabitats were found in any of the estuaries and in mangrove forests, a significant difference was found within only one of the eight (post-hoc tests, sig. Estuary \times Habitat \times Microhabitat interaction). As with maximum temperature, minimum temperatures were generally greater in the lower than the higher latitude estuaries (post-hoc tests, sig. Estuary \times Habitat \times Microhabitat interaction; Fig. 2B).

The difference in humidity between bare and oyster microhabitats varied between habitats, and among estuaries (PERMANOVA: sig. Estuary \times Habitat \times Microhabitat interaction; Appendix S1: Table S1). On rocky shores, where the humidity of bare rock averaged $74 \pm (1 \text{ SE}) 3\%$, a significant difference between microhabitats was found in four of the five estuaries sampled, the exception being the lowest latitude estuary (post-hoc tests, sig. Estuary \times Habitat \times Microhabitat interaction; Appendix S1: Fig. S1). In mangroves, where humidity outside of oyster patches averaged $87 \pm 1\%$, a significant difference was found in three of the five estuaries (post-hoc tests, sig. Estuary \times Habitat \times Microhabitat interaction; Appendix S1: Fig. S1). Differences in humidity between microhabitats were greater on rocky shores than in mangroves (post-hoc tests, sig. Estuary \times Habitat \times Microhabitat interaction; Appendix S1: Fig. S1).

Invertebrate communities

Latitudinal survey—At each of the rocky shore and mangrove sites, oyster microhabitat supported more abundant and taxon-rich invertebrate communities than the bare microhabitat, but the magnitude of this difference varied among estuaries, or, in the case of invertebrate abundance in mangroves, sites (PERMANOVA, post-hoc tests sig. Estuary \times Microhabitat and Site (Estuary) \times Microhabitat interactions, Appendix S2: Table S1). Overall, across both habitats, 96% of invertebrates were collected from oyster microhabitat. Of the 84 taxonomic groups identified across the two habitats, 67 (including all polychaetes, amphipods, isopods, crabs, chitons and bivalves) were found only in the oyster microhabitat during this study and none were unique to the bare microhabitat (Appendix S3: Table S1). Within the rocky shore samples, which contained 67% of the total invertebrates collected, only 2% of individuals came from bare microhabitat, whereas in the mangrove forest bare microhabitat provided 8% of the individuals.

The log-response ratio of invertebrate abundance in oyster as compared to bare microhabitat decreased with increasing latitude on rocky shores ($r^2 = -0.819$, $df = 6$, $p = 0.006$) but bore no relationship to latitude in the mangrove forest ($r^2 = 0.052$, $df = 6$, $p = 0.451$; Fig. 3). Similarly the log-response ratio of richness declined with increasing latitude on rocky shores ($r^2 = -0.800$, $df = 6$, $p = 0.008$) but not in mangroves ($r^2 = 0.052$, $df = 6$, $p = 0.451$; Fig. 3). In the bare microhabitat of rocky shores, differences among estuaries in the assemblage structure of invertebrate communities were correlated to differences in maximum temperature (RELATE: $r_s = 0.33$, $p < 0.01$) and temperature range (RELATE: $r_s = 0.18$, $p = 0.04$). By contrast, differences among

estuaries in invertebrate assemblage structure in the oyster microhabitat of rocky shores did not follow patterns in either temperature variable (maximum temperature: $r_s = 0.09$, $p = 0.17$; temperature range: $r_s = -0.04$, $p = 0.58$). In mangrove forests, invertebrate assemblages of the bare microhabitat showed no relationship to maximum temperature ($r_s = 0.005$, $p = 0.41$) or temperature range ($r_s = -0.05$, $p = 0.58$). Invertebrates living in oyster microhabitats of mangroves showed a significant correlation with maximum temperatures ($r_s = 0.18$, $p = 0.03$); however, there was no relationship with temperature range ($r_s = 0.12$, $p = 0.16$).

When species were combined into key groups, the abundance of each was significantly greater in oyster

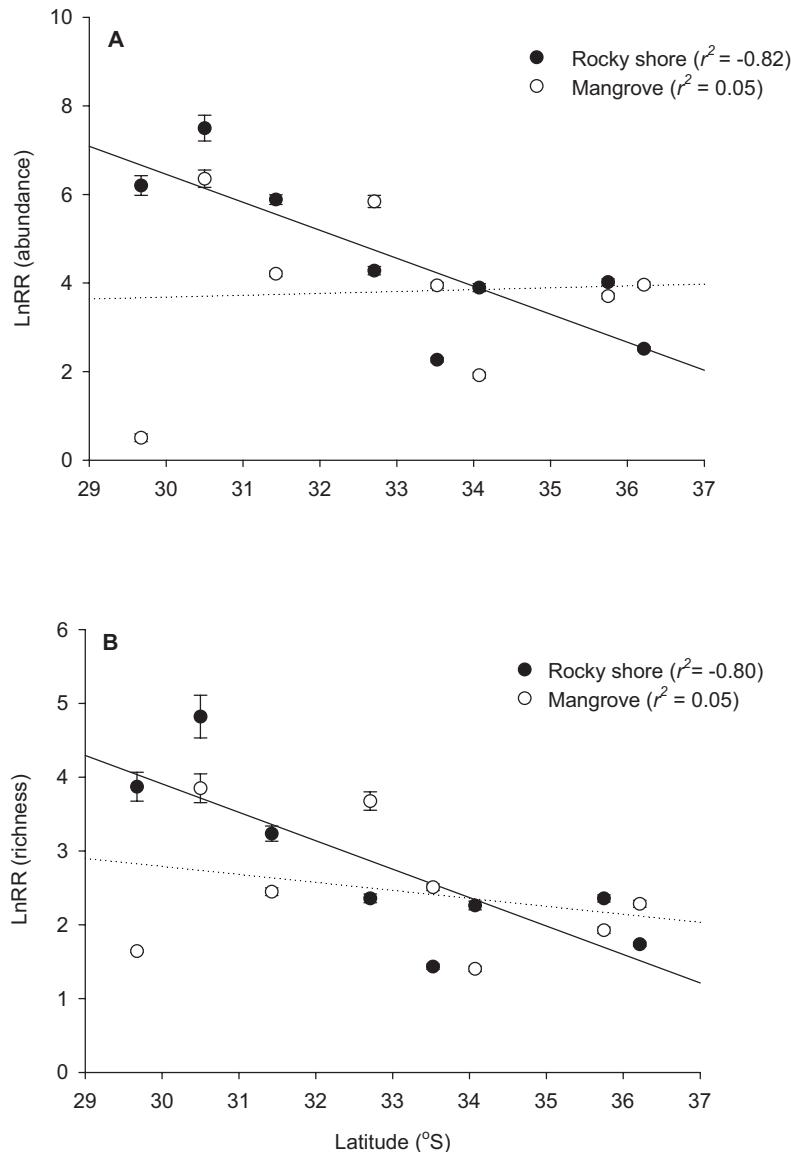


FIG. 3. Relationships between latitude and mean (± 1 SE) log-response ratio of (A) invertebrate abundance and (B) invertebrate richness between oyster and bare microhabitats. Mean log-response ratios were calculated from $n = 12$ replicate quadrats, sampled in each microhabitat of each estuary.

than bare microhabitat at every site at which it was present (PERMANOVA, post-hoc tests sig. Estuary \times Microhabitat and Site (Estuary) \times Microhabitat interactions, Appendix S2: Table S1; Fig. 4). The log-response ratio of gastropod abundance in oyster as compared to bare microhabitat decreased with increasing latitude on rocky shores ($r^2 = 0.83$, $df = 6$, $p = 0.001$), but no other group, on rocky shores or in mangroves, displayed a log-response ratio that was correlated with latitude (Fig. 4). Log-response ratios for bivalves were consistently greater on rocky shores than in mangroves (paired t -test, $t_{14} = 4.0$, $p = 0.01$), but for other groups did not

differ significantly between the two habitats (paired t -tests, $p > 0.05$). At a species level, the only taxa that were more abundant in the bare than the oyster microhabitat were the mud whelks *Batillatia australis* and *Pyrazus ebeninus* in the mangroves, and the limpet *Cellana tramoserica* on the rocky shore (Appendix S3: Table S3).

Generally, greater mean densities and smaller-sized live oysters were found in quadrats in the lower latitude estuaries (Appendix S4: Fig. S1). Multiple regressions indicated that morphological characteristics of oyster microhabitats explained 42–45% of variation in the

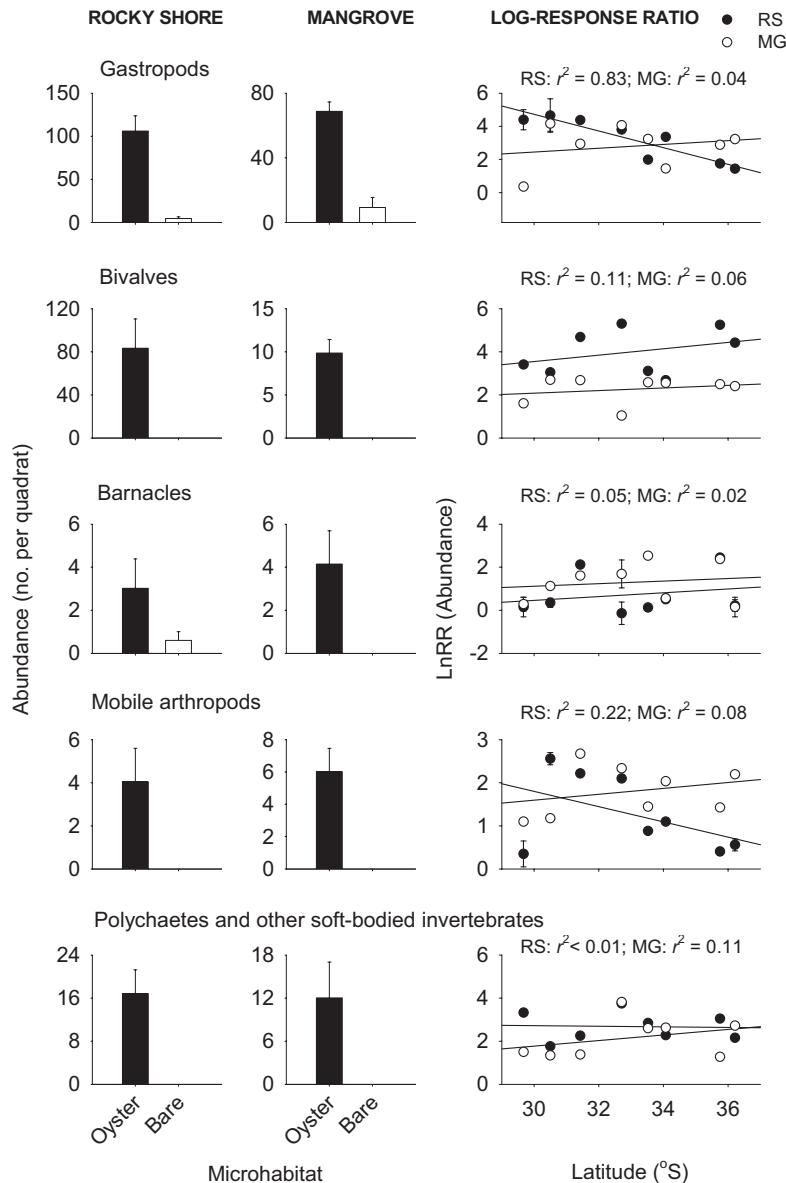


FIG. 4. Mean (± 1 SE) abundance of key invertebrate groups in oyster and bare microhabitat of rocky shores (RS) and mangroves (MG; $n = 8$ replicate estuaries). Relationships between latitude and the mean (± 1 SE) log-response ratio of invertebrate abundance between oyster and bare microhabitats are also shown. Mean log-response ratios were calculated from $n = 12$ replicate quadrats, sampled in each microhabitat of each estuary.

abundance of associated invertebrates on rocky shores and mangrove forests, and in the taxon richness of associated invertebrates in mangroves (Appendix S4: Table S1). By contrast, the variables explained only 15% of variation in invertebrate taxon richness on the rocky shore (Appendix S4: Table S1). Live oyster density and total surface area of oysters per quadrat had a significant influence on invertebrate abundance in both habitats (Appendix S4: Table S1).

Manipulative experiment—Of the invertebrates enumerated in our manipulative experiment, 53% were the gastropod *Bembicium auratum*, 18% were the limpet *Patelloida mimula*, and 8%, the gastropod *Bembicium nanum*. Molluscs also dominated the remaining biodiversity in this experiment which, for logistical reasons, only manipulated mobile species >3 mm in diameter.

Three weeks after defaunation, the abundance and richness of invertebrates recolonising plots in which oysters remained was greater than in plots where oysters had been cleared (post-hoc tests, sig. Estuary × Treatment interaction for abundance, main effect of Treatment for richness, Appendix S5: Table S1; Fig. 5). Within Port Hacking and Wagonga Inlet, the abundance and richness of invertebrates colonizing the defaunated oyster plots was statistically indistinguishable from in the undisturbed control plots of oysters (Fig. 5). At Port Macquarie, however, there was a significant difference in invertebrate abundance between these two treatments (Fig. 5). Treatments cleared entirely of oyster microhabitat received little recolonization of invertebrates following the disturbance, and within each estuary had abundances and richnesses that were statistically indistinguishable to unmanipulated bare microhabitat (post-hoc tests, Appendix S5: Table S1; Fig. 5). The number of invertebrates recolonising oyster habitat, and that were present in control oyster plots, was significantly greater in Port Macquarie than at Wagonga, but other pairwise comparisons among estuaries were not significant (post-hoc tests, sig. Estuary × Treatment interaction; Appendix S5: Table S1).

DISCUSSION

Although there are an increasing number of studies documenting spatial gradients in ecosystem engineering (Broitman et al. 2001, Wright et al. 2006, Silliman et al. 2011, Kimbro et al. 2014), it is unclear how these gradients vary among habitats. Our sampling of 32 sites distributed across eight estuaries has shown that the interaction strength of the Sydney rock oyster, *Saccostrea glomerata*, on invertebrate communities displays differing spatial patterns between rocky shores and mangroves. On rocky shores, the positive influence of oysters on the abundance and richness of intertidal invertebrates decreased with latitude. By contrast, in mangrove forests we found no evidence of latitudinal gradients in ecosystem engineering.

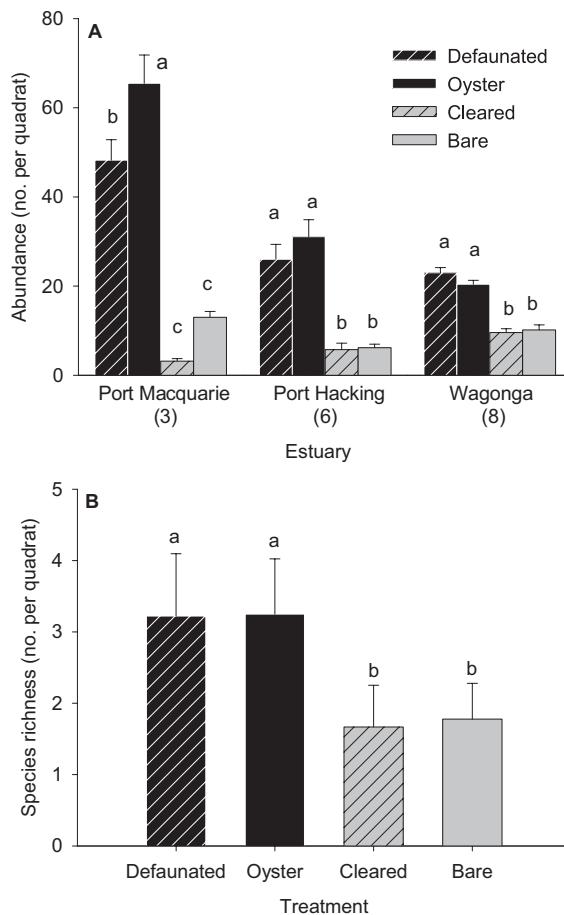


FIG. 5. Mean (+1 SE) (A) abundance and (B) richness of invertebrates re-colonizing defaunated experimental plots in which oysters remained (Defaunated), or were cleared (Cleared) and in unmanipulated control plots of oyster (Oyster) or bare (Bare) microhabitat. Letters denote significant differences in abundance among treatments (at $\alpha = 0.05$). Numbers denote the latitudinal position of estuaries (see Fig. 1). $n = 2$ sites per estuary, with $n = 3$ estuaries.

On rocky shores, oysters provided habitat that was cooler and more humid than bare microhabitat, thereby reducing temperature maxima and drying that occur at low tide and act to limit the distribution of intertidal invertebrates (Helmuth et al. 2006, Silliman et al. 2011). Consistent with a role of climate in determining invertebrate community structure (Helmuth et al. 2006), the invertebrate assemblages of the bare microhabitat of rocky shores were correlated to maximum temperature and temperature range. By contrast, in the cooler and more humid oyster microhabitat of rocky shores, there was no relationship between temperature and community structure. Although the approach of this study was primarily observational, the short-term manipulative experiment we conducted on mobile species on rocky shores and the results of previous studies examining longer-term responses of invertebrates to oysters (Underwood and Barrett 1990, Summerhayes et al. 2009, Hughes et al.

2014) suggest that differences in invertebrate communities between oyster and bare microhabitats were caused by oysters. In previous manipulative studies, the amelioration of temperature and desiccation stress has been identified as among the mechanisms by which habitat-forming bivalves facilitate invertebrate communities (Cole 2010, Silliman et al. 2011). Although oysters can serve as food resources for muricid gastropods and some species of crabs (Grabowski 2004, Wilkie and Bishop 2012), in this study these predatory taxa contributed a very small proportion of the total invertebrates associated with oysters. Hence, our conclusion is that the effects of oysters were primarily a result of ecosystem engineering, as opposed to trophic.

In shaded mangrove forests, where temperature ranges in bare habitat were on average 6°C less than on rocky shores and humidity that was 10% greater, differences in microclimate between oyster and bare microhabitats were much smaller than on the rocky shore and did not follow a latitudinal pattern. Nevertheless, even in the more abiotically benign mangrove environment, the oyster microhabitat on average supported over 11 times more invertebrates than the bare microhabitat. For most invertebrate groups, with the exception of bivalves, the extent to which oysters magnified abundance and richness was not consistently smaller in mangroves than on rocky shores, which was contrary to predictions. In mangroves, where the primary ecosystem engineer, the mangrove has a large influence on microclimate (Garside and Bishop 2014), the primary role of oysters may instead be in mitigating biotic stress caused by competition and/or predation.

The trunk and pneumatophores of mangroves provide some hard substratum in an otherwise sedimentary environment, but its availability is limited, and competition for space and food resources can be intense (Branch and Branch 1980, Minchinton and Ross 1999). Furthermore, although the structure of mangrove roots can lower the foraging efficiency of some larger predators (Primavera 1997), predation on invertebrates is nevertheless an important determinant of community structure in mangroves (Underwood and Barrett 1990, Bishop et al. 2008). The more complex and heterogeneous oyster matrices may reduce the intensity of competitive interactions and/or provide a refuge from predation (Underwood and Barrett 1990, Hughes et al. 2014). In east Australian mangrove forests, removal of oyster microhabitat results in mortality of gastropods (Underwood and Barrett 1990).

In mangrove forests, variation in the morphology of oyster microhabitat instead displayed a stronger relationship with the structure of associate invertebrate assemblages than did climate. The density and size of bivalves can influence structural complexity and surface area, which, in turn, has large effects on invertebrate assemblages (Gutiérrez et al. 2003). Although oyster morphometrics displayed no relationship to invertebrate richness on rocky shores, a relationship between oyster

density and invertebrate abundance was apparent, and may have contributed to the latitudinal gradient in the oyster-invertebrate interaction strength. Gastropods, the group that displayed the strongest latitudinal gradient in their association with oysters, are well protected by their shell against desiccation stress (McMahon 1990). Instead, their abundance may be responding to oyster shell area, which provides substrate for attachment and grazing (Branch and Branch 1980, Minchinton and Ross 1999).

The results of our study reinforce the view that although invertebrate assemblages are clearly influenced by large-scale environmental gradients (Hutchins 1947), in many instances local-scale interactions among species are sufficiently strong to mitigate these. The distribution of some organisms were obligately dependent on the ecosystem engineer's amelioration of abiotic stress (e.g., soft-bodied polychaetes that were not found outside of oyster microhabitat), while for others, the relationship with oysters was facultative. Overall, however, habitat modification by oysters was sufficient to alter biogeographic patterns in invertebrate assemblage composition, disrupting the latitudinal gradients displayed by invertebrates on the bare rocky shore. The role of oysters in disrupting gradients, presumably set by thermal stress, supports the notion that conservation and restoration of these and other habitat-forming species that ameliorate environmental stress may be a key strategy in assisting biodiversity to adapt to environmental change (Byers et al. 2006, Crain and Bertness 2006).

This is the first study that has to our knowledge examined spatial variation in ecosystem engineering by a single species across habitat contexts in which the species is a primary versus a secondary ecosystem engineer. Despite predictions that the role of ecosystem engineers may be reduced in environments where they coexist with others in nested assemblages, to the contrary, we found the overall interaction strength of a single ecosystem engineer did not vary markedly between these contexts. In the case of the oyster, this may be because there is limited redundancy in habitat amelioration between oysters and mangroves. Although both provide hard substratum and modify microclimate, they do so at very different spatial scales. The universally positive effect of oysters across environmental contexts is consistent with predictions that where ecosystem engineers enhance the complexity of an ecosystem, they will increase biodiversity (Gutiérrez et al. 2003). We predict that as redundancy between primary and secondary habitat formers increases, the effect of the secondary ecosystem engineer may decrease.

Nevertheless, in line with our prediction, we did find that latitudinal gradients in ecosystem engineering were greater when oysters were primary rather than secondary ecosystem engineers. Primary ecosystem engineers modify the biotic and abiotic environment, providing a new context for secondary ecosystem engineering (Angelini et al. 2011). Hence, spatial variation in secondary ecosystem engineers may be better predicted from

spatial variation in traits of the primary ecosystem engineer, rather than factors of the physical environment. Our results suggest that whether an ecosystem engineer has a net positive or negative effect on biodiversity can be predicted by its effect on habitat complexity, but the magnitude of this effect will be dependent on the abiotic and biotic environmental context.

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