

Research article

Complexity-functioning relationships differ across different environmental conditions

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ABSTRACT

Habitat complexity is widely considered an important determinant of biodiversity, and enhancing complexity can play a key role in restoring degraded habitats. However, the effects of habitat complexity on ecosystem functioning – as opposed to biodiversity and community structure – are relatively poorly understood for artificial habitats, which dominate many coastlines. With Greening of Grey Infrastructure (GGI) approaches, or eco-engineering, increasingly being applied around the globe, it is important to understand the effects that modifying habitat complexity has on both biodiversity and ecological functioning in these highly modified habitats. We assessed how manipulating physical (primary substrate) and/or biogenic habitat (bivalves) complexity on intertidal artificial substrata affected filtration rates, net and gross primary productivity (NPP and GPP, respectively) and community respiration (CR) – as well as abundance of filter feeders and macro-algae and habitat use by cryptobenthic fish across six locations in three continents. We manipulated both physical and biogenic complexity using 1) flat or ridged (2.5 cm or 5 cm) settlement tiles that were either 2) unseeded or seeded with oysters or mussels. Across all locations, increasing physical and biogenic complexity (5 cm seeded tiles) had a significant effect on most ecological functioning variables, increasing overall filtration rates and community respiration of the assemblages on tiles but decreasing productivity (both GPP and NPP) across all locations. There were no overall effects of increasing either type of habitat complexity on cryptobenthic fish MaxN, total time in frame or macro-algal cover. Within each location, there were marked differences in the effects of habitat complexity. In Hobart, we found higher filtration, filter feeder biomass and community respiration on 5 cm tiles compared to flat tiles. However, at this location, both macro-algae cover and GPP decreased with increasing physical complexity. Similarly in Dublin, filtration, filter feeder biomass and community respiration were higher on 5 cm tiles compared to less complex tiles. In Sydney, filtration and filter feeder biomass were higher on seeded than unseeded tiles, and fish MaxN was higher on 5 cm tiles compared to flat

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tiles. On unseeded tiles in Sydney, filter feeder biomass also increased with increasing physical complexity. Our findings suggest that GGI solutions via increased habitat complexity are likely to have trade-offs among potentially desired functions, such as productivity and filtration rates, and variable effects on cryptobenthic fish communities. Importantly, our results show that the effects of GGI practices can vary markedly according to the environmental context and therefore should not be blindly and uniformly applied across the globe.

1. Introduction

The United Nations General Assembly declared 2021–2030 to be the ‘Decade of Ecosystem Restoration’ – a global effort ‘to prevent, halt and reverse’ the degradation of ecosystems for the benefit of both people and nature. Urbanisation is one of the leading causes of ecosystem degradation that occurs through conversion of natural habitats to built infrastructure, such as buildings and roads (Grimm et al., 2008). In an effort to offset or mitigate damage resulting from urbanisation, nature-based solutions (NbS) are increasingly being used (Dorst et al., 2019). Nature-based solutions are defined by IUCN (2020) as “*actions to protect, sustainably manage, and restore natural or modified ecosystems ... simultaneously providing human well-being and biodiversity benefits*”, and can range from restoration of natural habitats to green-grey infrastructure approaches (Naylor et al., 2017; Airoidi et al., 2021) which are increasingly used to support biodiversity on hard infrastructure in highly urban contexts (Strain et al., 2018; Oral et al., 2020). While a growing body of work has assessed how such manipulations affect biodiversity (Evans et al., 2016; Strain et al., 2021; Bishop et al., 2022; Wooster et al., 2022) very little is known about (a) how these interventions influence ecological functioning that underpin key ecosystem services, including habitat provision and (b) how these effects vary across environmental context.

In urban coastal areas, construction is a major cause of natural ecosystem degradation (Bulleri and Chapman, 2010; Bugnot et al., 2020) and efforts for ‘greening of grey infrastructure’ (GGI hereafter) using eco-engineering solutions have gained traction to ‘rehabilitate’ these ecosystems (Evans et al., 2021). GGI practices in the marine environment often involve the modification of built infrastructure (grey) by enhancing habitat complexity – a process argued to increase biodiversity and restore lost ecological functions (Browne and Chapman, 2011; Firth et al., 2016, but see Grasselli and Airoidi, 2021). Although many studies report increased richness and abundance of species in more complex habitats (e.g. Heck Jr and Wetstone, 1977; Matias et al., 2010; Loke and Todd, 2016), results from small-scale eco-engineering experiments across the globe have shown that the relationship between habitat complexity and biodiversity is not always positive and can vary with local biotic and abiotic conditions (O’Shaughnessy et al., 2021; Strain et al., 2021; Clifton et al., 2022). It is therefore expected that the responses of ecosystem functions to changes in complexity may, similarly, vary across environmental conditions, such as latitude (see e.g. Bracewell et al., 2018). Nevertheless, there is a notable lack of empirical research addressing how habitat complexity influences the ecological functions of systems, and specifically artificial habitats (but see Mayer-Pinto et al., 2023).

Increasing habitat complexity – either through changes in the topography of the primary substratum (hereafter referred to as physical complexity) or through the addition (seeding) of habitat forming species such as bivalves and macro-algae (hereafter referred to as biogenic complexity) – can affect ecosystem functioning through several mechanisms. Complexity might affect the ecological functioning of habitats by changing, for example, the abundance and identity of colonising species due to their substrate preferences (e.g. Matias et al., 2010), altered abiotic conditions, biological interactions or changes in the performance of individual organisms (Mumby et al., 2011; Montalto et al., 2016; Mayer-Pinto et al. 2018, 2020; Lim et al., 2020). Consequently, effects of habitat complexity on functioning may not necessarily mirror effects on biodiversity, and may vary with the type of

habitat complexity being modified as well as the environment in which complexity is changed (Mayer-Pinto et al., 2023).

In urbanised coastal habitats, GGI approaches often manipulate not only the physical complexity of the artificial substrata, e.g. by adding habitats such as water-retaining features (Evans et al., 2016; Firth et al., 2016) or pits (Martins et al. 2010, 2016), but also through the addition of key or threatened habitat-forming species (Perkol-Finkel et al., 2012; Bradford et al., 2020). Therefore, here, we assessed how increasing habitat complexity in artificial habitats, through physical changes to the primary substratum and/or the addition of habitat-forming bivalves (hereafter referred to as seeding) can affect ecological functions, including habitat provision, across different abiotic and biotic contexts.

Habitat-forming bivalves, such as oysters and mussels, serve as secondary substrata for attachment and refuge for other organisms. Consequently, their addition to the primary substrata can enhance the physical complexity provided by the primary substrate while simultaneously influencing the functioning of systems in other non-structural ways (e.g. Mayer-Pinto et al., 2023). Bivalves can influence the functioning of habitats through changes in biological communities, via provision of habitat and/or food, as well as through their feeding and metabolic processes such as filtration, ammonia excretion and respiration (Boucher and Boucher-Rodoni, 1988). Given that GGI often aims to not only enhance biodiversity, but also desired ecosystem services, it is important to understand how habitat complexity-induced changes in biodiversity translate to changes in ecosystem functioning that underpins these services, such as filtration rates and productivity. For example, increased filtration rates on seawalls in urban areas could result in improved local water quality due to the capacity of bivalves to accumulate pollutants through their feeding, therefore ‘cleaning’ the water column (Vaughn and Hoellein, 2018).

Using small-scale experiments at six locations across the globe, we investigated how tiles of different physical complexity (flat, 2.5 cm or 5 cm complex), and biogenic complexity (with and without seeded bivalves), attached to coastal infrastructure influenced primary and net productivity, filtration and respiration rates and filter feeder biomass. These variables are directly linked to the provision of services such as clean water and fisheries (Downing et al., 1990; Vaughn and Hoellein, 2018). Based on previous experiments using similar tiles and treatments (Ushijima et al., 2019; Strain et al., 2020; Vozzo et al., 2021; Mayer-Pinto et al., 2023), we hypothesised that filtration rates would be higher on complex tiles seeded with bivalves compared to unseeded and flat tiles, due to increased number (biomass) of bivalves on these tiles. In contrast, we predicted that primary and net productivity would be greater on flat, unseeded tiles, as algal growth may be limited on complex tiles due to increased shading by ridges, and on seeded tiles due to increased competition with sessile and mobile invertebrates and potential consumption of algal propagules by filter-feeders (Santelices and Martinez, 1988). Macroalgae are the dominant primary producers on hard-substrata habitats (Tait and Schiel, 2010), such as seawalls. Understanding how GGI approaches on seawalls influence the biomass of producers can help managers devise tailored eco-engineering approaches according to the main objectives of the intervention.

We also looked at the effects of complexity on cryptobenthic fish assemblages. Cryptobenthic fish are defined as reef-associated fish that are <50 mm in length, and are visually and/or behaviourally cryptic (Depczynski and Bellwood, 2003; Brandl et al., 2019). These benthic fish are particularly useful in looking at habitat-fish interactions because of their strong association with specific habitats (Bellwood et al., 2006)

and their rapid response to environmental change due to their short life spans (Depczynski and Bellwood, 2004). Critically, cryptobenthic fish are an important trophic link between primary producers and higher trophic levels (Brandl et al., 2019), and are predicted to not only be impacted by marine urbanisation, but also to equally benefit from mitigation strategies such as GGI practices (Ushiamo et al., 2019). Nevertheless, most research to date has focused on pelagic fish (but see Morris et al., 2017; Ushiamo et al., 2019; Strain et al., 2020). We predicted complex tiles would have a positive effect on cryptobenthic fish relative abundance and time spent near tiles, and that this relationship would be stronger on tiles that had been seeded with bivalves, due to increased food availability.

2. Methods

2.1. Study sites and experimental design

The experiment was replicated in Sydney (Australia), Hobart (Australia), Plymouth (UK), Dublin (Ireland), Ravenna (Italy) and Arraial do Cabo (Brazil). At each location, we established two sites >100 m apart. All sites were in estuaries or bays along urbanised coastlines, with semi-diurnal tidal regimes and well-mixed marine waters. Within locations, each site comprised a vertical seawall or breakwater that extended from the shallow subtidal or the low intertidal to the high intertidal zone. At each site, tidal elevation was measured using pressure loggers to record inundation period, temperature was measured using iButton data loggers, and distance to nearest port or Marina was measured from satellite images (Table S1). Sites were all in the mid or high tide zone, and varied in temperature, maximum tidal range and distance to port or marina (Table S1). See Strain et al. (2021) for details on measurements of environmental parameters.

At each site, we manipulated habitat complexity on the intertidal seawalls or breakwaters by deploying 0.25×0.25 m concrete tiles, that were either: (1) flat with fine-scale <1 mm grooves that mimicked the texture on each of the complex tiles created by 3D printing (hereafter 'flat'; surface area = 0.0625 m^2); (2) complex with vertically orientated 2.5 cm high ridges separated by 1.5–5 cm wide crevices ('2.5 cm'; surface area = 0.090 m^2); or (3) complex with vertically orientated 5 cm high ridges separated by 1.5–5 cm wide crevices ('5 cm'; surface area = 0.136 m^2) (Strain et al., 2021). Tiles were cast using a marine concrete mix commonly used for seawall construction (i.e., Portland cement), from 3D printed moulds designed by Reef Design Lab (Melbourne, Australia). On half of the tiles, complexity was further increased by attaching ('seeding') native bivalves to the tiles (either mussels or oysters) before deployment (Table 1). Bivalves were added in groups of 4 or

5 in equal numbers in crevice and ridge habitats, covering 33% of the tiles, and were attached with non-toxic epoxy glue (Strain et al., 2020; Vozzo et al., 2021).

At each site, five replicate tiles of each treatment were deployed between early spring to late autumn of 2015 or 2016, during the period of greatest species recruitment and growth, and were deployed for a total of 12 months. Tiles were deployed in random order with respect to the experimental treatments in a single horizontal row in the mid-intertidal zone.

Unfortunately, not all variables could be recorded at all locations due to logistical issues and capacity of the local team. Therefore, the range of variables recorded at each location differed. Nevertheless, all variables were measured in at least three locations (six sites) (see details in Table 1). After 12 months of deployment, filtration and biomass of dominant filter feeders were measured at Sydney, Dublin and Hobart, while macro-algal cover, net primary productivity (NPP), gross primary productivity (GPP) and community respiration were measured at Dublin, Plymouth and Hobart. Before tiles were retrieved from the field, cryptobenthic fish MaxN and total time in frame (as proxies for relative abundance and habitat use, respectively) and fish species richness were measured at Sydney, Ravenna and Arraial do Cabo. In Hobart, measurements were not completed for 2.5 cm complex tiles.

2.2. Functional measurements of tiles

After 12 months, all tiles were removed from the field and brought to the laboratory where they were immediately incubated in sealed chambers with seawater to assess productivity, respiration and filtration rates under light and dark conditions. Incubation times and volumes of water used in incubations varied among locations. Differences in incubation time were due to differences in total volume in the chambers and/or biomass of assemblages. Incubations were done for 20 min in Sydney and Hobart (water volume of 4 and 27 L, respectively); 60 min in Dublin (water volume of 6 L) and 90 min in Plymouth (water volume of 18 L). Throughout incubations water was mixed using pumps or electric coffee stirrers. Filtration rates were calculated by counting the difference in number of particles in the seawater before and after incubations under light conditions, with particles counted in $10 \mu\text{m}$ size classes between 10 and $100 \mu\text{m}$ (Mayer-Pinto et al., 2018; Vozzo et al., 2021). Measurements were standardised by time, volume and initial particle count, and analyses were done separately for each location to avoid any potential confounding factors. After incubations, we recorded the identity and percentage cover (pooling across primary and secondary growth) of all algae on each tile. All sessile filter-feeder organisms were removed from tiles and oven dried at 60°C for 3–5 days to ensure that weights were constant for biomass measurements.

Dissolved oxygen was measured in both light and dark incubations using a HQ30D Hach portable dissolved oxygen meter in Dublin, PreSens Microx 4 Fiber Optic Oxygen Transmitter (PreSens, Regensburg, Germany), in Plymouth, and HOBO® DO loggers in Hobart. Oxygen fluxes were then calculated, standardising for total surface area (m^2) of the primary substratum of each tile type (i.e. complex and flat; $\mu\text{mol m}^{-2} \text{ h}^{-1}$) and time of incubation (details above) as per Mayer-Pinto et al. (2023). Tile gross primary productivity (GPP) was calculated by subtracting dark O_2 flux rates (community respiration; CR) from light O_2 flux rates (i.e. net primary productivity (NPP), which estimates community respiration plus community productivity (Sutherland et al., 2017)).

Fish abundance measurements.

At Sydney, Ravenna and Arraial do Cabo, cryptobenthic fish communities were censused using underwater cameras (GoPro® Hero) at high tide prior to tile removal. Cameras were focused on a single tile each, and filmed the four tile types that showed greatest differences in benthic communities (Strain et al., 2021 and unpublished data): (1) flat unseeded, (2) flat seeded, (3) 5 cm unseeded and, (4) 5 cm seeded. Cameras were positioned such that they fitted an entire tile in view and

Table 1

Summary of measurements taken at each location. NPP = Net Primary Productivity, GPP = Gross Primary Productivity, CR = Community Respiration.

Location	Seeded Bivalve	Variables measured
Sydney, Australia	<i>Saccostrea glomerata</i> (Oyster)	Filtration rates, Filter Feeder Biomass Fish MaxN, Time in Frame and Richness
Hobart, Australia	<i>Mytilus planulatus</i> (Mussel)	Filtration rates, Filter Feeder Biomass Macroalgae Cover, CR, NPP, GPP
Dublin, Ireland	<i>Mytilus</i> spp. (Mussel)	Filtration rates, Filter Feeder Biomass Macroalgae Cover, CR, NPP, GPP
Plymouth, UK	<i>Mytilus</i> spp. (Mussel)	Macroalgae Cover, CR, NPP, GPP
Ravenna, Italy	<i>Crassostrea gigas</i> (Oyster)	Fish MaxN, Time in Frame and Richness
Arraial do Cabo, Brazil	<i>Perna perna</i> (Mussel)	Fish MaxN, Time in Frame and Richness

recorded for 180-min. For each camera, 60-min of footage was analysed, between 40 min and 100 min after the camera was positioned to remove any effects of disturbance associated with deploying and retrieving cameras. Videos were analysed frame by frame, with one frame taken every 2 s (i.e., 1800 frames in the 60 min period) and the number of species observed (species richness) recorded. For each cryptobenthic fish species identified on each video, we calculated MaxN – the maximum number observed in a single video frame during the 60-min of footage (Cappo et al., 2007) – as a proxy of abundance. Time in frame – the number of seconds each species is present across the 60-min video period – was also determined for each fish species as a metric of its habitat occupancy (as per Lanham et al., 2021; Martínez-Baena et al., 2022). To estimate panel occupancy and use, we calculated MaxN (the maximum number of cryptobenthic fish of each species observed in a single video frame during the 60-min video period, used as a proxy of abundance) and time in frame (number of seconds fish of each species are present across the 60-min video period, which can be used as a proxy for interaction with tiles). At some of the sites and locations, replicates were missing due to battery failure or tidal conditions, where, for example at microtidal sites in Ravenna, persistent high-pressure conditions produced lower tides and plots were not fully submerged for enough time. Given the low number of replicate tiles videoed as well as cryptobenthic fish species counted, we pooled data from the two sites within locations, so site was removed from the analyses. Also, given that only two species of cryptobenthic fishes were found in Arraial do Cabo (Brazil) and one species in Ravenna (Italy), we did not test for differences in species richness at these locations. Further, for each location, rather than analysing MaxN for each species separately, we summed these to calculate a total MaxN, which was then compared among treatments (Schultz et al., 2014).

Statistical analysis.

Due to differences in seeded species identity across global locations, locations were analysed separately. To test the generality of effects of physical and biogenic complexity on functional responses of colonising assemblages across the various locations, a meta-analysis was conducted. To do this, we calculated standardised mean differences between the treatments (flat seeded, 2.5 cm unseeded, 2.5 cm seeded, 5 cm unseeded, and 5 cm seeded) vs. the control (flat unseeded) for each functional and fish abundance measure, within sites. The measures analysed were: filtration rates and biomass of suspension feeders, CR, NPP, GPP, macro-algae abundance (as % cover), and MaxN and time in frame of cryptobenthic fish. Effect sizes were calculated using the Hedges' *g* standardised mean difference (SMD) for all response variables, using the 'escalc' function from the package 'metafor' in R (Viechtbauer, 2010). SMD was used for meta-analyses due to the large number of zeroes in the data, and because some response variables (GPP and NPP) were positive or negative, depending on location (Borenstein et al., 2010). The effects of physical complexity and seeding on the response variables were tested using a multilevel random effects model with site (random, 6 sites within 3 locations) nested in location (Viechtbauer, 2010). Site was not included in the models for fish MaxN and time in frame, as data from sites within each location was pooled due to limited replicates.

Within each location, generalised linear models (GLM) were used to test for effects of physical complexity (fixed, 3 levels: flat, 2.5 cm, 5 cm, or, for Hobart, fixed, 2 levels: flat, 5 cm), seeding (fixed, 2 levels: unseeded and seeded) and site (fixed, 2 levels) on the measures of productivity (CR, NPP, GPP), macro-algae percent cover, filter feeder biomass, and filtration rate. We treated sites as fixed because of statistical limitations (i.e. only 2 sites were sampled per location). Although, modern mixed model estimations (as opposed to traditional models using sum-of-squares) need a 'reasonable' number of levels (usually considered to be more than 5 – as in the analyses above) to calculate variance among levels effectively (Gelman and Hill, 2006; Harrison, 2015) they allow greater flexibility in the choice of response variable distributions. Each location was analysed separately due to differences in methodology and deployment period. Type-II ANOVA was used to

assess significance using the 'Anova' function from the 'Car' package (Fox et al., 2012). CR, NPP, GPP and filtration data were modelled using a Gaussian distribution, while biomass and macro-algae percent cover were modelled using a Tweedie distribution with a log-link function (using 'tweedie' family with variance power 1.75, link = 0 from the package 'statmod', Smyth et al., 2017) as both are response variables with zeroes and positive continuous values (percent cover was not limited to 100% due to both primary and secondary cover being considered). For filtration rate analyses, initial particle count was found to have a significant linear relationship with filtration rate (as particles/mL/min) across all locations, as has been shown in previous studies (Mayer-Pinto et al., 2018; Vozzo et al., 2021). Therefore, for all models, filtration rates were calculated as the difference in number of particles at the beginning and at the end of incubations, divided by time, volume and initial particle count. Additionally, we ran two GLMs for filtration rate; one with total filter feeder biomass included as a covariate, and the other without this covariate. This was done to assess whether any effects on filtration were explained by suspension feeder biomass and/or due to changes in their efficacy (per unit biomass), or because of differences in environmental conditions among treatments. For each test, model-fit and assumptions of normality and homogeneity of variance were assessed graphically (Q-Q and Residual vs Fitted values plots). Where significant interactions were detected, post-hoc pairwise comparisons were run using the 'emmeans' package in R (Lenth et al., 2019).

To test the effect of habitat complexity (fixed, 2 levels: flat, 5 cm) and seeding (fixed, 2 levels: unseeded and seeded) on measurements of cryptobenthic fish MaxN and time in frame, we used linear models with a gaussian distribution constructed using the 'manyglm' function from the 'mvabund' package (Wang et al., 2022). Type-II ANOVA (as above) was again used to test for significance. Site was not included in models due to a lack of replication across sites (i.e. at Ravenna's southern site, there was only one replicate for the flat unseeded treatment). Data were log-transformed to meet assumptions where necessary and post-hoc pairwise comparisons made using 'emmeans' (see above).

All analyses were run in R Version 4.1.2 (Team, 2016).

3. Results

3.1. General effects of physical and biogenic complexity across locations (meta-analyses)

When results were combined across locations, adding just biogenic complexity to flat tiles (i.e., seeding with bivalves) had no significant effect on any of the functional measures (Fig. 1; Table 2; Table S2). Similarly, we found no effects of biogenic complexity (seeding) on the functions of complex tiles (i.e., 2.5 cm unseeded vs 2.5 cm seeded, and 5 cm unseeded vs 5 cm seeded; Table S2).

In contrast, there were significant effects of increased physical complexity and increased biogenic and physical complexity on functional measures. Across all locations, tiles with 5 cm ridges (seeded and unseeded) had significantly higher filtration rates than flat unseeded tiles or flat seeded tiles. We found significantly greater filtration rates on 2.5 cm seeded tiles compared to flat unseeded tiles. 5 cm seeded tiles also had greater filtration rates than 2.5 cm unseeded ones (Fig. 1; Table 2; Table S2). Patterns of filtration only partly reflected patterns in the biomass of filter-feeders, with significant differences found only between 5 cm seeded tiles vs. flat seeded and flat unseeded tiles (Fig. 1; Table 2; Table S2).

There were significantly lower rates of productivity (both GPP and NPP) on 5 cm seeded tiles when compared to flat tiles, both seeded or unseeded (Fig. 1; Table 2; Table S2). NPP was also significantly lower on 2.5 cm seeded and 2.5 cm unseeded tiles compared to flat unseeded tiles (Fig. 1; Table 2; Table S2). These results did not correspond to patterns in macro-algal cover, which was not significantly affected by physical complexity or seeding (Fig. 1; Table 2; Table S2). Community respiration rates of colonising assemblages were significantly higher on 5 cm

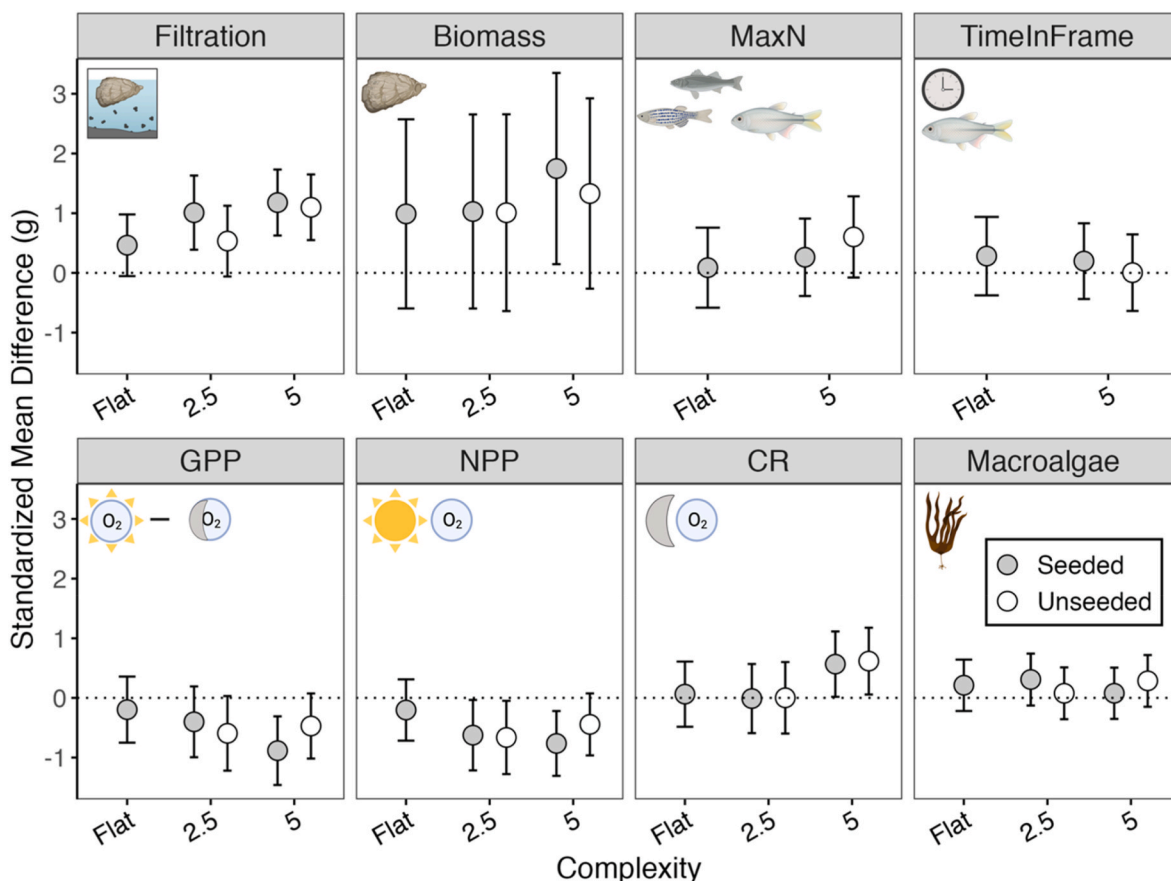


Fig. 1. Effect of increasing physical and biogenic complexity on the standard mean difference (SMD \pm CI) for a) filtration rates (particles/mL/min), b) biomass of filter feeders, c) Fish MaxN, d) Fish Time in Frame, e) GPP (Gross Primary Productivity), f) NPP (Net Primary Productivity), g) CR (community respiration), and h) macro-algal percent cover. Flat unseeded tiles were used as a control comparator for all treatments. Grey points = Seeded treatments; White points = Unseeded treatments. Error bars are 95% confidence intervals. Effects are significant if the confidence intervals do not overlap with zero (dashed line). Figure created with [Biornder.com](https://www.biornder.com).

Table 2

Summary of results comparing standard mean difference (SMD) between control and treatment groups for separate models. Flat unseeded tiles were used as a control for all treatments. Separate models were run for each response variable. Significant results ($p < 0.05$) are in bold. N/A = Not Applicable. Significant post-hoc comparisons between complexity types are also shown. The full table of results can be found in supplementary (Table S2).

	Flat Seeded	2.5 cm Seeded	2.5 cm Unseeded	5 cm Seeded	5 cm Unseeded	Significant Post-Hoc Comparisons ($p < 0.05$)
Filtration	0.079	0.002	0.078	<0.001	<0.001	5 cm Seeded > Flat Seeded 5 cm Seeded > 2.5 cm Unseeded 5 cm Unseeded > Flat Seeded 5 cm Seeded > Flat Seeded
Filter feeder biomass	0.221	0.215	0.23	0.033	0.102	
MaxN	0.798	N/A	N/A	0.429	0.083	
Time in Frame	0.402	N/A	N/A	0.542	0.992	
GPP	0.485	0.185	0.063	0.003	0.091	Flat Seeded > 5 cm Seeded
NPP	0.437	0.038	0.034	0.006	0.094	Flat Seeded > 5 cm Seeded
CR	0.823	0.969	0.996	0.043	0.031	5 cm Unseeded > 2.5 cm Seeded 5 cm Unseeded > Flat Seeded 5 cm Unseeded > 2.5 cm Unseeded
Macroalgae	0.337	0.166	0.729	0.725	0.198	

unseeded tiles than on flat and 2.5 cm seeded and unseeded tiles, and on 5 cm seeded tiles than on flat unseeded tiles (Table 2, Table S2, Fig. 1).

Overall, there were no significant effects of physical or biogenic complexity on the abundance of fish (MaxN or Time in Frame), potentially due to the high variability and low replication among locations (Fig. 1; Table 2; Table S2).

Effects of physical complexity and seeding on filter feeder biomass and filtration rates for each location.

A summary of the main results for each location can be found in Fig. 2 as well as in the supplementary material (Fig. S1 and Table S3).

After 12 months, the seeded oyster species (*Saccostrea glomerata*) was the most abundant filter feeder on the tiles deployed in Sydney, followed by barnacles of various species (*Amphibalanus variegatus*, *Austrobalanus imperator*, *Chthamalus antennatus*, *Hexaminius* sp.) (Fig. S2). At both sites, the biomass of filter feeders was significantly greater on seeded than on unseeded tiles (Fig. 3; Table 3; Table S4). Among the seeded tiles, we found no effects of physical complexity, i.e., flat tiles had similar biomass of filter feeders relative to complex tiles (2.5 cm and 5 cm). However, on the unseeded tiles, there were site-dependent effects of physical complexity. At site 1, 5 cm tiles had similar biomass of filter

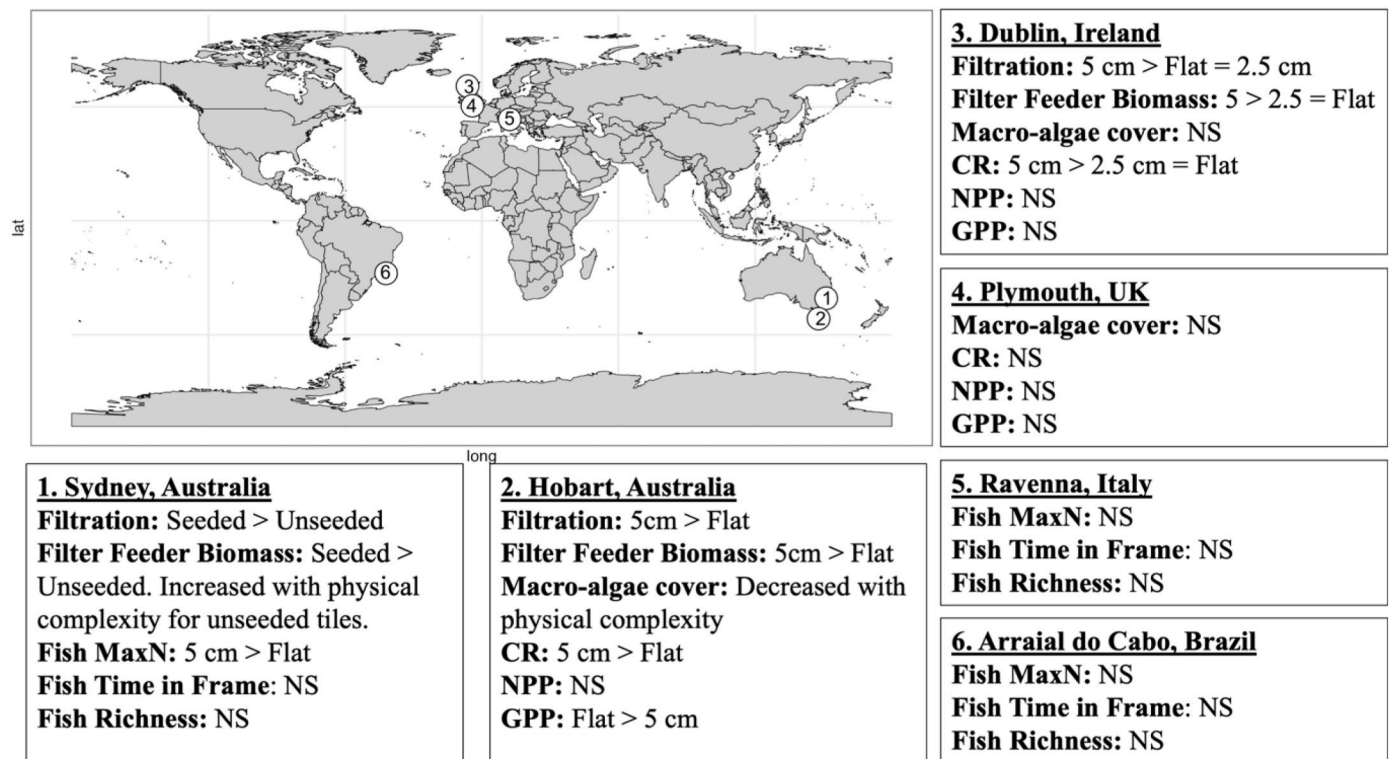


Fig. 2. Map showing location of study sites and summary of main results by location. Results have been simplified to show main effects of physical and biogenic complexity on variables measured at each location. Summarised results do not show interactions between site and biogenic or physical complexity, or main effects of site within locations.

feeders to 2.5 cm tiles and both treatments had greater biomass than flat tiles while at site 2, 5 cm unseeded tiles had more biomass of filter feeders than flat or 2.5 cm tiles. Without biomass of filter feeders as a covariate, filtration rates were significantly higher on seeded than unseeded tiles. However, when biomass was included in the model as a covariate, filtration rates increased with increased biomass of filter-feeders and there was no significant effect of seeding (Table 3; Table S5).

In Hobart, many of the seeded mussels moved off the tiles due to epoxy glue failure. However, mussels (*Mytilus planulatus*) were the dominant contributor to filter feeder biomass, followed by barnacles (*Chthamalus antennatus* and *Chamaesipho tasmanica*) (Fig. S2). Contrary to Sydney, we found that 5 cm tiles had significantly higher biomass of filter feeders than flat tiles, regardless of seeding treatment or site. We found no effects of seeding on the total biomass of filter feeders (Fig. 3; Table 3; Table S6). Although we found significant differences in biomass between sites, results were consistent in direction (i.e., 5 cm tiles had greater biomass than flat tiles on both sites) (Table S6). Similar to filter feeder biomass, filtration rates were significantly greater on 5 cm than flat tiles, regardless of whether biomass of filter feeders was included as a model covariate (Table 2; Table S9).

In Dublin, most seeded mussels (*Mytilus edulis*) had died or fallen off tiles by 12 months (i.e., 83% of seeded tiles had no mussels recorded), so barnacles were the most abundant filter feeders and the species for which biomass was calculated (Fig. S2). We found no effects of seeding on the biomass of barnacles, but 5 cm tiles had, on average, the greatest biomass of barnacles (Fig. 3; Table 3; Table S7). Filtration rates were also significantly higher on 5 cm tiles than on 2.5 cm or flat tiles when biomass of filter feeders, i.e. barnacles, was not included as a model covariate (Fig. 3; Table S10). When biomass was included as a covariate, we only found significant effects between sites, with no effects of physical or biogenic complexity (Table 3; Table S10).

Effects of physical complexity and seeding on macro-algae abundance, GPP, NPP and CR at each location.

In Hobart, we only found significant differences in macro-algae cover among treatments at site 2, with more macro-algae on flat seeded, 2.5 cm seeded and unseeded tiles and 5 cm unseeded tiles than on 5 cm seeded tiles (Fig. S3; Table 4; Table S11). At this location, flat tiles had significantly greater gross primary productivity (GPP) than 5 cm tiles, with the opposite pattern for community respiration (CR; i.e., 5 cm > flat tiles). Neither GPP, NPP nor CR responded to seeding, though each variable displayed site differences (Fig. 4; Table 4; Table S12). Neither physical complexity, seeding, nor their interaction influenced net primary productivity (NPP) at this location. Interestingly, we found negative NPP at one site, but positive NPP at the another (Fig. 4; Table 4; Table S12). In Dublin there were no significant differences in macro-algal cover between sites, complexity or seeding (Fig. S3; Table 4; Table S11).

Similar to Hobart, CR rates in Dublin were greater for assemblages on 5 cm tiles compared to 2.5 cm or flat tiles, regardless of whether they were seeded or not, and across both sites. However, there were no effects of physical complexity or seeding on total cover of macro-algae, GPP or NPP of assemblages at this location, and mean NPP rates were consistently positive across sites (Fig. 4; Table 4; Table S12).

In Plymouth, there was large variability within treatments, and we found no significant effects of physical complexity, seeding or sites, for any of the variables (GPP, NPP, CR) measured, with no macro-algae found at site 2 (Fig. 4; Fig. S3; Table 4; Table S11; Table S12).

Effects of physical complexity and seeding on cryptobenthic fish for each location.

Cryptobenthic fish species richness ($S = 7$) was greatest in Sydney (see details in Table S16). The most abundant species at this location was the oyster blenny (*Omobranchius anolius*), with a mean MaxN of 1.35 (± 0.29 SE), followed by the eastern jumping blenny (*Lepidoblennius haplodactylus*), with a mean MaxN of 0.68 (± 0.23 SE). We found no effects of physical complexity or seeding on fish species richness (analysed for Sydney only) (Fig. 5g; Table 5; Table S13) or on total time in frame

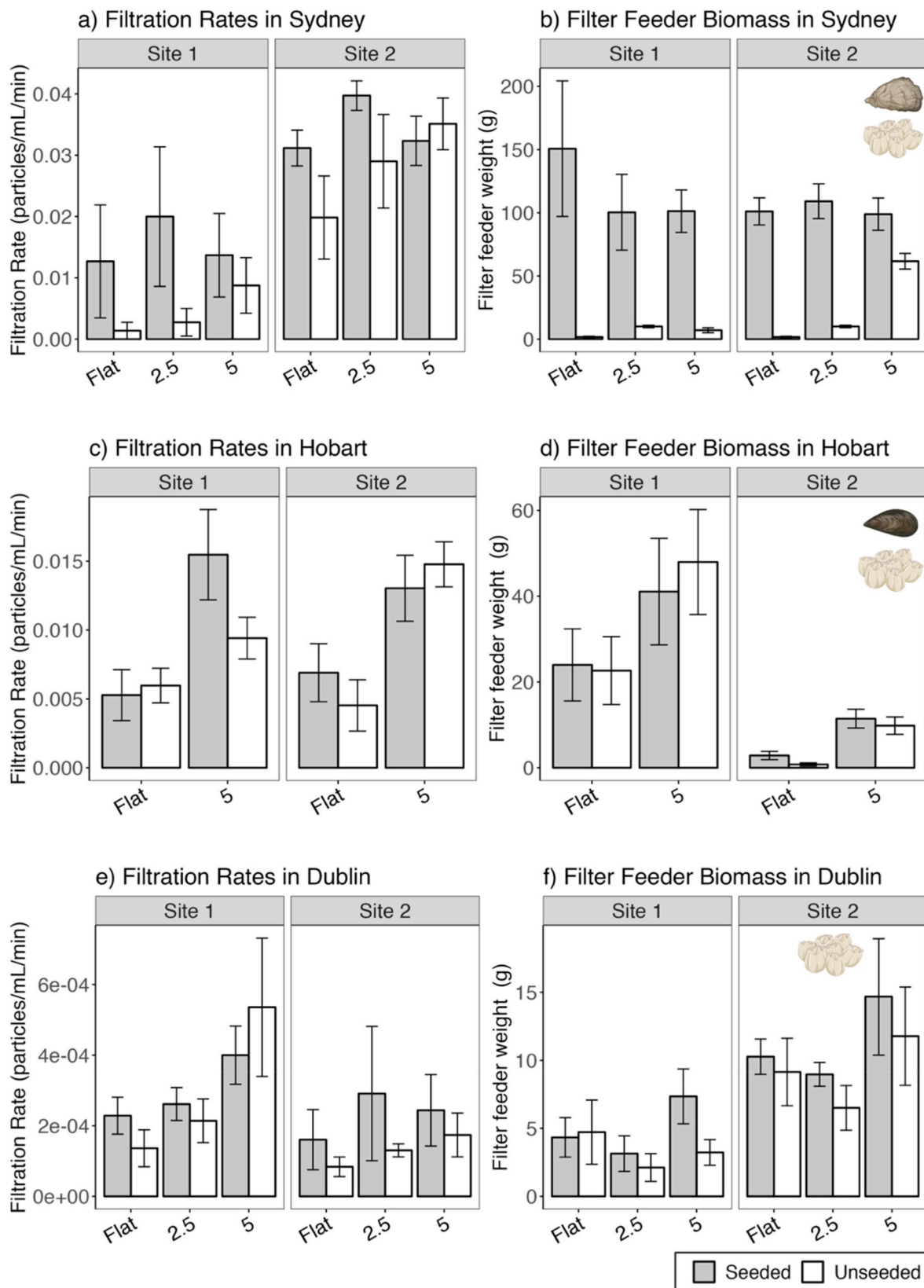


Fig. 3. Mean (\pm SE, N = 5) rate of filtration (particles/mL/min) in a) Sydney, c) Hobart and e) Dublin, and mean (\pm SE) biomass (g) of dominant filter feeders in b) Sydney, d) Hobart and f) Dublin on Flat, 2.5 and 5 cm tiles, seeded with bivalves or not. Flat = Flat tiles; 2.5 = tiles with 2.5 cm high ridges; 5 = tiles with 5 cm high ridges. Rate of filtration is divided by initial particle count. Biomass of dominant filter feeders included weight of oysters and barnacles in Sydney (3 b), mussels and barnacles in Hobart (3 d) and barnacles in Dublin (3f), as indicated by the icons in the corner of each graph. Grey bars = Seeded treatments; White bars = Unseeded treatments. Images created with [BioRender.com](https://www.biorender.com).

Table 3

Summary results from analyses in Sydney, Hobart and Dublin testing how a) filtration rate, b) filtration rate with biomass as a covariate and c) total biomass of filter feeders varied between seeded and unseeded tiles, and between complex and flat tiles. NS = Not Significant; N/A = Not Applicable; given interaction factor was significant, * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.0001$.

	Filtration – No biomass	Filtration – With Biomass	Filter feeder Biomass
SYDNEY			
Complexity	NS	NS	N/A
Seeding	*	NS	N/A
Site	***	***	NS
Biomass	–	*	–
Complexity × Seeding	NS	NS	***
Complexity × Site	NS	NS	**
Seeding × Site	NS	NS	**
Complexity × Seeding × Site	NS	NS	**
Post-hoc	Site 2 > Site 1 Seeded > Unseeded	Site 2 > 1 Filtration increased with biomass	Seeded > Unseeded Seeded: 5 = 2.5 = Flat Unseeded: 5 = 2.5 > Flat
HOBART			
Complexity	***	***	N/A
Seeding	NS	NS	NS
Site	NS	NS	N/A
Biomass	–	NS	–
Complexity × Seeding	NS	NS	NS
Complexity × Site	NS	NS	**
Seeding × Site	NS	NS	NS
Complexity × Seeding × Site	NS	NS	NS
Post-hoc	5 cm > Flat	5 cm > Flat	Site 1: 5 cm > Flat Site 2: 5 cm > Flat
DUBLIN			
Complexity	*	NS	*
Seeding	NS	NS	NS
Site	*	*	***
Biomass	–	NS	–
Complexity × Seeding	NS	NS	NS
Complexity × Site	NS	NS	NS
Seeding × Site	NS	NS	NS
Complexity × Seeding × Site	NS	NS	NS
Post hoc	5 > Flat Site 1 > Site 2	Site 1 > Site 2	5 > 2.5 5 = Flat Flat = 2.5 Site 2 > Site 1

(Fig. 5d; Table 5; Table S15). However, we did find more cryptobenthic fish (i.e., greater MaxN) on 5 cm tiles than on flat tiles in Sydney (Fig. 5a; Table 5; Table S14).

4. Discussion

Greening of the grey approaches are increasingly used to enhance the biodiversity of infrastructure (Strain et al., 2018; Oral et al., 2020). Few studies have, however, assessed whether GGI influences the ecological functions that underpin key ecosystem services, including habitat provision for cryptobenthic fish. Furthermore, the few assessments on functions have generally been done within similar environmental contexts, e.g. within Sydney Harbour (e.g. Vozzo et al., 2021; Mayer-Pinto et al., 2023), such that their generality across different environmental conditions is unclear. Here, we tested how enhancement of physical (topographic) and biogenic (through seeding) complexity influences functional processes on marine infrastructure spanning six locations and

Table 4

Summary from generalised linear models testing the effects of physical complexity; 3 levels: flat, 2.5 cm, 5 cm for Dublin and Plymouth, and 2 levels: flat and 5 cm for Hobart) or seeding (2 levels: seeded, unseeded) and site (2 levels: site 1, site 2) on total cover of macro-algae, community respiration (CR), Net Primary Production (NPP) and Gross Primary Production in Hobart, Dublin and Plymouth. NS = Not Significant; N/A = Not Applicable; given interaction factor was significant, * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.0001$.

	Macro-algae	CR	NPP	GPP
HOBART				
Complexity	N/A	*	NS	**
Seeding	N/A	NS	NS	NS
Site	N/A	***	***	**
Complexity × Seeding	N/A	NS	NS	NS
Complexity × Site	N/A	NS	NS	NS
Seeding × Site	N/A	NS	NS	NS
Complexity × Seeding × Site	**	NS	NS	NS
Post-hoc	Site 2 Flat seeded, 2.5 cm seeded, 2.5 cm unseeded; 5 cm unseeded > 5 cm seeded	5 cm > Flat Site 2 > Site 1	Site 2 > Site 1	Flat > 5 cm Site 1 > Site 2
DUBLIN				
Complexity	NS	**	NS	NS
Seeding	NS	NS	NS	NS
Site	NS	NS	NS	NS
Complexity × Seeding	NS	NS	NS	NS
Complexity × Site	NS	NS	NS	NS
Seeding × Site	NS	NS	NS	NS
Complexity × Seeding × Site	NS	NS	NS	NS
Post-hoc		5 cm > Flat 5 cm > 2.5 cm Flat = 2.5 cm		
PLYMOUTH				
Complexity	NS	NS	NS	NS
Seeding	NS	NS	NS	NS
Site	***	NS	NS	NS
Complexity × Seeding	NS	NS	NS	NS
Complexity × Site	NS	NS	NS	NS
Seeding × Site	NS	NS	NS	NS
Complexity × Seeding × Site	NS	NS	NS	NS
Post-hoc	Site 1 > Site 2			

three continents across which marine colonists differed (see Strain et al., 2021). Despite biological and environmental differences among the locations, the meta-analyses showed some common effects of the manipulations. This result corroborates previous research in showing that habitat complexity can, at least over short time scales, affect ecosystem functions, and that these changes may not be directly dependent on species identity (Mayer-Pinto et al., 2023).

The meta-analyses showed that across locations, filtration rates increased with both physical complexity individually and physical complexity combined with seeding with bivalves. There is growing stakeholder demand for GGI solutions to provide a range of outcomes besides increased biodiversity, such as improvement of water quality (Evans et al., 2017). Interventions that can increase the biomass of filter-feeders, thus increasing local filtration rates, have the potential to improve water quality through the removal of particles and contaminants from the water column (Ostroumov and Widdows, 2006; Beck et al., 2011; Hawkins et al., 2020). Nonetheless, it is important to assess how these increased rates can influence other important factors such as

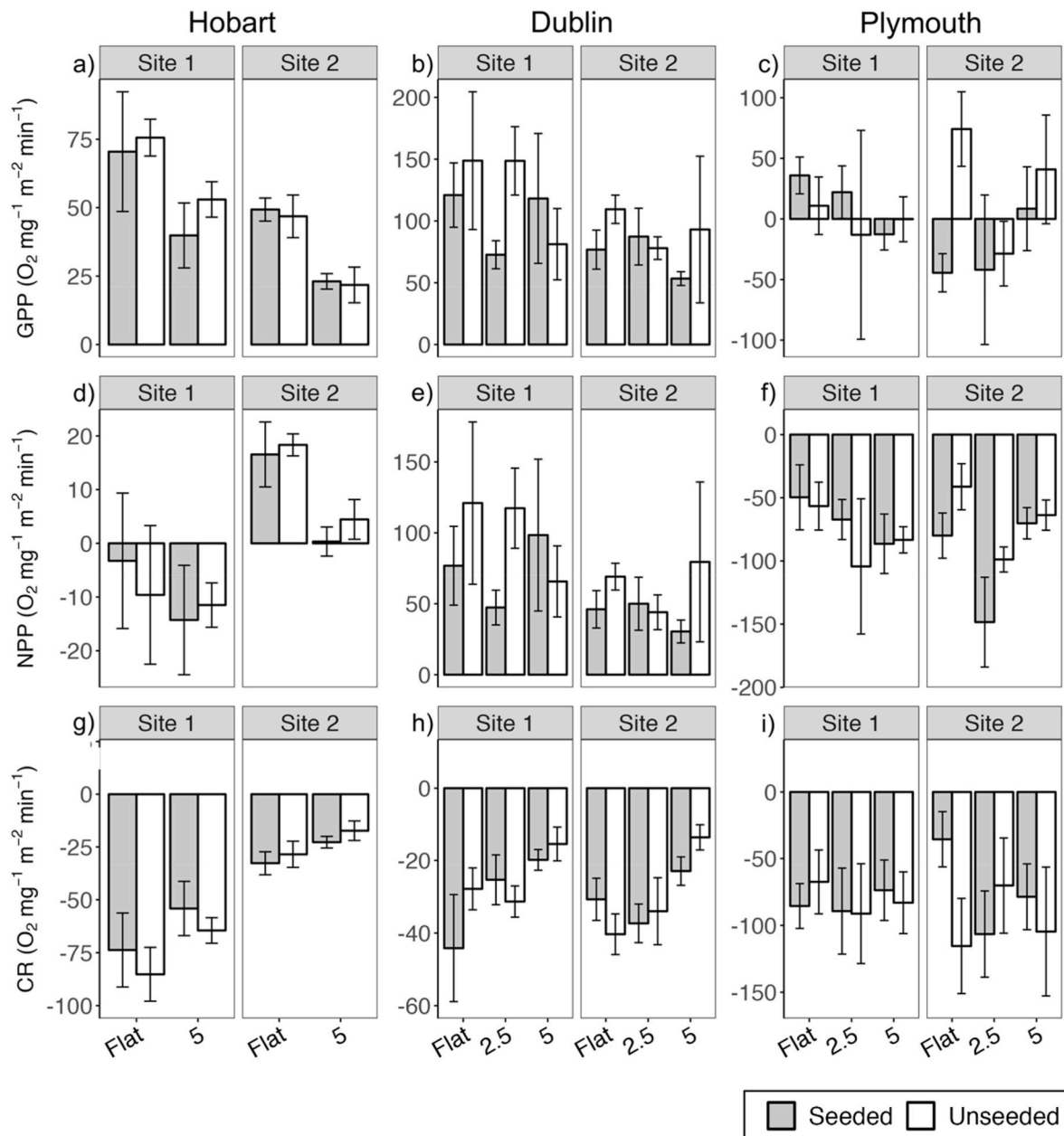


Fig. 4. Mean (\pm SE, $N = 5$) rates of Gross Primary Productivity ($\text{O}_2/\text{mg}/\text{m}^2/\text{min}$) (a, b, c), Net Primary Productivity ($\text{O}_2/\text{mg}/\text{m}^2/\text{min}$) (d, e, f) and Community Respiration ($\text{O}_2/\text{mg}/\text{m}^2/\text{min}$) in Hobart, Dublin and Plymouth on complex and flat tiles, seeded with bivalves or not. Note that axis scale is not consistent between graphs due to the wide range in values measured. Flat = Flat tiles; 2.5 = tiles with 2.5 cm high ridges; 5 = tiles with 5 cm high ridges. Grey bars = Seeded treatments; White bars = Unseeded treatments.

nutrient cycling and species richness, as filter-feeders can also filter propagules and/or larvae (Malerba et al., 2019). Future studies could also assess how changes in the biomass of bivalves modify biodeposits in the sedimentary habitats adjacent to seawalls as those can also have important consequences for the nearby habitats.

Differences among treatments within each location could be due to differences in aspects of the abiotic environment that influence filtration, such as temperature and particle size distribution (Jørgensen et al., 1990; Newell et al., 2001) and/or the identity and biomass of filter feeders that subsequently recruited into the tiles (Comeau et al., 2008; Richard et al., 2022). Such differences corroborate previous results that while one type of manipulation might be successful at one place, this is not necessarily true for other places/environments (e.g. O'Shaughnessy et al., 2021; Strain et al., 2021). In Dublin, Hobart, and Plymouth, where no effects of seeding were seen, most of the seeded mussels fell off or

died during the experiment resulting in a reduced efficacy of the seeding treatment. In the future, similar studies using mussels should facilitate natural attachment of these animals to tiles using byssal threads rather than gluing individuals. Nevertheless, the reduced efficacy of the seeding treatment may be compounded as seeding can provide chemical cues and/or biological conditions that facilitate additional recruitment of conspecifics from the wild (Seed, 1969). In Sydney, where there was significantly higher filter feeder biomass on seeded than on unseeded tiles, and subsequent natural recruitment of oysters (Strain et al., 2020), we found increasing filtration rates with increasing biomass of filter-feeders. Dublin and Hobart are also cooler climates than Sydney and the tiles were seeded with mussels from the genus *Mytilus* as opposed to *Saccostrea* oysters. Previous studies have shown, for example, that increased temperatures can increase the rates of filtration of the clam *Anomalocardia flexuosa* (Carneiro et al., 2020) and that different

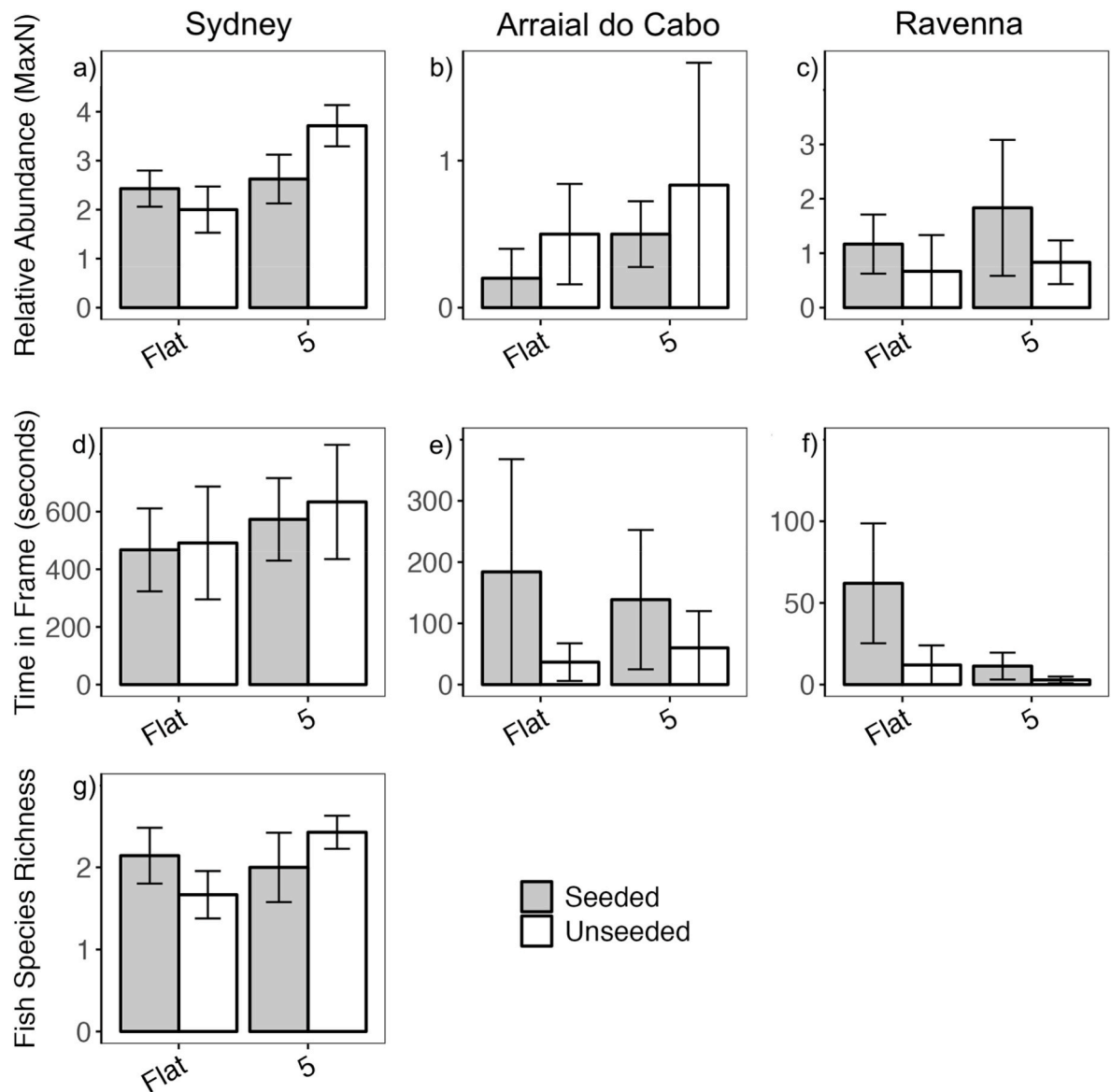


Fig. 5. Mean (\pm SE) MaxN (a, b, c), Time in Frame (d, e, f) and species richness (g) in Sydney, Arraial do Cabo and Ravenna, on complex and flat tiles, seeded with bivalves or not. Flat = Flat tiles; 5 = tiles with 5 cm high ridges. Grey bars = Seeded treatments; White bars = Unseeded treatments. N = 7–9 for each treatment in Sydney; in Arraial do Cabo, N = 6, except for flat seeded tiles where N = 5 and in Ravenna, N = 6, except for flat unseeded where N = 3.

Table 5
Linear models testing for the interactive effects of complexity (2 levels: flat and 5) or seeding (2 levels: seeded or unseeded) on Time in Frame (seconds) and MaxN for all sites and fish species richness for Sydney only. NS = not significant; N/A = not applicable; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.0001$.

	Time in Frame	MaxN	Species Richness
SYDNEY			
Complexity	NS	*	NS
Seeding	NS	NS	NS
Complexity x Seeding	NS	NS	NS
Post-hoc		5 cm > Flat	
RAVENNA			
Complexity	NS	NS	
Seeding	NS	NS	
Complexity x Seeding	NS	NS	
ARRAIAL DO CABO			
Complexity	NS	NS	
Seeding	NS	NS	
Complexity x Seeding	NS	NS	

species of bivalves can have different filtration rates, with e.g. the oyster *Crassostrea virginica* clearing significantly fewer particles than the blue mussel *Mytilus edulis* (Comeau et al., 2008).

Meta-analyses looking at the effect sizes between treatment tiles (with added physical and/or biogenic complexity) vs. control tiles (Flat unseeded) across locations showed that tiles with 5 cm ridges that had been seeded with bivalves were the treatment that significantly influenced the most functional variables across locations. Seeding by itself, had no effects on the productivity (gross and net) or respiration rates of assemblages on tiles, regardless the type of tile (i.e., flat, 2.5 cm or 5 cm). Across all locations, increasing physical complexity decreased productivity (both GPP and NPP) of assemblages, with the biggest, significant, decreases seen on the 5 cm seeded tiles. Interestingly, this finding does not reflect patterns of the percentage cover of macro-algae found here, suggesting that more subtle effects or complex interactions are happening (see e. g discussion in Mayer-Pinto et al., 2023).

We found that respiration rates (CR) of assemblages on tiles in some instances increased with physical complexity and/or seeding, consistent with Mayer-Pinto et al. (2023). This is likely due to the greater cover of

sessile invertebrates in more complex habitats (Strain et al., 2021; Vozzo et al., 2021; Mayer-Pinto et al., 2023). Effects of increasing physical complexity on productivity and respiration of assemblages, however, varied markedly among locations. In Plymouth, for example, we found no effects of complexity on any of the studied functional variables, most likely due to no significant differences in assemblages among tile types (Strain et al., 2021), while in Hobart and Dublin we found increased respiration rates on 5 cm tiles compared to flat tiles, regardless of whether they had been seeded or not. Although experiments here were done at relatively small scale (centimetres to metres), large scale interventions using similar concepts are being increasingly done across the globe (Sawyer et al., 2020; Bishop et al., 2022). Thus, results from this study provide key information for managers. Our results support the growing assertion that the magnitude and, in some instances, even the direction of effects of habitat complexity on benthic assemblages varies across environmental settings (Hsiung et al., 2020; O'Shaughnessy et al., 2021; Strain et al., 2021; Clifton et al., 2022). Therefore, it is important for managers and relevant stakeholders to have clear goals for GGI interventions and local knowledge of the system being manipulated (Mayer-Pinto et al., 2017).

The number and abundance of cryptic fish species found on tiles was, apart from in Sydney, extremely low (1–2 species). Consequently, it is unsurprising that effects of complexity on fish abundance and habitat occupation were few. Although there was a trend of lower interaction time of cryptobenthic fish species on unseeded tiles compared to seeded ones (i.e., time spent in frame) in both Ravenna and Arraial do Cabo, these differences were not significant. In Sydney, where we found a total of nine species of cryptobenthic fish, there were significantly greater abundances (MaxN) of these fishes on physically complex tiles (i.e., 5 cm) compared to flat ones, but we found no effects of physical complexity or seeding on time in frame. A study that looked at effects of water retaining features (flowerpots) on seawalls found no differences in the density of benthic fish between flowerpots and controls (Morris et al., 2017), however, Ushima et al. (2019) did find that cryptobenthic fish, such as those found in Sydney, interacted more with physically complex tiles. Recent work also suggested that the structure of the fish assemblages associated with artificial habitats could be strongly influenced by the nature of the surrounding habitat (e.g. dominance of sedimentary vs rocky natural habitats), so it is possible that effects of GGI could be greater in some habitat settings than others (Franzitta and Airolidi, 2019; Komyakova and Swearer, 2019). Moreover, given that cryptobenthic fish are often territorial and thus only 1–2 individuals would occupy the same tile, further studies with greater replication and done in areas with different habitat settings and higher diversity of fish would greatly enhance our understanding on how eco-engineering influence assemblages of cryptobenthic fish and their habitat use, and how these, in turn, might influence functions such as productivity.

Well managed urban ecosystems can support rich biodiversity and provide essential ecosystem services such as clean air and water (Haase et al., 2014; Elmqvist et al., 2015), but more often, urbanisation results in impacts including loss of habitat and biodiversity as a consequence of fundamental modification of the physical habitat (Alberti, 2005; McKinney, 2006; Shen et al., 2008). Given that marine infrastructure has a significant footprint in many urbanised estuaries, modifying in some cases more than 50% of coastlines (Chapman and Bulleri, 2003; Gittman et al., 2015), GGI interventions can be an effective way to improve the overall health of these ecosystems.

GGI practices involving increasing habitat complexity either through changes in the physical substrata or biogenically (e.g., seeding with macro-algae or bivalves) are increasingly being applied in marine environments as efforts to mitigate effects of construction on these ecosystems (Firth et al., 2016; Bishop et al., 2022). Although there is strong evidence that adding complexity to coastal built infrastructure often increases overall biodiversity, we found that such manipulations are likely to have trade-offs among potentially desired functions, such as productivity and filtration rates. Ours and previous results (Mayer-Pinto

et al., 2023) suggest that increasing physical complexity can often decrease productivity (GPP and NPP) of habitats, but increase filtration rates (see also Vozzo et al., 2021). Therefore, if the main objective of GGI is, for example, to increase local productivity to attract some species of fish, a more appropriate manipulation might be seeding the infrastructure with native seaweeds rather than increasing the physical complexity of the substrate. Conversely, where managers want to improve local water quality, they might consider the latter or seeding with local bivalves.

5. Conclusions

A robust evaluation of the potential trade-offs arising from interventions that incorporates consultations with different stakeholders, including First Nations people (Porri et al., 2023), is needed to assess both potential risks and benefits of GGI and inform managers so interventions can be implemented at large scales. Nevertheless, we found clear differences in the potential benefits of GGI across locations. Thus, it is important to re-emphasise that such manipulations should not be blindly and uniformly applied without local, expert knowledge, and that there is no silver bullet to mitigate effects of marine construction (Firth et al., 2020; Airolidi et al., 2021).

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Research data

Data and code used for this manuscript are publicly available through Mendeley Data, DOI: 10.17632/sggzrtf5dz.1.

CRediT authorship contribution statement

Mariana Mayer-Pinto: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Amelia Caley:** Data curation, Formal analysis, Writing – review & editing. **Antony M. Knights:** Funding acquisition, Investigation, Methodology, Writing – review & editing, Conceptualization. **Laura Airolidi:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Melanie J. Bishop:** Conceptualization, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Paul Brooks:** Data curation, Investigation, Methodology, Writing – review & editing. **Ricardo Coutinho:** Data curation, Funding acquisition, Investigation, Writing – review & editing. **Tasman Crowe:** Data curation, Funding acquisition, Writing – review & editing. **Paolo Mancuso:** Data curation, Investigation, Methodology, Writing – review & editing. **Lais P.D. Naval-Xavier:** Data curation, Investigation, Methodology, Writing – review & editing. **Louise B. Firth:** Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Rafael Menezes:** Data curation, Investigation, Methodology, Writing – review & editing. **Luciana V.R. de Mesiano:** Data curation, Investigation, Methodology, Writing – review & editing. **Rebecca Morris:** Investigation, Methodology, Writing – review & editing. **Donald J. Ross:** Data curation, Supervision, Writing – review & editing. **Joanne X.W. Wong:** Data curation, Investigation, Methodology, Writing – review & editing. **Peter Steinberg:** Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. **Elisabeth M.A. Strain:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

We only found two fish cryptobenthic species in Arraial do Cabo (*Scartella cristata* and *Parablennius pilicornis*, Table S17) and one in Ravenna (*Parablennius incognitus*, Table S18). The most abundant species in Arraial do Cabo, Brazil, was the molly miller blenny *Scartella cristata* (Table S17). Contrary to Sydney, there were no effects of complexity (physical or biogenic) on MaxN in either Arraial do Cabo (Fig. 5b–Table 5; Table S14) or Ravenna (Fig. 5c–Table 5; Table S14). Similar to Sydney, there was no effect of physical or biogenic complexity on the total time in frame (Fig. 5e and f; Table 5; Table S15).

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2024.120370>.

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