The environmental context and traits of habitat-forming bivalves influence the magnitude of their ecosystem engineering

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ABSTRACT: The effective use of ecosystem engineers in biodiversity conservation is contingent on an understanding of those factors that influence the magnitude and direction of their effects. At patch scales, effects of ecosystem engineers on associated communities can range from positive to negative according to how the ecosystem engineer modifies environmental conditions. In a meta-analysis of 68 empirical studies, we assessed how, for a widespread group of ecosystem engineers — the marine habitat-forming bivalves — bivalve taxon, density, habitat, tidal elevation and latitude, as well as habit, or lifestyle, of associated taxa, influences the magnitude and direction of their effect on associated invertebrates. Overall, marine bivalves had a positive effect on both species abundance and species density, but effect sizes varied considerably according to bivalve traits and environmental setting. Oysters enhanced invertebrate abundance to a greater extent than either mussels or pinnids, perhaps because of the greater habitat heterogeneity they provide. Nevertheless, the effect of mussels on associated communities was generally more responsive to spatial variation in engineer traits and environmental context than the effect of oysters or pinnids. Positive effects of mussels on associated species abundance decreased at high mussel densities, were greater at subtidal than mid–low intertidal elevations and differed among faunal habits depending on habitat setting. Knowledge of those conditions under which positive effects of bivalves on associated biodiversity is greatest will help in identifying which species of ecosystem engineer, at which sites, should be prioritised for conservation and restoration, where the goal is enhancement of biodiversity.

KEY WORDS: Facilitation · Competition · Stress-gradient hypothesis · Ecosystem engineer · Foundation species · Oyster · Mussel · Pinnid

INTRODUCTION

There is growing interest in the use of ecosystem engineers as a tool for conserving biodiversity (Byers et al. 2006, Crain & Bertness 2006). Ecosystem engineers maintain, modify and create habitats by causing state changes to biotic and/or abiotic materials, which serve as resources for other organisms (Jones et al. 1994, 1997). At landscape scales, ecosystem engineers generally have net positive effects on biodiversity because they increase the diversity of available habitats (Jones et al. 1997). However, at the smaller scales at which conservation and restoration is often conducted, the effect of ecosystem engineers on biodiversity may range from positive to negative (Jones et al. 1994, 1997) according to spatial variation in resource availability and the extent that this is modified by the engineer (Jones et al. 1997). Additionally, even where the net effect of ecosystem engineers on biodiversity is positive, individual groups of organisms may be positively, neutrally or negatively affected, depending on their resource requirements and how the engineer affects these (Jones et al. 1997). The successful use of ecosystem engineers as a

tool for conservation is contingent on a predictive understanding of how traits of the ecosystem engineer, traits of the associated community and environmental context interact to influence the direction and magnitude of effects of ecosystem engineers (Byers et al. 2006, Crain & Bertness 2006).

At patch scales, the effects of ecosystem engineers are generally predicted to be positive where they enhance habitat complexity and negative where they reduce it (Crooks 2002). Hence, across morphologically similar groups of ecosystem engineers, there may be a high degree of functional redundancy (Crooks 2002), although this has rarely been tested (but see Wilkie et al. 2012). Traits of ecosystem engineers may be expected to have a particularly large influence on associated communities where they influence the availability of limiting resources (Bruno & Kennedy 2000, van Hulzen et al. 2007, Irving & Bertness 2009, Harley & O'Riley 2011). For example, in sedimentary marine environments where the availability of hard substratum for attachment is limited, morphologies of ecosystem engineers that provide a greater surface area may lead to greater positive effects on hard substrate-dependent taxa (Bishop et al. 2009, 2013, Summerhayes et al. 2009).

In addition to traits of ecosystem engineers, environmental context may also be an important determinant of their effect on associated communities. Ecological theory predicts that the frequency of positive interactions among species should increase with abiotic (e.g. temperature and desiccation) and/or biotic (e.g. competition and predation) stress, due to the enhanced benefits of associational refuge (Bertness & Callaway 1994). In empirical studies, primarily conducted on individual ecosystem engineers in terrestrial environments (but see Silliman et al. 2011, Kimbro et al. 2014, McAfee et al. 2016 for some marine exceptions), the effects of ecosystem engineers increase across abiotic gradients of temperature (Bertness & Leonard 1997, Callaway et al. 2002), aridity (Armas et al. 2011) and wind velocity (Cavieres et al. 2002) as well as biotic gradients of herbivory or predation (Callaway et al. 2005, Graff et al. 2007). Such effects may result not only from direct effects of the environment, but also from indirect effects of the environment determining population-level traits of the ecosystem engineer such as density (Bulleri et al. 2011) and patch size (Irving & Bertness 2009), or individual-level traits such as size and shape (Bishop et al. 2009), which in turn influence associated communities by modifying resource availability.

Studies are needed that assess the generality of trait and environmental effects in mediating species interactions across functional groups of ecosystem engineers. Bivalves are widespread ecosystem engineers in coastal environments (Gutierrez et al. 2003, Buschbaum et al. 2009) that in many parts of the world have suffered up to 90% reductions in the habitats they form since industrialisation (Beck et al. 2011). Bivalves modify the environment by (1) enhancing the availability of hard substrate for attachment of sessile and epifaunal organisms (Seed 1996, Gutierrez et al. 2003, Grabowski & Peterson 2007), (2) providing interstices between their valves and, in the case of mussels among byssal threads, where mobile fauna can seek refuge from predators (Seed 1996, Grabowski & Peterson 2007, Cinar et al. 2008), physical disturbance from waves and currents (Widdows et al. 2002), and desiccation stress during low tide at intertidal elevations (Cole 2010), (3) accumulating pseudo-faeces and sediments that can provide food and habitat for associated species (Hammond & Griffiths 2004, Calcagno et al. 2012), and (4) improving water clarity through the filtration of suspended materials (Newell 2004, Bos & van Katwijk 2007, Grabowski & Peterson 2007, Wall et al. 2008). They support dense and diverse invertebrate and algal communities (Seed 1996, Borthagaray & Carranza 2007, Markert et al. 2010). With increasing realisation of the extent of bivalve loss from historic overharvest (e.g. Alleway & Connell 2015), there is increasing interest in conservation and restoration of bivalve reefs to reinstate their ecosystem functions, including provision of habitat (Grabowski & Peterson 2007). Developing effective strategies for restoring and conserving bivalve habitats for biodiversity benefits is dependent on understanding those factors that determine when and where bivalves have the strongest positive effects on associated communities.

Here, we present the results of a meta-analysis that uses differences in the abundance and species density of invertebrates between otherwise similar patches of habitat with and without bivalves to assess how the effect size of ecosystem engineering by habitat-forming bivalves varies at the patch scale according to bivalve traits (taxonomic group and density), associated community traits (faunal habit, or mode of life) and environmental context (habitat, tidal elevation and latitude). Previous studies examining sources of intraspecific variation in the structure and function of bivalves at the patch scale have found their effects on associated communities to range from positive to negative compared with adjacent similar habitat without bivalves according to age (Koivisto et al. 2011), complexity (Prado & Castilla 2006), biomass (Valdivia & Thiel 2006) and

environmental context (Saier 2002, Thiel & Ullrich 2002). Although low–intermediate densities of small–medium-sized bivalves might facilitate invertebrates by providing habitat and stress amelioration, high densities of large bivalves may suppress invertebrate recruitment by preying on larvae (Khaitov 2013). Most studies (but see Buschbaum et al. 2009) have been limited to individual species or regions and so variability among studies is common. Therefore, it is unclear whether the effects of bivalves vary predictably among taxonomic groups of bivalves and across larger geographic scales. Cross-study analyses, such as meta-analysis, are able to detect patterns among multiple studies among which findings may vary (Rosenberg et al. 2000).

MATERIALS AND METHODS

Data collection

Hypotheses about effects of habitat-forming bivalves on invertebrate abundance and species density were tested using data from surveys and peer-reviewed papers published prior to June 2016. Habitat-forming bivalves were defined as epibenthic or infaunal bivalves that form a biogenic reef that protrudes from the surrounding substrate. Infaunal bivalves that spend the majority of their time wholly buried in the sediment were not included. Literature was located through searches in Google Scholar, Science Direct and Web of Science using the following search terms: 'bivalve', 'mussel', 'oyster' or 'pinnid' with 'habitat-forming', 'invertebrate community', 'associated community', 'facilitation', 'competition', 'mutualism', 'infauna', 'epifauna', 'mobile fauna', 'abundance' or 'richness'. As meta-analysis compares effect sizes calculated between experimental and control treatments, only those studies reporting the individual or total abundances of associated invertebrate taxa, and/or associated invertebrate species density (i.e. species richness per unit area) in otherwise similar habitat with (experimental) and without bivalves (control; see 'Analyses' below) were considered. To be included in analyses, papers also needed to include (1) means, (2) estimates of variation about the means and (3) sample sizes or raw data necessary to calculate effect sizes, for both patches with and without bivalves. In total, 68 studies were suitable for inclusion in analyses (Table 1, Fig. 1). Of these, 31 reported effects of bivalves on both abundance and species density, 34 reported effects on abundance only and 3 papers reported effects on species density only. This gave a total of 65 papers that could be used in analyses of species abundance and 34 that could be used for species density.

Of the 65 studies reporting effects of bivalves on abundances of species, 42 studies reported these at the level of individual taxa. These studies were used in analyses that separately assessed whether the effects of bivalves on the abundances of 9 common invertebrate phyla associated with the benthic habitat of bivalves (annelids, arthropods, molluscs, nemerteans, cnidarians, echinoderms, platyhelminthes, tunicates and priapulids) were positive, negative or neutral. For each of the 42 studies, we summed abundances within each of these 9 phyla to produce a mean (plus variation) abundance of organisms for both bivalve and bare microhabitat at each study site or environmental context. Within phyla, individual taxa were not considered as replicates due to issues of spatial non-independence arising from these being sampled from the same plots. These analyses revealed that effects of bivalves on invertebrate abundance were similar among taxa. Hence, for all other analyses, we used total invertebrate abundance or species density as our metric for analysis. The 65 studies with sufficient information to calculate or use total abundances in analyses provided a total of 195 different comparisons of total abundance, across the multiple study sites and habitat contexts sampled by the studies. The 34 studies reporting effects on species density across multiple study sites and habitat contexts gave 131 comparisons for species density.

To test hypotheses about how the effect of habitat-forming bivalves on total invertebrate abundance and species density varied according to bivalve traits, contrasts were categorised according to bivalve taxon (mussel, oyster or pinnid) and the density of bivalves (Table 1). We expected that oysters, due to their highly plastic morphology, would increase habitat complexity and therefore total abundances and species density (Menge et al. 1985, Sueiro et al. 2011) to a greater extent than mussels and pinnids. We predicted that invertebrate species density and total abundance would initially increase with bivalve density, as habitat modification increased, but then decline at high densities due to competition between the bivalves and the associated fauna for resources such as space and food (see Stachowicz 2001).

Additionally, to assess how traits of associated invertebrate communities influence their response to bivalves, and how such effects depend on habitat setting, these communities were categorised according to their habit, or mode of life, and the broader habitat context in which they were found. Habits

Table 1. Summary of the studies, their locations and focal taxa. N/A = data not available. In all cases, intertidal sampling was conducted at locations with a semi-diurnal tidal range

Study number	Reference	Study location	Substrate	Tidal elevation	Latitude (°N)	Longitude (°E)	Density (bivalves m⁻²)	Habitat-forming bivalve	Abundance/ species density
1	Altieri et al. (2007)	USA	Rocky	Mid intertidal	41.67	−71.33	N/A	Mussel	Abundance
2	Altieri et al. (2010)	USA	Rocky	Mid intertidal	41.67	−71.33	N/A	Mussel	Both
3	Angelini et al. (2015)	USA	Sedimentary	Mid intertidal	31.41	−81.29	4–320	Mussel	Abundance
4	Beadman et al. (2004)	Wales	Sedimentary	Low intertidal	53.23	−4.12	Tested, but not quantified	Mussel	Both
5	Bell et al. (2015)	South Africa	Rocky	Low intertidal	−34.06	23.38	N/A	Mussel	Abundance
6	Bertness et al. (2004)	USA	Rocky	Mid intertidal	43.84	−69.51	N/A	Mussel	Abundance
7	Bonnici et al. (2012)	Malta	Rocky	Mid intertidal	35.83	14.53	16550	Mussel	Both
8	Buschbaum et al. (2009)	Germany	Sedimentary	Low intertidal	54.92	8.35	1871	Mussel	Species density
		Chile			−41.48	−72.87	3442		
		South Korea			34.35	126.5	1927		
		Australia			−34.62	135.5	18393		
9	Commito (1987)	USA	Sedimentary	Low intertidal	44.55	−67.35	1130	Mussel	Both
10	Commito et al. (2005)	USA	Sedimentary	Mid intertidal	44.53	−67.88	5950	Mussel	Both
11	Creese et al. (1997)	New Zealand	Sedimentary	Low intertidal	−36.89	174.88	12500	Mussel	Both
12	Crooks & Khim (1999)	USA	Sedimentary	Low intertidal	32.78	−117.23	2500	Mussel	Both
13	Crooks (1998)	California	Sedimentary	Low intertidal	32.78	−117.23	Variable densities	Mussel	Both
14	Cummings et al. (1998)	New Zealand	Sedimentary	Subtidal	−36.5	174.73	N/A	Pinnid	Both
15	Cummings et al. (2001)	New Zealand	Sedimentary	Subtidal	−36.5	174.73	N/A	Pinnid	Both
16	Dittmann (1990)	Germany	Sedimentary	Low intertidal	55.03	8.43	1301	Mussel	Both
17	Duarte et al. (2006)	Chile	Sedimentary	Low intertidal	−41.53	−73.02	3000 / 750	Mussel	Both
18	Escapa et al. (2004)	Argentina	Sedimentary	Low intertidal	−41.19	−62.22	60	Oyster	Abundance
19	Fariñas-Franco et al. (2013)	Ireland	Sedimentary	Subtidal	54.5	−5.07	N/A	Mussel	Abundance
20	Ferraro & Cole (2012)	USA	Sedimentary	Low intertidal	45.53	−123.92	100	Oyster	Both
21	Grabowski et al. (2005)	USA	Sedimentary	Low intertidal	34.68	−73.57	N/A	Oyster	Abundance
22	Green & Crowe (2013)	Ireland	Rocky	Low intertidal	55.12	−7.2	N/A	Oyster	Both
23	Günther (1996)	Germany	Sedimentary	Mid intertidal	55.59	6.67	1750	Mussel	Abundance
24	Harding & Mann (2010)	USA	Sedimentary	Low intertidal and subtidal	37.53	−76.38	N/A	Oyster	Abundance
25	Harwell et al. (2011)	USA	Sedimentary	Mid intertidal	34.18	−77.85	N/A	Oyster	Abundance
26	Hollander et al. (2015)	Sweden	Sedimentary	Subtidal	58.87	11.17	N/A	Mussel Oyster	Both
27	Holsman et al. (2006)	USA	Sedimentary	Low intertidal	46.72	−124.01	N/A	Oyster	Abundance
28	Hosack et al. (2006)	USA	Sedimentary	Low intertidal	46.72	−124.01	N/A	Oyster	Abundance
29	Hughes et al. (2014)	Australia	Sedimentary	Low intertidal	−34.02	151.18	21 / 51	Oyster	Both
30	Humphries et al. (2011)	USA	Sedimentary	Subtidal[a]	29.25	−90.92	N/A	Oyster	Abundance
31	Kent et al. (2016)	Wales	Sedimentary	Subtidal	54.92	−4.57	N/A	Mussel	Abundance
32	Keough (1984)	Australia	Sedimentary	Subtidal	−35.08	137.73	N/A	Pinnid	Abundance
33	Kimbro et al. (2014)	USA	Sedimentary	Low intertidal	37.74	−76.59	N/A	Oyster	Abundance
					33.92	−77.9			
					32.34	−80.5			
					31.87	−81.08			
					29.7	−81.24			
					29.58	−81.16			

Table 1 (continued)

Study number	Reference	Study location	Substrate	Tidal elevation	Latitude (°N)	Longitude (°E)	Density (bivalves m^{-2})	Habitat-forming bivalve	Abundance/ species density
34	Kochmann et al. (2008)	Germany	Sedimentary	Low intertidal	55.07	8.43	3000 750	Oyster and mussel	Abundance
35	Koivisto & Westerbom (2010)	Finland	Rocky	Subtidal[b]	59.8	23.2	N/A	Mussel	Both
36	Lejart & Hily (2011)	France	Sedimentary Rocky	Mid intertidal	48.38	−4.48	368 5686	Oyster	Both
37	Lemieux & Cusson (2014)	Canada	Rocky	Low intertidal	48.62	−68.18	1320	Mussel	Both
38	Lohrer et al. (2013)	New Zealand	Sedimentary	Subtidal	−36.48	174.73	N/A	Pinnid	Abundance
39	Macreadie et al. (2014)	Australia	Sedimentary	Subtidal	−33.03	151.63	N/A	Pinnid	Abundance
40	McAfee et al. (2016)	Australia	Rocky	Mid intertidal	−34.43 −34.07 −36.36	152.9 151.13 150.2	129	Oyster	Both
41	McLeod et al. (2014)	New Zealand	Sedimentary	Subtidal	−36.98	175.27	N/A	Mussel	Abundance
42	Mistri (2002)	Italy	Sedimentary	Subtidal	44.85	12.28	N/A	Mussel	Abundance
43	Munari (2008)	Italy	Sedimentary	Subtidal	44.85	12.28	N/A	Mussel	Both
44	Nevins et al. (2014)	USA	Sedimentary	Subtidal	29.92	−93.87	N/A	Oyster	Abundance
45	Norkko et al. (2006)	New Zealand	Sedimentary	Subtidal[b]	−36.44	174.72	N/A	Pinnid	Both
46	Norling & Kautsky (2007)	Sweden	Sedimentary	Subtidal	58.87	11.15	352	Mussel	Both
47	Norling & Kautsky (2008)	Finland	Sedimentary	Subtidal	58.78	17.6	N/A	Mussel	Both
48	Norling et al. (2015)	Sweden	Sedimentary	Subtidal	58.85	11.17	N/A	Mussel Oyster	Both
49	Ojeda & Dearborn (1989)	New England, USA	Rocky	Subtidal	43.83	−69.52	N/A	Mussel	Both
50	Padilla (2010)	USA	Rocky	Mid intertidal	48.38	−123	N/A	Oyster	Abundance
51	Peterson & Heck (2001)	USA	Sedimentary	Subtidal[a]	30	−85.5	500	Mussel	Abundance
52	Ragnarsson & Raffaelli (1999)	Scotland	Sedimentary	Low intertidal	57.03	−1.98	N/A	Mussel	Both
53	Robillard et al. (2010)	USA	Sedimentary	Subtidal	28.65	−96.58	N/A	Oyster	Abundance
54	Rodney & Paynter (2006)	USA	Sedimentary	Subtidal	39.98	−75.95	173	Oyster	Abundance
55	Sellheim et al. (2010)	USA	Rocky	Subtidal	38.27	123	N/A	Mussel	Both
56	Shervette & Gelwick (2008)	USA	Sedimentary	Subtidal	30.33	−88.38	N/A	Oyster	Species density
57	Silliman et al. (2011)	Patagonia	Rocky	Mid and low intertidal	−38.4 −39.5 −43.6 −46.5 −47.6 −48.9 −50.2 −53.0	−58.1 −62.1 −65.3 −67.47 −65.78 −67.4 −69.1 −68.5	N/A	Mussel	Both
58	Stunz et al. (2010)	USA	Sedimentary	Subtidal[a]	29.57	−9.93	N/A	Oyster	Both
59	Taylor & Bushek (2008)	USA	Sedimentary	Low intertidal	39.07	−75.17	N/A	Oyster	Abundance
60	Thiel & Dernedde (1994)	Germany	Sedimentary	Mid and low intertidal	54.9	8.33	N/A	Mussel	Abundance
61	Thiel & Reise (1993)	Germany	Sedimentary	Mid and low intertidal	54.9	8.33	N/A	Mussel	Abundance
62	Tokeshi & Romero (1995)	Peru	Rocky	Low intertidal	−11.77	−77.2	N/A	Mussel	Abundance
63	Tolley & Volety (2005)	USA	Sedimentary	Low intertidal	26.43	−82.07	N/A	Oyster	Abundance
64	van der Zee et al. (2015)	Netherlands	Sedimentary	Low intertidal	53.42	5.73	N/A	Mussel	Species density
65	Witman (1985)	USA	Rocky	Subtidal	42.97	−70.62	N/A	Mussel	Abundance
66	Ysebaert et al. (2009)	Denmark	Sedimentary	Subtidal	56.93	9.07	3911	Mussel	Both
67	Zhang et al. (2015)	China	Sedimentary	Subtidal	36.17	120.3	N/A	Oyster	Abundance
68	Zimmerman et al. (1989)	USA	Sedimentary	Subtidal[a]	29.22	−94.9	N/A	Oyster	Abundance

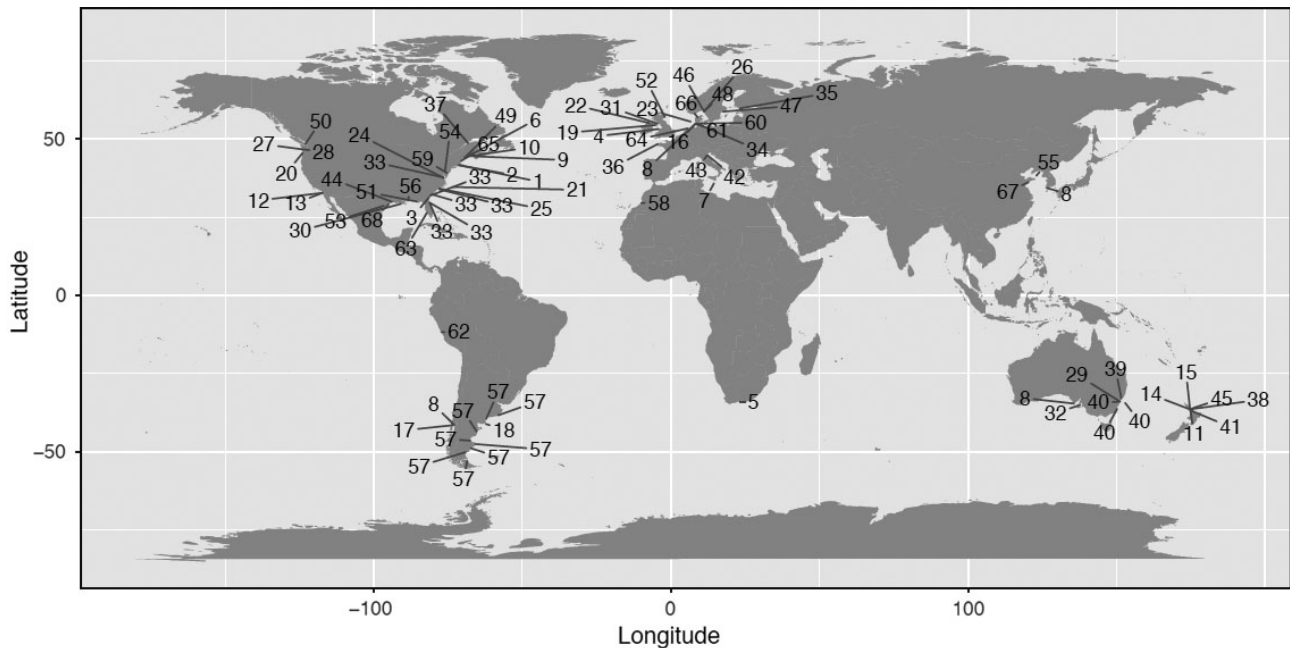[a]Site had a diurnal tide.; [b]Site was not tidal

Fig. 1. The location of studies from which data were extracted. Studies are numbered as in Table 1

were (1) infaunal—living in sediment under the bivalve matrix or in sediment trapped in the interstices of the bivalve matrix, (2) mobile epifaunal—living on the surface of the bivalve matrix or bare substratum with a mobile adult life-history stage, or (3) sessile epifaunal—also living on the surface but with a non-mobile adult life-history stage. Habitats were categorised as soft sediment or rocky shore. Because hard substrate is scarce on sedimentary shorelines, and sediments are scarce on rocky shores, it was predicted that for each of sessile and mobile epifauna, the positive effect of bivalves on abundance would be greater on sedimentary than rocky shores, but for infauna, the positive effect of bivalves would be greater on rocky than sedimentary shores. Consequently, we expected that in sediments, bivalves would have a greater effect on sessile and mobile epifauna than infauna, but on rocky shores effects on infauna would be greatest. Across all habits of invertebrates, it was predicted that bivalve enhancement of species density would be greater on sandy shores where hard substrate is otherwise lacking, than on rocky shores.

To determine whether the effect of habitat-forming bivalves on invertebrate abundance and species density varies with abiotic stress, we compared ecosystem engineering across environmental gradients of known stressors to intertidal invertebrates, including tidal elevation (Connell 1972) and latitude, over which abiotic stressors such as temperature and humidity may vary (Morley et al. 2012). Three tidal elevations were considered: mid intertidal (aerially exposed for ≥4 h but no more than 8 h per semi-diurnal tidal cycle), low intertidal (aerially exposed on every tidal cycle, but for <4 h per semi-diurnal tidal cycle) and subtidal elevations (permanently submerged). High intertidal elevations could not be included due to insufficient data. All sites at which intertidal sampling was conducted had a semi-diurnal tidal cycle. Although most of the subtidal sampling was also done at sites with a semi-diurnal tide, 5 studies conducted subtidal sampling at sites that had a diurnal or no tide (Table 1). Analyses examining relationships between ecosystem engineering and latitude utilised only data collected from the intertidal zone of either sedimentary or rocky shores, as this is where invertebrates are exposed to the greatest variations in climatic factors, such as temperature and humidity, that can induce stress (Tsuchiya 1986, Jenewein & Gosselin 2013). In line with the Bertness & Callaway (1994) stress-gradient hypothesis, it was predicted that the effect of bivalves on invertebrate abundance and species density would increase with tidal elevation, across which temperature and desiccation stress is broadly acknowledged to increase (Connell 1972), and increase with decreasing latitude, across which temperature increases (McAfee et al. 2016). Studies from tropical, sub-tropical and temperate systems were considered for latitudinal analysis.

Analyses

Hedges' *d* (Hedges & Olkin 1985) was used to calculate the effect size by which invertebrate abundances or species density differed between patches of habitat-forming bivalves and otherwise similar bare substrate. Hedges' *d* was used in preference to other statistics, such as Hedges' *g*, as it better accounts for small sample sizes (Rosenberg et al. 2000), which were apparent in around one-quarter of papers examined. Weighted variances of effect size were calculated and used to determine the 95% confidence interval of each. Effect sizes were considered significant if the 95% confidence interval did not include 0. Homogeneity assumptions were assessed using the I^2 statistic (Higgins et al. 2003). Where I^2 was greater than 75%, heterogeneity was considered too large to proceed with the analysis (Higgins et al. 2003). Prior to each analysis, we assessed whether results were influenced by publication bias using funnel plots (Figs. S1–S5 in the Supplement at www. int-res.com/articles/suppl/m563p095_supp.pdf). These plot effect size against sample size, checking for a funnel shape that is indicative of an absence of bias (Palmer 1999).

Separate categorical random-effects models were conducted in MetaWin 2.0 (Rosenberg et al. 2000) on total invertebrate abundance and species density data to test hypotheses about the overall effect of habitat-forming bivalves, and the effects of bivalve taxon, associated faunal habit, habitat and tidal elevation on effect size. In the event that bivalve effects on invertebrate abundance and species density differed among bivalve taxa, analyses of the effects of bivalve density, associated community habit, bivalve habitat and environmental gradients on total abundance and species density were conducted separately for each bivalve taxon. Where categorical analyses were significant at α = 0.05, categorical random-effects models assessed pair-wise differences among treatments.

Effects of bivalve density and latitude on effect size were examined using weighted-least squares regressions. As effect size was hypothesised to have a non-linear association with density; data were examined with curve-fitting software (Curve Expert 1.3, Hyams 1997), which recommended a linear model.

RESULTS

Of the 65 studies in which effects of bivalves on the total abundance of one or more invertebrate taxa was

quantified (Table 1, Fig. 1), 32% reported significant positive effects (i.e. Hedges *d* > 0, and 95% confidence interval excluding 0), 39% reported non-significant positive effects (i.e. Hedges *d* > 0, but 95% confidence interval including 0), 17% reported non-significant negative effects (i.e. Hedges *d* < 0, but 95% confidence interval including 0) and 12% significant negative effects (i.e. Hedges *d* < 0, but 95% confidence interval excluding 0; Table 1). Bivalves had a significant positive effect on invertebrate species density in 29% of the 34 studies in which their effects on species density were assessed; there was a non-significant positive effect in 48%, a non-significant negative effect in 20% and a significant negative effect in 3% (Table 1). Funnel plots indicated that analyses were not influenced by publication bias (Figs. S1–S5 in the Supplement).

In analyses partitioning invertebrates by phylum, habitat-forming bivalves did not have a significant negative effect on any of the phyla examined. Bivalves had a significant positive effect on the abundances of 5 of the 9 groups examined, a non-significant positive effect on cnidarians and platyhelminthes, and a non-significant negative effect on tunicates and priapulids, each of which had only 2 data points available (Fig. 2). Consequently, when phyla were pooled, habitat-forming bivalves affected both invertebrate abundances and species density positively (*d* ± 95% CI; abundance: 0.87 ± 0.20; species density: 1.00 ± 0.28).

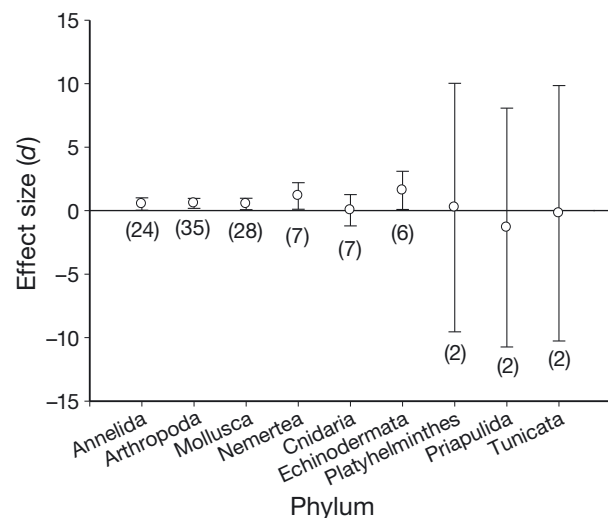The effects of bivalves on associated invertebrate abundance and species density varied as a function

Fig. 2. Mean (±95% CI) effect size (calculated using Hedges' *d*) by which habitat-forming bivalves enhanced the abundance of each of 9 invertebrate phyla. Numbers in parentheses indicate the number of comparisons used to determine effect size
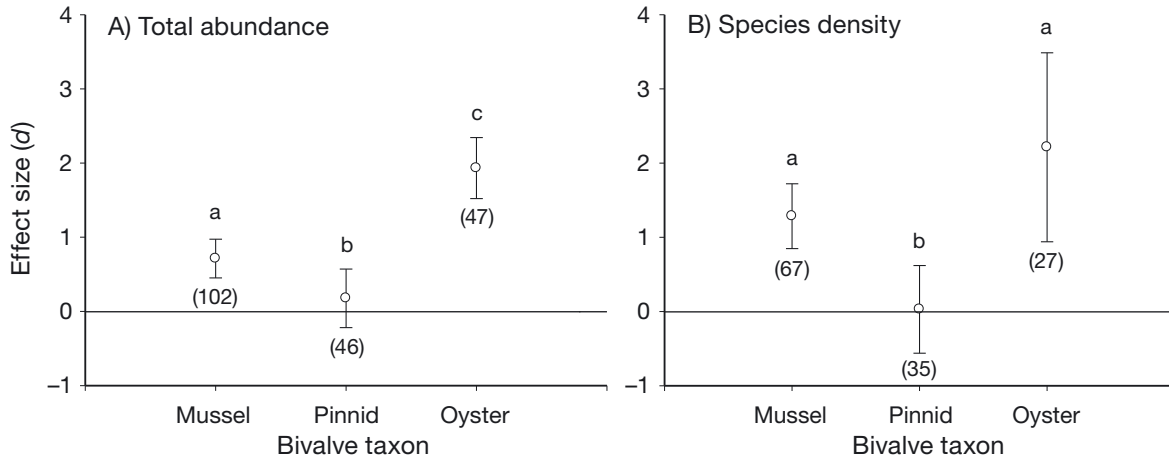
Fig. 3. Mean (±95% CI) effect size (calculated using Hedges' d) by which bivalve taxa (mussel, pinnid, oyster) enhanced (A) total faunal abundance and (B) total faunal species density. Letters denote treatments found to differ significantly at p = 0.05 using post-hoc tests for significant meta-analyses. Numbers in parentheses indicate the number of comparisons used to determine effect size

of bivalve taxon (abundance: Qb, which describes the difference in cumulative effect sizes between groups based on a Chi squared distribution [Rosenberg et al. 2000], = 40.96, df = 2, p = 0.001; species density: Qb = 18.58, df = 2, p = 0.001). Oysters increased total invertebrate abundance by a significantly greater effect size than did mussels, and mussels had a greater effect on invertebrate abundance than did pinnids, with the effect size of pinnids not deviating significantly from 0 (p < 0.05 post-hoc tests, oyster > mussel > pinnid; Fig. 3). The effect of oysters on invertebrate species density did not differ significantly from the effect of mussels, but both bivalve taxa had a greater effect on species density than did pinnids (p < 0.05 post-hoc tests, oyster = mussel > pinnid; Fig. 3), the latter of which did not deviate significantly from 0.

Of the 3 bivalve taxa, only mussels had data of sufficient density spread to test for a relationship between bivalve density and the abundance and species density of associated invertebrates. As the density of mussels increased, their effect on total invertebrate abundance decreased linearly (R^2 = 0.271, df = 1, p < 0.001; Fig. 4), but their effect on invertebrate species density did not vary predictably (R^2 = 0.013, df = 1, p = 0.426; Fig. 4).

The effect of mussels on invertebrate abundance varied by faunal habit (i.e. infauna, mobile epifauna, sessile epifauna) on sedimentary, but not rocky substrates (sedimentary: Qb = 8.79, df = 2, p = 0.012; rocky: Qb = 4.14, df = 1, p = 0.065). On sedimentary substrates, the positive effect of mussels was greater on sessile and mobile epifauna, which did not significantly differ from one another, than on infauna,
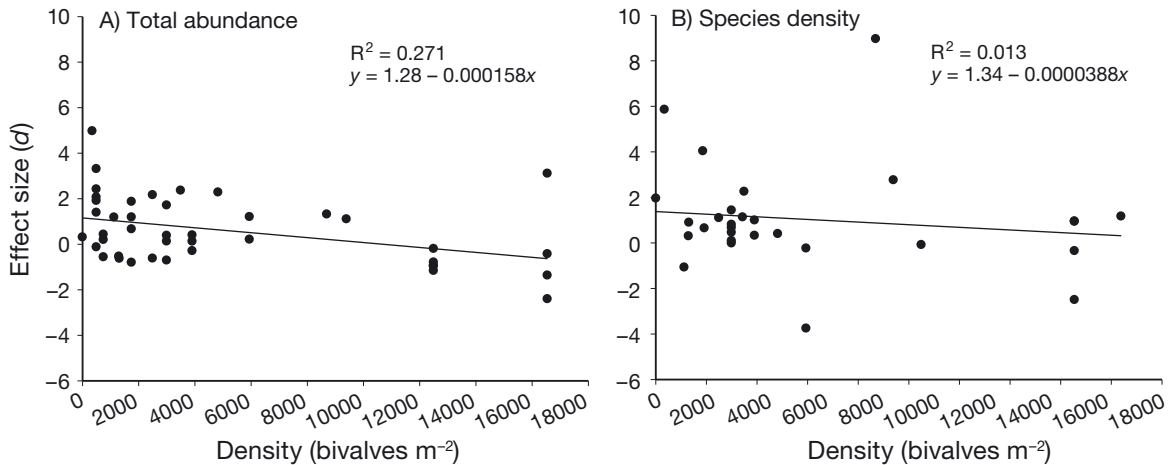

Fig. 4. Weighted relationship between the density of mussels and their effect size (calculated using Hedges' d) on invertebrate (A) abundance and (B) species density. Values weighted against the inverse sum of study variance and pooled variance
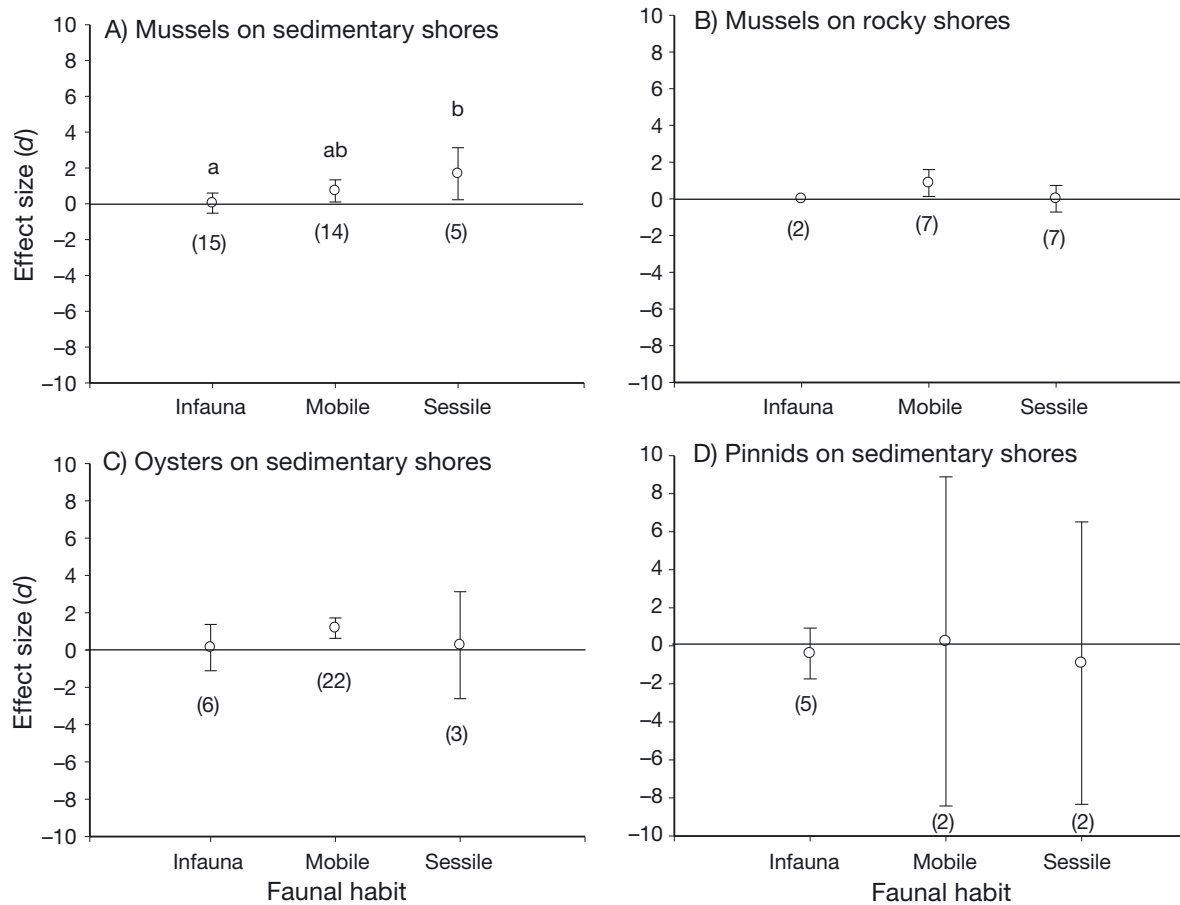
Fig. 5. Mean (±95% CI) effect size (calculated using Hedges' d) by which (A, B) mussels, (C) oysters and (D) pinnids enhanced total abundance of infauna, mobile epifauna and sessile epifauna on (A, C, D) sedimentary and (B) rocky substrates. Letters denote treatments found to differ significantly at p = 0.05 using post-hoc tests for significant meta-analyses. Numbers in parentheses indicate the number of comparisons used to determine effect size

which did not deviate from 0 (post-hoc tests; Fig. 5). On rocky substrates, the effect of mussels on infauna could not be tested due to insufficient data, but their significant positive effect on mobile epifauna did not differ from their non-significant positive effect on sessile epifauna (Fig. 5). Mussels had a greater effect on sessile epifaunal abundance on sedimentary than on rocky shores (Qb = 5.82, df = 1, p = 0.049), but their effect on mobile epifauna (Qb = 0.34, df = 1, p = 0.564) and infauna (Qb = 1.52, df = 1, p = 0.233) did not differ between habitat settings. In contrast, neither the effect of oysters nor pinnids differed among faunal habits on sedimentary shorelines (oysters: Qb = 4.53. df = 2, p = 0.178; pinnids: Qb = 1.63, df = 2, p = 0.501; Fig. 5), with only the effect of oysters on sessile epifauna significantly differing from 0 (Fig. 5). Compared with mussels, there were few studies on oysters or pinnids, and there were insufficient data to assess whether groups of fauna differed in their response to oysters on rocky shores. Pinnids are

infaunal bivalves that are only found on sedimentary substrates.

The effect of mussels on invertebrate species density was greater on rocky than sedimentary substrates, but the effect of oysters on invertebrate species density was greater on sedimentary than rocky substrates (mussels: Qb = 6.122, df = 1, p = 0.039; oysters: Qb = 9.634, df = 1, p = 0.011; Fig. 6). Comparisons could not be made for pinnids.

The effect of mussels on invertebrate abundance and species density varied among tidal elevations. Mussels had a significant positive effect on invertebrate abundance at subtidal elevations, which did not differ significantly from their effect at low-intertidal elevations, which was also significantly greater than 0. Their effect at both of these tidal elevations was greater than their effect at mid intertidal elevations, which did not deviate from 0 (abundance: Qb = 9.60, df = 2, p = 0.025; post-hoc tests; Fig. 7). Similarly, the significant positive effect of mussels on invertebrate

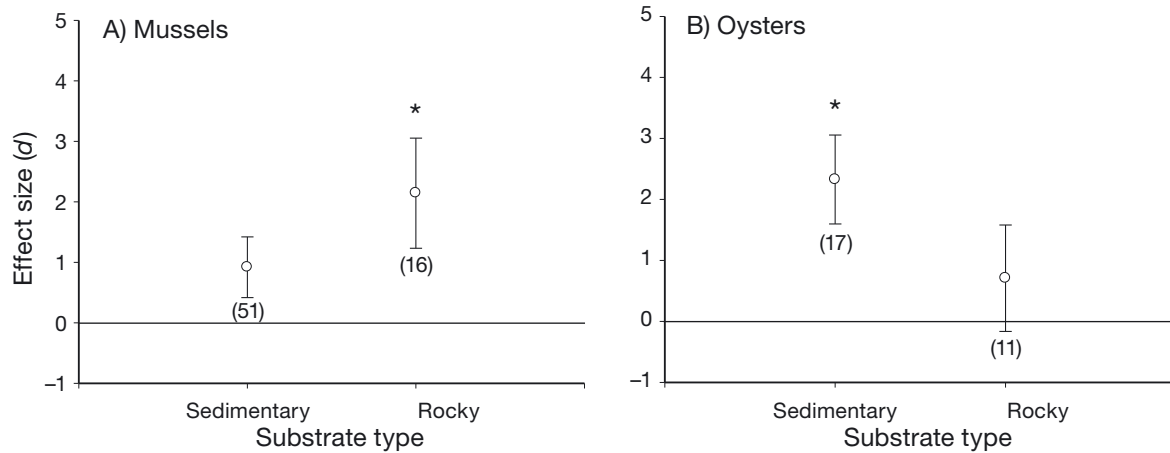Fig. 6. Mean (±95% CI) effect size (calculated using Hedges' *d*) by which (A) mussels and (B) oysters enhanced invertebrate species density on rocky and sedimentary substrates. Asterisk denotes treatment found to differ significantly at p = 0.05. Numbers in parentheses indicate the number of comparisons used to determine effect size
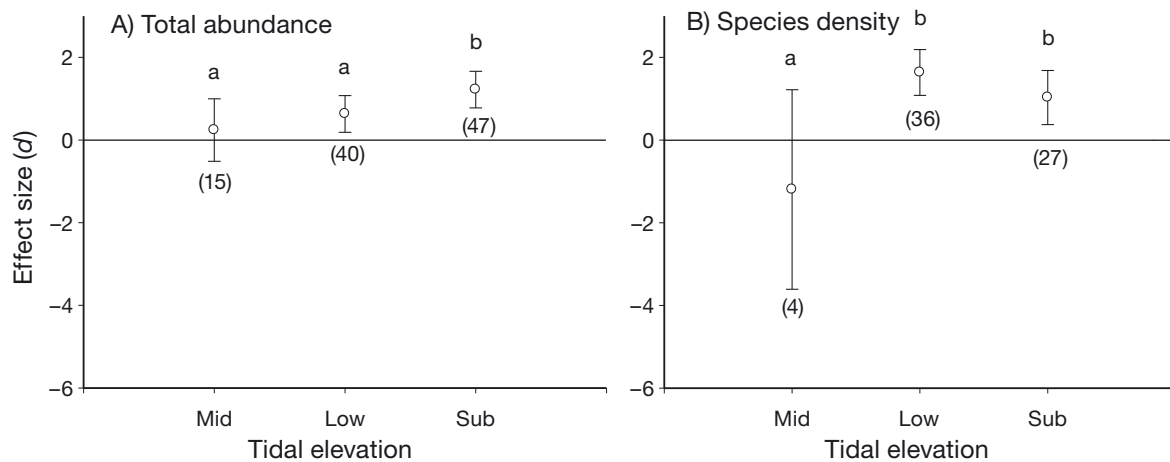

Fig. 7. Mean (±95% CI) effect size (calculated using Hedges' *d*) by which mussels affected (A) total faunal abundance and (B) total faunal species density at different tidal elevations (Mid = mid intertidal; Low = low intertidal; Sub = subtidal). Letters denote treatments found to differ significantly at p = 0.05 using post-hoc tests for significant meta-analyses. Numbers in parentheses indicate the number of comparisons used to determine effect size

species density at subtidal and low intertidal elevations was greater than their negative non-significant effect at mid intertidal elevations (species density: Qb = 12.89, df = 2, p = 0.011; post-hoc tests; Fig. 7). The effect of oysters on both associated invertebrate abundance and species density did not differ among tidal heights (abundance: Qb = 2.71, df = 2, p = 0.343; species density: Qb = 1.714, df = 2, p = 0.521; Fig. 7). Tests were not conducted for pinnids as all data for this bivalve taxon were from subtidal elevations.

Within the intertidal, the effect of mussels on associated invertebrate abundance and species density did not vary in relation to latitude (abundance: R^2 = 0.021, df = 1, p = 0.146; species density: R^2 = 0.024, df = 1, p = 0.374). Similarly, the effect of oysters on associated invertebrate abundance displayed no sig-

nificant relationship with latitude (abundance: R^2 = 0.026, df = 1, p = 0.220). There were insufficient data on the species density of invertebrates associated with oysters or the abundance or species density of invertebrates associated with pinnids to enable effect sizes to be compared among latitudes.

DISCUSSION

Effective use of ecosystem engineers as a tool for biodiversity conservation requires an understanding of those factors that determine when and where ecosystem engineers have the greatest influence on biodiversity. Several empirical studies have demonstrated how intraspecific variation in traits of individual eco-

system engineers can influence their effects (Bruno & Kennedy 2000, van Hulzen et al. 2007, Irving & Bertness 2009, Harley & O'Riley 2011) and ecological theory makes predictions of how interactions should vary across environmental stress gradients (Bertness & Callaway 1994). This paper provided one of the first cross-study assessments of how traits of ecosystem engineers and habitat context influence ecosystem engineering in marine environments. As expected (see review by Seed 1996), habitat-forming bivalves had an overall positive effect on invertebrate abundance and species density across the studies considered. Nevertheless, the magnitude of their effects varied considerably, from zero to highly positive according to engineer and associated community identity, as well as environmental setting.

The magnitude of bivalve effects on invertebrates was influenced by each of the bivalve characteristics examined by this study — bivalve taxon and bivalve density. Of the 3 bivalve taxa considered, oysters provided a greater enhancement of invertebrate abundance than mussels and pinnids, and both oysters and mussels enhanced invertebrate species density to a greater extent than pinnids. Differences in the magnitude of ecosystem engineering between the 3 taxa may reflect differences in their physical structure, the environmental setting in which they are found or the magnitude of key ecological functions, such as filtration (Gutiérrez et al. 2003, Kochmann et al. 2008). Whereas oysters and mussels are gregarious, directly attaching to one another, pinnids are typically solitary. Oysters and mussels are epibenthic, found either on sediments or on rock, whereas pinnids are infaunal, with only a small proportion of their shell above the sediment–water interface. The complexity and heterogeneity of bivalve habitat influences the quality of refuge (Grabowski 2004), flow and boundary layers (Cummings et al. 2001), which in turn influence larval deposition (Lapointe & Bourget 1999), as well as the area of hard substrate available to fouling organisms (Gutiérrez et al. 2003, Summerhayes et al. 2009). Bivalve habitat may influence the area of shell surface above the sediment surface and the identity and traits of associated assemblages that may respond to the ecosystem engineer. Filtration rates influence entrainment and mortality of settling larvae (Wilkie et al. 2013) and benthic–pelagic coupling, which determine sediment characteristics (Kochmann et al. 2008). Experiments on rocky and sedimentary shorelines comparing the effect of structural mimics and live bivalves would be required to disentangle the key traits responsible for differences in the magnitude of ecosystem engineering among the 3 taxa.

Unfortunately, we did not find studies that had sampled at sufficiently low bivalve densities to fully test for relationships between ecosystem engineering and bivalve density across the full range of densities possible. We had predicted that the magnitude of ecosystem engineering would increase from low to medium bivalve densities as the number of structural elements and the capacity for associational defence increases (McAfee et al. 2016), but decrease at high densities due to competition between bivalves and associated species for space and other resources (see Stachowicz 2001). Assessments of changes in invertebrate communities from intermediate to high mussel densities revealed that mussel effects on their abundance but not species density decreased across this density range. At high densities of habitat-forming bivalves, interstitial spaces for organisms may be reduced (Cole 2010). Additionally, for gregarious habitat-forming bivalves, such as mussels and oysters, bivalves tend to decrease in size as density and competition for space increases (Cole 2010, McAfee et al. 2016). Relationships between length and each of surface area and biomass are square to cubic (McKinney et al. 2004) such that when the length of bivalves is reduced, their surface area and biomass decrease in a non-linear way (Alunno-Bruscia et al. 2000, McKinney et al. 2004). Our examinations assessed invertebrate communities in relation to the number of bivalves m^{-2} and did not take changing bivalve biomass or surface area into account. Since associated invertebrates respond strongly to bivalve surface area (Gutiérrez et al. 2003, Summerhayes et al. 2009), changes in biomass and surface area may have potentially offset the effect of increasing density per se.

The nature and the magnitude of ecosystem engineering by habitat-forming bivalves was influenced by the traits of the associated community and bivalve habitat setting for mussels, but not for oysters or pinnids, for which fewer studies were available and among which variation in effect sizes was high. In sedimentary habitats where bivalves enhance the availability of hard substrate for mobile and sessile epifauna, but may compete for resources with infaunal invertebrates (Seed 1996, Gutierrez et al. 2003), the effect of mussels on epifaunal abundance was positive, but on infauna was neutral. In contrast, in rocky habitats at mid and lower intertidal elevations where habitat-forming bivalves may compete for settlement space with other sessile invertebrates (Menge 1976), we found the effect of mussels on sessile epifaunal abundance was neutral. Whether bivalves had a greater effect on invertebrate species density on rocky or sedimentary substrate varied

with the identity of the habitat-forming bivalve taxon. Although we had expected each of the bivalve taxa to have greater effects on sandy shores, where hard substrate is otherwise lacking, the reverse pattern of greater enhancement of species density on rocky than sedimentary shores was apparent for mussels. The habitat heterogeneity provided by bivalves may not only provide a greater substrate for invertebrate attachment, but may provide refuge from predation and environmental stressors (Menge et al. 1985, McAfee et al. 2016).

Earlier studies suggest that amelioration of temperature and desiccation stress is a key mechanism by which bivalves facilitate fauna in the intertidal zone (Bertness & Leonard 1997, Cole 2010, McAfee et al. 2016). Hence, we expected that effects of bivalves on abundance and species density would increase from subtidal to intertidal elevations — the paradigmatic gradient of temperature and desiccation stress on rocky shores (Connell 1972) — and increase from cooler, high-latitude to warmer, low-latitude climates. Instead, we found the effect of mussels on invertebrate abundance and species density was greater at subtidal than intertidal elevations and neither the effect of oysters or mussels on invertebrate abundance nor species density exhibited any relationship with latitude. Unfortunately, our analyses were unable to include the high intertidal elevation, at which desiccation stress is most severe (Connell 1972), due to a paucity of studies presenting such data. The greater effect of mussels at subtidal than low intertidal elevations may be driven by associational defence from marine vertebrate predators such as fish and rays to which subtidal invertebrates are more exposed. Our analyses failed to detect latitudinal gradients in ecosystem engineering in spite of a previous study documenting latitudinal gradients in the facilitation of invertebrates by an individual species of oyster (McAfee et al. 2016). In the present study, detection of global-scale patterns may have been hampered by methodological differences among studies, and small-scale variation in associated invertebrate diversity and other environmental factors not considered in our analyses (Seed 1996). Consequently, in addition to meta-analyses that synthesise results across studies, studies that adopt consistent methodology to sample across broad biogeographic scales are needed (see Smith et al. 2006, McAfee et al. 2016).

Overall, ecosystem engineering by mussels displayed stronger variation with respect to the bivalve traits and the environmental conditions examined by this study than ecosystem engineering by either oysters or pinnids. Although oysters and pinnids did not vary predictably with many of the factors examined, they displayed high among-study variation in their effects. Whereas studies on mussel bed communities display fairly consistent methodologies for sampling across studies, predominantly based on coring, oyster communities are sampled using a variety of techniques including quadrats, seine nets and benthic traps, which may contribute to this high variation. In addition, oysters exhibit great morphological plasticity (O'Beirn et al. 2000), potentially giving rise to high variability in the response of the associated community, making distinctions in ecosystem engineering difficult to detect across the gradients we tested. In the case of pinnids, the high variability in the invertebrate communities associated with pinnids may reflect the lower degree of habitat-modification and therefore less-consistent ecosystem engineering compared with mussels and oysters.

Overall, our analyses indicate that habitat-forming bivalves facilitate dense and diverse communities of associated invertebrates. The magnitude of their ecosystem engineering, however, exhibits considerable spatial variability according to traits of the ecosystem engineer, the associated community, as well as environmental context. The high spatial variability of ecosystem engineering highlights the need to understand the context dependency of ecological interactions, if use of ecosystem engineers in restoration and conservation is to be effective. We have shown that environmental context can directly influence ecosystem engineering and may indirectly influence ecosystem engineering, where it affects traits of the ecosystem engineer such as density and taxonomic identity. Our findings not only serve to inform future conservation efforts aimed at restoring the ecological communities supported by marine bivalves, but also broaden the current knowledge of ecosystem engineering in marine environments.

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