


RESEARCH ARTICLE

Physical and biogenic complexity mediates ecosystem functions in urban sessile marine communities

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Abstract

1. The influence of habitat complexity on biodiversity is a central theme in ecology, with many studies reporting positive relationships. Reconciliation approaches in urbanised areas, such as eco-engineering, have increasingly focused on 'rebuilding' the complexity of degraded and/or homogenised habitats to support biodiversity. Yet, the effects of increasing complexity and biodiversity on ecological functions are rarely measured.
2. We assessed how increasing the physical and/or biogenic complexity of habitats affects the net primary productivity (NPP) and gross primary productivity (GPP), community respiration and nutrient cycling (specifically dissolved inorganic phosphorus and nitrogen) of intertidal sessile marine communities at three sites. We manipulated physical complexity using two types of settlement tiles: 'complex', with crevices and ridges, and 'flat'. We increased biogenic complexity on half the replicates of each tile type by seeding with oysters.
3. Increased physical and biogenic complexity resulted in greater sessile species richness at all sites. Although many variables assessed varied with sites and time of measurements, overall, GPP and NPP were greater on flat tiles than on complex ones. These patterns were not explained by differences in the total surface area of tiles.
4. Daily flux rates of dissolved inorganic phosphorus had a significant positive relationship with biogenic complexity. There were no effects of biogenic or physical complexity on the net fluxes of dissolved inorganic nitrogen.

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5. Effects of habitat complexity on the productivity and nutrient cycling of marine sessile communities were largely unrelated to diversity measures, such as richness or abundance of key taxa and functional groups.
6. *Synthesis and applications.* Eco-engineering practices that manipulate habitat complexity might benefit from explicit functional targets that also consider associated ecosystem services, as we found that under some conditions there is a trade-off between biodiversity and functional targets. Our results suggest that increasing habitat complexity has a positive effect on sessile species richness, but not necessarily on productivity (GPP and NPP). The species pool available as well as light availability is likely to mediate effects of complexity on assemblages, so local environment needs to be a key consideration when designing interventions.

KEYWORDS

artificial structures, coastal management, coastal systems, eco-engineering, ecosystem functioning, habitat complexity, habitat-formers, urban infrastructure

1 | INTRODUCTION

The complexity of habitats and how this affects ecological communities has long been a key interest in ecology (MacArthur & MacArthur, 1961; Matias et al., 2010). The ecological effects of habitat complexity have become particularly relevant in the Anthropocene era, when human activities have often homogenised and simplified habitats across the globe, causing declines in biodiversity and changing ecosystem functioning (Fahrig, 2003; McKinney, 2006; Rogers et al., 2014). Urbanisation is a key driver of habitat homogenisation (McKinney, 2006), transforming, for example, forests and other natural ecosystems into cities, where urban infrastructure replaces ecological habitats, and the few green spaces lack habitat complexity (Byrne, 2007). As a result, reconciliation efforts (i.e. modifying human-dominated ecosystems; sensu Rosenzweig, 2003), such as eco-engineering, are increasingly aimed at enhancing biogenic complexity in urban habitats to enhance biodiversity and ecological functioning in degraded systems (Airoldi et al., 2021; Firth et al., 2016; Miller & Hobbs, 2007). Nevertheless, most studies have focused solely on assessing the effects of eco-engineering interventions on biodiversity (Block et al., 2001; Evans et al., 2016; Suding, 2011), with the implications for desired ecosystem functioning being inferred, rather than directly measured (Johnston, Mayer-Pinto, & Crowe, 2015). However, the direct translation of increased biodiversity to functional change in urban ecosystems can lead to errors (Johnston, Mayer-Pinto, & Crowe, 2015; McMahon et al., 2012) and is currently mostly speculative as we have limited knowledge of the relationships between biodiversity and functioning in an urban context (Mayer-Pinto, Dafforn, et al., 2018). Consequently, there remains a lack of empirical data on how the addition of habitat complexity by eco-engineering efforts influences critical ecosystem functions, such as productivity and nutrient cycling. This can limit the effectiveness of coastal management strategies, if increasing habitat

complexity through eco-engineering does not translate to desired changes in key functions.

The addition of habitat complexity involves manipulating the structural components of habitats (i.e. structural complexity) and the relative abundance of different structural components (i.e. the heterogeneity of habitats) (Downes et al., 1998; McCoy & Bell, 1991). Habitat complexity can therefore be influenced by topographic features of the primary physical substratum such as protrusions, crevices and depressions (hereafter simply referred to as physical complexity) or features of the secondary biogenic substrata provided by habitat-forming organisms (hereafter referred to as biogenic complexity). Habitat complexity can influence assemblages by increasing species richness as a function of species-area relationships (Heck Jr & Wetstone, 1977), as well as through the provision of more niches, including microhabitats (Menge & Sutherland, 1976), which allow for coexistence of different species (Schoener, 1974). The physiology, metabolism and/or behaviour of individuals can also be affected by changes in abiotic and/or biotic factors (Cartar & Real, 1997; Mayer-Pinto et al., 2016; Wright et al., 2001). In aquatic systems, habitat complexity can affect water flow with consequences for the performance (e.g. growth and feeding) of suspension feeders such as oysters (Lenihan, 1999). In addition, it can affect the response of organisms and/or assemblages to disturbances (Gosper et al., 2015; Mayer-Pinto et al., 2016) or mediate species interactions, such as predation and competition (Finke & Denno, 2002; Grabowski et al., 2008), by regulating availability of refugia and food (Crowder & Cooper, 1982; Srivastava, 2006; Taniguchi & Tokeshi, 2004). Furthermore, habitat complexity can dictate what sizes of organisms can utilise a habitat (McAbendroth et al., 2005), meaning it can favour particular taxa, life-history stages and/or functional groups over others (Bracewell et al., 2018; Lassau et al., 2005; Scharf et al., 2006).

Physical and biogenic complexity can, thus, affect the functioning of systems through changes in the performance of individual

organisms (Mayer-Pinto et al., 2020; Mayer-Pinto, Cole, et al., 2018; Montalto et al., 2016; Mumby et al., 2011), changes in species richness, abundance and composition (e.g. Matias et al., 2010), or by altering food-webs through top-down or bottom-up changes in trophic levels (or taxa) performing particular functions (McQueen et al., 1989; Srivastava, 2006). For instance, by providing refuge from physical stressors in the intertidal zone, increased physical complexity via the addition of crevices and/or habitat-forming bivalves like oysters can facilitate the colonisation of mobile invertebrates (Jackson, 2009), including grazers (Klein et al., 2011). This may then decrease the richness, abundance and/or composition of macroalgae (Underwood, 1980), ultimately affecting the primary productivity of these habitats (Griffin et al., 2010). Alternatively, oysters themselves can serve as a substrate, providing additional space and/or nutrients for the settlement, development and growth of micro and macro-algae (e.g. Bracken, 2004), which may then counteract possible negative effects of grazers, resulting in either no net changes, or increased primary productivity. Therefore, changes in the number and composition of species and/or key groups might not be readily translated to corresponding changes in ecosystem functioning.

This is further complicated when increased habitat complexity is achieved through the addition of habitat forming species (biogenic complexity), since some species that contribute to physical complexity can also influence the functioning of systems in other non-structural ways. Examples include the provision of food (Nielsen, 1974; Steneck et al., 2002) and nutrients to the system via waste products in the case of bivalves (Commito & Boncavage, 1989), and detritus in the case of primary producers (Moore et al., 2004). Furthermore, increases in complexity via the addition of habitat-forming species such as bivalves can affect the functioning of systems, not only by modifying biological communities (as described above), but also due to the biological functions that the added organisms themselves perform. Oysters are likely to influence habitat function through their feeding and metabolism, such as ammonia excretion and respiration (Boucher & Boucher-Rodoni, 1988) and by accelerating mineralisation of organic substances (Ostroumov & Widdows, 2006). Therefore, for a given area, eco-engineering strategies that involve increasing biogenic and physical complexity may be more effective in increasing particular ecosystem functions compared to strategies that focus solely on physical complexity.

Here, we assessed how increasing habitat complexity through the manipulation of both physical and biogenic complexity by adding crevices and ridges and/or oysters to settlement tiles (see Strain et al., 2020; Ushima et al., 2019) influences the functioning of sessile marine assemblages. Such manipulations are commonly done in small-scale eco-engineering interventions aiming to increase the biodiversity and ecological functioning of artificial habitats, such as seawalls, in urbanised coastal areas worldwide (Chapman & Underwood, 2011; Loke & Todd, 2016; Strain et al., 2020, 2021). However, functional outcomes of these interventions, such as changes in productivity and nutrient cycling, have rarely been measured (Vozzo et al., 2021). Determining which ecological intervention

strategies provide the largest increases in ecosystem function per unit, such as productivity, can be used by managers to assess the most cost-effective ways to increase desired functions.

We hypothesised that enhancing the physical and biogenic complexity of tiles would have an interactive effect on the functions of the colonising assemblages, whereby tiles with both forms of complexity would have the highest rates of primary productivity and community respiration (CR) compared to tiles with a single form of, or lacking, complexity. We expected that these patterns would be related to the richness and abundance of sessile species/functional groups that colonised the tiles. Previous studies that added biogenic and physical complexity to seawalls found greater diversity overall on complex seeded tiles (Strain et al., 2020; Vozzo et al., 2021). Moreover, we predicted that increased species richness would increase the efficiency by which organisms assimilate inorganic resources as suggested by previous studies (see e.g. Cardinale et al., 2011), leading to a higher uptake of inorganic nutrients (i.e. being sinks of inorganic nutrients). Associated with this, we expected greater effluxes of inorganic nitrogen and phosphorus on tiles seeded with oysters than on unseeded tiles.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

Eco-engineering interventions in marine systems are commonly undertaken on seawalls, which often are less complex than natural habitats such as rocky shores and support less biodiversity (Bulleri & Chapman, 2010; Chapman, 2003). Therefore, three vertical seawalls in Sydney Harbour, Sydney, Australia, were selected as experimental sites: Illoura Reserve (33°51'29.7"S, 151°11'46.7"E), Sawmillers Reserve (33°50'45.1"S, 151°12'05.9"E) and Clarke's Point Reserve (33°50'34.7"S, 151°10'27.4"E; Figure S1). Sites were located 1.5–3.0 km apart. All sites have vertical sandstone seawalls and are subjected to the same tidal levels (~2 m). All three sites are in the inner part of the Harbour (west of the Harbour Bridge; Johnston, Mayer-Pinto, Hutchings, et al., 2015) and are all relatively sheltered, but Illoura Point seawall receives the most waves from boating activity, while Clarke's receives the lowest. In addition, seawalls at Illoura Reserve and Clarke's Point face east, while the seawall at Sawmillers faces south-west and is shaded by tree canopy above the seawall, so is therefore less exposed to direct sunlight. Mean temperatures recorded at all three sites for 6 months during the period of the study were ~17°C at each site (Table S1). Maximum temperatures recorded varied from 36.7°C at Clarke's to 33.0°C at Illoura Reserve, and minimum temperatures at all sites were approximately 8°C (Table S1). Concrete tiles were deployed at each site in the low intertidal zone (0.2–0.4 m below Mean Low Water Springs; MLWS). Physical complexity was manipulated by adding complex tiles with crevices and ridges (increased physical complexity) or by adding flat tiles (no physical complexity) to the seawall. On half of the tiles, we further increased complexity by attaching ('seeding') the live native

oyster *Saccostrea glomerata* (i.e. biogenic complexity) before deployment. We had a complete orthogonal design with four treatments: complex tiles with and without oysters (seeded and unseeded, respectively), and flat tiles with and without oysters (seeded and unseeded, respectively). Concrete tiles were made using 3D-printed moulds designed by Reef Design Lab (Melbourne, Australia). Tiles with ridges and crevices (hereafter referred to as complex tiles) (250×250×50mm) had 17–65mm wide ridges of 5 cm height, each separated by 15–50mm wide crevices (see Strain et al., 2018). Flat tiles were 250×250×20mm, made from the same concrete. Oysters were attached in clusters on both the ridges and crevices of complex tiles and on flat tiles (Figure S2A) and were sourced from stock cultivated at the Port Stephens Fisheries Institute. The oysters were 2 months old and had an average length of 4.6 cm ± 0.6 cm. Oysters were glued onto tiles using epoxy (Megapoxy®, Vivacity Engineering Pty Ltd). This epoxy has been used previously and shown to be non-toxic (e.g. Bugnot et al., 2015). The surface area of each tile including the main face and sides was 0.0825 m² for flat tiles and 0.174 m² for complex tiles. An area of 0.0242 m² was seeded with oysters on the flat and complex tiles. Each treatment had nine replicate tiles at each of the three sites (i.e. 36 tiles at each site, totalling 108 tiles). Tiles were fastened to the seawalls with anchor bolts in March (2016). Primary production and CR rates of tiles deployed at all three locations were measured twice, in November and December 2016 (Austral summer). Rates of inorganic nutrient fluxes between the tiles and the water column were measured once at one site (Illoura Reserve) in December (2016). Biological diversity of tiles was assessed in situ once, in October 2016 (i.e. 1 month prior to first functional measurements). Ethics approval was not required for this study, as only sessile invertebrates were studied. Field work was carried out under the scientific collection permit no. P13/0007-2.0 from the Department of Primary Industries, NSW, Australia.

2.2 | Biodiversity assessment and functional measurements of tiles

The sessile assemblages and species richness on tiles were assessed with photographs in October 2016, after 7 months of deployment. Percentage cover of sessile organisms on tiles was assessed by overlaying a grid with 100 point-intersections using the software CoralNet (Lozada-Misa et al., 2017). Using the methodology described above, the same area of the tile (i.e. 25 cm × 25 cm) was assessed for biodiversity measurements regardless of tile treatment. Organisms were identified to the lowest possible taxonomic level. Since these were non-destructive samples, and there were no large mobile invertebrates observed (e.g. sea-urchins, sea stars, chitons) the richness and abundances of small mobile invertebrates were not assessed because these could not be easily identified through photos. Furthermore, although mobile species were not actively removed from the tiles before incubations, the retrieval and transport of tiles from the field to the laboratory likely resulted in the loss of mobile species (especially mesofauna such as amphipods). We do not

expect small mobile invertebrates (mesofauna) to have substantially influenced our functional measures.

After 8 months of deployment, we measured oxygen and inorganic nutrient flux rates between the water column and the tiles during light and dark conditions using chamber incubations (e.g. Kelaher et al., 2013). Specifically, three replicate tiles of each treatment, from each site, were haphazardly selected and removed from the seawalls. Tiles were then transferred to custom-made chambers (30×30×30cm) for incubations in an outdoor mesocosm under in situ conditions of temperature and light where they were completely submerged to simulate high tide conditions (Figure S2B). Oxygen flux measurements were taken twice (in November 2016 and December 2016), and different replicate tiles were used each time to ensure independent measurements between times. Incubations were done by placing tiles in closed-system chambers. Prior to incubation, tiles were submerged in a flow-through tank for 2–3h with water pumped directly from Rozelle Bay, Sydney Harbour (~1 km from the Illoura Reserve site) for acclimation. Chambers with tiles were then sealed and placed in a water bath supported by a flow-through system directly connected to the harbour to minimise variations in temperature (Figure S2B). To account for diel rhythms in community function, the timing of these incubations corresponded with real-world light/dark cycles. During the light cycles, tiles were incubated as close to midday as possible to standardise potential differences in primary production rates due to time of day. Each light and dark incubation was run over 1.5h with measurements of dissolved oxygen (DO) concentrations taken every 10min during the incubation with HOBOTM DO loggers. Tiles were oriented vertically in the chambers to match high-tide conditions on the seawalls and were oriented in the outdoor mesocosms according to the aspect of the seawall where they had been deployed (i.e. north or south facing). Throughout acclimatisation periods and the following incubations, internal overlying water in each chamber was circulated using small aquarium pumps to homogeneously mix the water column and avoid stratification. After incubations, tiles were carefully re-attached to the seawalls as previously described.

We calculated oxygen fluxes per total surface area (m²) of the primary substratum of each tile type (i.e. complex and flat; μmol m⁻² h⁻¹). Dark and light DO flux rates were calculated by making linear regressions of DO and time, which were then normalised by tile area and chamber volume. Tile gross primary productivity (GPP) was calculated by subtracting dark O₂ flux rates (CR) from net light flux rates (i.e. net primary productivity [NPP], which is the net sum of CR and community productivity during the light cycle (Sutherland et al., 2017)).

For measurements of inorganic nutrient fluxes between tiles and the water column, we collected 30ml water samples at the start and end of each light and dark incubation period. Samples were collected from tiles deployed at Illoura Reserve in December (2016). Samples were filtered through 45 μm cellulose acetate filters (Sartorius Minisart®) into clean polypropylene tubes and immediately stored at -20°C for later dissolved nutrient analysis. Nutrient concentrations were determined by flow injection analysis (Lachat™ QuikChem 8000) at the University of Canberra Ecochemistry Laboratory using standard

methods. Ammonia (NH₃-N) was analysed by the automated phenate method, phosphate (PO₄³⁻-P) by the automated ascorbic acid reduction method and NO_x (nitrite and nitrate) by the automated cadmium reduction method. Reference material used for nutrient analyses was produced at the Ecochemistry Laboratories (Canberra, Australia). This material was cross checked against certified reference materials produced by QLD Health Scientific Services (Queensland, Australia).

The flux of nutrients (F) (μmol m⁻² h⁻¹) was calculated using the following formula:

$$F = ([C_{t1} - C_{t0}] \times V / SA) / T,$$

where C_{t0} = molar nutrient concentration at incubation start (mmol L⁻¹), C_{t1} = molar nutrient concentration at incubation end (mmol L⁻¹), V = volume of overlying water in the chamber (L), SA = total surface area of tile (m²) and T = incubation time (h). Net daily nutrient flux was calculated by averaging nutrient flux rates measured during light and dark incubations (Sutherland et al., 2017).

2.3 | Statistical analyses

Univariate tests for differences in diversity and functional response variables according to manipulation of the physical features of the primary substratum and biogenic features of the habitat were tested with linear models (LMs) or generalised linear models (GLMs), whenever appropriate based on assessment of residuals, using the `lme4` package in R v.4.0.1.

Response variables of diversity included: the total number of species (species richness), the percentage cover of bare space (i.e. no visible macro-organism colonisation), as well as the most abundant individual species or taxa and functional groups among treatments using LM or GLM, whenever appropriate. Since it was not possible to differentiate the individually 'seeded' oysters from those that naturally recruited over time, in all subsequent analyses we included oyster abundance (percentage cover) as a continuous co-variate in the model (biogenic complexity).

Fixed factors were: 'physical complexity' (i.e. complex or flat tiles) and sites; 'biogenic complexity' was included as the percentage cover of oysters (continuous covariate). Three replicate tiles of each treatment at each site were analysed. We treated locations as fixed because of statistical limitations. 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) to calculate variance among levels effectively. If number of levels is low, then random effects are not properly estimated, and it can also lead to convergence problems (Gelman & Hill, 2006; Harrison, 2015). Although we appreciate that this is not necessarily ideal as it means our results cannot be generalised to other sites, it does provide the opportunity to discuss the spatial variability around these patterns. We also tested for two- or three-way interactions between 'physical complexity', 'biogenic complexity' and 'site'. Square root transformations were performed where necessary to improve the model fit

and fulfil model assumptions. We assumed a binomial distribution for the abundance of functional groups and bare space and a normal distribution for total number of species. While Poisson distribution is often more appropriate to use for count data, such as total number of species, the residuals of the model when using a Poisson distribution were very fan-shaped, therefore, to improve residuals, we chose to use a normal distribution for total number of species.

Post hoc comparisons were undertaken using the package `EMMEANS` to identify sources of treatment effects where significant (Lenth et al., 2018). The abundance of primary producers or filter-feeders, when significantly different among treatments, were included as covariates in the models estimating functional variables (described below). This was done to assess whether any functional differences among treatments (e.g. productivity) were influenced by community composition on the tiles using data from matched replicates.

Multivariate analyses were performed to determine whether community patterns (i.e. overall species composition and abundance) followed the same patterns as observed for species richness, functional groups and/or functional variables (e.g. GPP, NPP). We compared assemblage composition (using the lowest taxonomic resolution possible for each taxa) among treatments using permutational analyses of variance (PERMANOVA) with the same design as described above, that is, including 'physical' complexity and 'sites' as fixed factors, and 'biogenic' complexity (as percentage cover of oysters) as a continuous covariate. Analyses used a Bray-Curtis dissimilarity matrix on square-root transformed data, with significance determined from 9999 permutations of the data (Anderson, 2005). Multivariate analyses were done using the 'adonis' and 'pairwise.adonis' functions in the R 'VEGAN' package.

Functional variables analysed were GPP, NPP and CR, normalised per total surface area of tiles. Analyses of net daily metabolism (NDM) are in Supporting Information. The design was similar to described above with 'physical complexity' (i.e. complex or flat tiles), site and sampling time (one or two) as fixed factors and 'biogenic' complexity (as percentage cover of oysters) as a continuous covariate. We also tested for significant interactions among factors. Details of each analysis are described in the relevant tables and in Supporting Information.

For comparisons of nutrient cycling among treatments (performed at one site and sampling time), we used LMs including 'physical' complexity as a fixed factor and 'biogenic' complexity as a continuous covariate. We also tested for a significant interaction between these factors.

3 | RESULTS

3.1 | Effects on diversity

After 7 months of deployment, we found a total of 16 taxa of filter-feeders, including the bryozoan *Watersipora subtorquata*, the barnacles *Megabalanus coccopoma* and *Balanus trigonus*, colonial ascidians such as *Didemnum* sp. and *Botrylloides* sp. as well as oysters (seeded

and recruited), sponges, hydroids and polychaete tube worms. There were 15 taxa of macro-algae (classified as primary producers), including the kelp *Ecklonia radiata*, the green algae *Ulva* spp. and *Codium fragile*, the brown algae *Dictyota* sp., *Sargassum* sp. and *Colpomenia sinuosa*, as well as *Corallina officinalis* and encrusting brown algae, such as *Ralfsia* sp. and other unidentified filamentous and turfing algae. We found the highest species richness at Clarke's and the lowest at Sawmillers. The dominant algae on tiles differed among sites, with *C. officinalis* being the most abundant overall at Illoura Reserve and *Ulva* spp. the most abundant at Clarke's Point Reserve (Figure S3). Among the filter-feeding organisms, besides oysters, the bryozoan *Watersipora subtorquata* was, in general, the most abundant (Figure S3; Table S3). Generally, the abundance of all three taxa decreased with increasing biogenic complexity (Figure S3), though we did find differences among sites and times (Table S3).

Physical and biogenic complexity did not interact to increase sessile species richness (i.e. the total number of species found) as predicted, however, each factor had independent effects on richness. More sessile species occurred on complex tiles, regardless of biogenic complexity ($p = 0.004$; Table 1; Table S2; Figure 1). Similarly, sessile species richness increased with biogenic complexity (i.e. oyster abundance; $p = 0.013$), independently of physical complexity. We found interactive effects of physical and biogenic complexity, as well as site, on the total abundance of primary producers and bare space on tiles (Table 1; Table S2; Figure 1). Overall, we found a negative relationship between primary producers and biogenic complexity (Figure 1; Table S2). Bare space on complex tiles was positively related to percentage cover of oysters (biogenic complexity) at all sites (Table S2; Figure 1), but effects of biogenic complexity on the amount of bare space on flat tiles was only significant at two of the three sites (Clarke's Reserve and Illoura). When comparing the abundance of filter-feeders, excluding oysters, we found an interaction between physical and biogenic complexity as well as effects of sites

(Table 1; Table S2; Figure 1). At Illoura, for example, the abundance of filter-feeders (other than oysters) increased with increasing biogenic complexity on both complex and flat tiles, while at Clarke's, the opposite pattern was found. At Clarke's, there was a negative relationship between abundance of other filter-feeders and biogenic complexity, regardless of the type of tiles. At Sawmillers, there was no effect of biogenic complexity on flat tiles, but we found that, on complex tiles, filter-feeders decreased with increasing biogenic complexity (Table 1; Table S2; Figure 1).

In the multivariate analyses, we found independent effects of physical and biogenic complexity, as well as sites, on the composition and relative abundance of assemblages (Figure S4; Table S4). Results from analyses with untransformed data to account for the presence of rare and dominant species were very similar to analyses with transformed data (data not presented).

3.2 | Effects on functioning

We found an interactive effect of physical and biogenic complexity as well as site on the GPP of tiles ($F_{1,2} = 3.74$; $p < 0.05$; Table 2; Table S5; Figure 2). Although post hoc tests detected significantly greater GPP on complex tiles at Time 1, this was driven by Clarke's, where we found almost double the GPP on complex tiles compared to flat tiles (Table S6). In all other cases (i.e. 5/6 site×time combinations), flat tiles had greater GPP than complex tiles (Table S6; Figure 2). Similarly, only at Clarke's did GPP increase with biogenic complexity on flat tiles (Table 2). However, when the abundance of producers was added as a covariate, GPP increased significantly with increasing biogenic complexity, regardless of sites or whether tiles were complex or flat (Table S7). Similar patterns occurred for NPP, with greater NPP on flat tiles than on complex tiles, except at Clarke's reserve at Time 1 (Table 2; Tables S5 and S6; Figure 2).

TABLE 1 Summary of the main biodiversity results based on the hypothesis regarding the addition of physical (complex vs. flat) and biogenic (oyster seeding) complexity

	Richness	Primary producers	Filter-feeders (no oysters)	Bare space
Physical	*	n/a	n/a	n/a
Biogenic	*	n/a	n/a	n/a
Sites	*	n/a	***	n/a
Physical×Biogenic	ns	n/a	***	ns
Physical×Biogenic×Sites	ns	***	ns	***
Comments	Complex > Flat Increased species richness with increasing biogenic complexity Site effect	Primary producers decreased with biogenic complexity on both complex and flat tiles at all sites	Direction and magnitude of relationship differed between sites	Bare space increased with biogenic complexity on complex tiles at all sites. Effects on flat tiles varied with sites

Please note that only the factors and interactions of main interest (i.e. biogenic×physical and biogenic×physical×site) were included here for simplicity. Full results are found in Supporting Information (Table S2). Richness = total number of species found; primary producers = percentage cover of primary producers; filter feeders = percentage cover of filter feeders, excluding oysters; bare space = percentage cover of bare space; ns = no significant effect. * $p < 0.05$; *** $p < 0.0001$. n/a = not applicable, given interaction factor was significant.

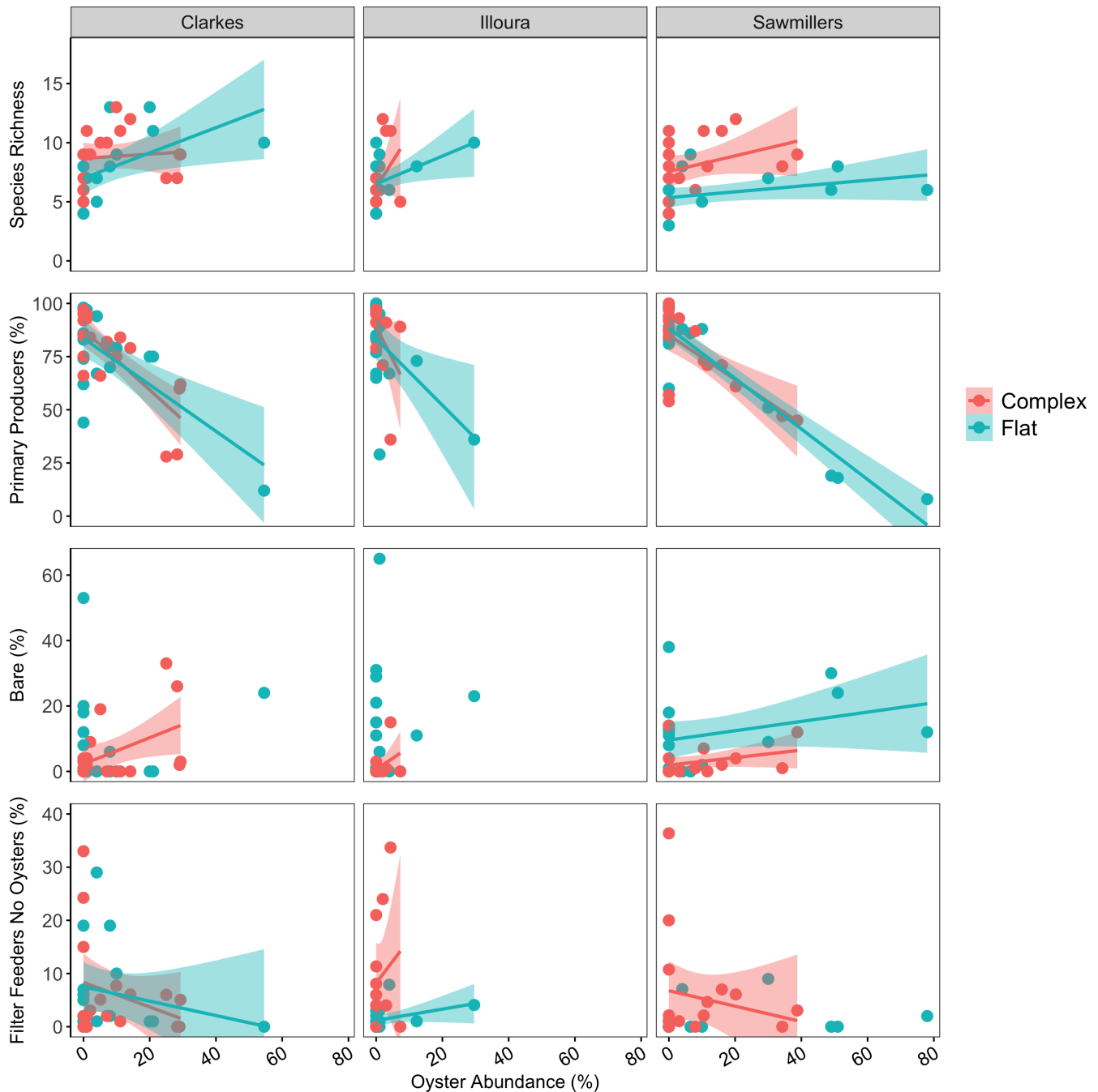


FIGURE 1 Relationship between biogenic complexity (as percentage cover of oysters) and total number of species, percentage cover of primary producers, bare space and filter feeders (excluding oysters) found on complex and flat tiles at each site. Lines are fitted values calculated from the generalised linear model (GLM) for each site (where there was a significant effect of biogenic complexity; $p < 0.05$), and shading represents a 95% confidence interval.

CR rates decreased with increased biogenic complexity on flat tiles at Clarke's Reserve at both sampling times ($F_{1,2} = 4.56$; $p < 0.05$; Table 2; Tables S5 and S6; Figure 2). Almost all functional variables varied across site and sample time (Table 2; Table S5). When considering productivity and respiration rates per tile rather than per unit of surface area, we found significantly greater GPP and NPP on flat tiles than on complex tiles, and the opposite pattern for CR (i.e. greater CR on complex tiles compared to flat tiles). We also found that when standardised per tile unit, CR decreased with

increasing biogenic complexity regardless of physical complexity or site (Table S10; Figure S6).

Dissolved inorganic phosphorus (DIP) net daily flux rates between tiles and the water column had a significantly positive relationship with biogenic complexity (RSS = 426; $p < 0.01$; Table S9; Figure 3). We found that most flat tiles, which also had low biogenic complexity overall, were either neutral or a source of ammonia (NH_4^+), while complex tiles acted mostly as sinks of NH_4^+ , except for one replicate, which also had relatively high biogenic complexity

TABLE 2 Summary of the main functional results based on the hypothesis regarding the addition of physical (complex vs. flat) and biogenic (as percentage cover of oysters) complexity

Complexity	GPP	NPP	CR
Physical	n/a	n/a	n/a
Biogenic	ns	ns	n/a
Sites	n/a	n/a	n/a
Time	n/a	n/a	n/a
Physical × Biogenic	n/a	ns	n/a
Biogenic × Time	ns	ns	ns
Physical × Time	*	*	ns
Site × Time	***	***	**
Physical × Biogenic × Sites	*	ns	*
Biogenic × Site × Time	ns	ns	ns
Comments	<p><i>Clarkes:</i> Flat tiles: GPP increased with increasing biogenic complexity No effect of biogenic complexity for other sites or tiles Time 1: Complex > Flat Time 2: Complex = Flat</p>	<p>TIME 1: Complex = Flat <i>Illoura</i> > <i>Clarkes</i> <i>Illoura</i> > <i>Sawmillers</i> <i>Clarkes</i> = <i>Sawmillers</i> TIME 2: Complex = Flat <i>Clarkes</i> > <i>Sawmillers</i> <i>Illoura</i> > <i>Sawmillers</i> <i>Illoura</i> = <i>Clarkes</i> <i>Clarkes</i>: Time 1 < Time 2 <i>Illoura</i>: Time 1 = Time 2 <i>Sawmillers</i>: Time 1 = Time 2</p>	<p><i>Clarkes:</i> Flat tiles → CR decreased with increasing biogenic complexity No effect of biogenic complexity for other sites or tiles TIME 1: <i>Clarkes</i> = <i>Illoura</i> = <i>Sawmillers</i> TIME 2: <i>Sawmillers</i> > <i>Clarkes</i> <i>Clarkes</i> = <i>Illoura</i> <i>Illoura</i> = <i>Sawmillers</i> <i>Clarkes</i>: Time 1 > Time 2 <i>Illoura</i>: Time 1 = Time 2 <i>Sawmillers</i>: Time 1 = Time 2</p>

Please note that only the factors and interactions of interest (i.e. biogenic × physical and the triple interaction, with sites) were included here for simplicity. Full results can be found in Supporting Information. CR, community respiration; GPP, gross primary productivity; NPP, net primary productivity; all functional variables were standardised by total surface area. Ns, no significant effect. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$. n/a = not applicable, given interaction(s) factor(s) was (were) significant.

(Figure 3). No effects of biogenic or physical complexity were found on the net fluxes of NO_x (Table S9; Figure 3).

4 | DISCUSSION

We empirically assessed how increasing the physical and biogenic complexity of habitats can influence metabolism and nutrient fluxes of urban intertidal assemblages on seawalls. Contrary to our hypotheses, the two forms of complexity did not interact to increase the richness of assemblages, although each factor affected richness independently. More sessile species colonised physically complex tiles than flat tiles and sessile species richness increased with increasing biological complexity (i.e. oyster abundance). Overall, we found that cover of producers decreased with increasing biogenic complexity. The effect of biogenic complexity on filter-feeders (excluding oysters) varied with site. We predicted that productivity and respiration would be enhanced by the combined effects of increasing biogenic and physical complexity; however, our results do not support this prediction. Importantly, we found that effects of complexity on

community productivity (GPP and NPP) and respiration varied with site as well as times of measurement. This suggests that the local environmental conditions and available species pool can mediate the effects of complexity and, therefore, should be a key consideration when devising management interventions, such as eco-engineering.

Increasing the biogenic complexity of tiles through the seeding of oysters had little, if any, effect on rates of productivity (both GPP and NPP), being significant only at one site (Clarke's). Although there was no statistically significant effect of physical complexity on rates of productivity, when measurements were standardised by the total surface area of tiles, flat tiles had, generally, greater GPP and NPP when compared to complex tiles, except at Clarke's Point at Time 1. Overall, we found that diversity measures had clearer, stronger responses to changes in complexity than functional measures when standardised per the total surface area of tiles. However, effects of complexity on functional measures were clearer when considering tiles as a unit, that is, considering the same surface area for both types of tiles (complex and flat). In such cases, we found greater GPP and NPP on flat tiles, regardless of biogenic complexity or site of deployment and no effects of biogenic complexity. We also found

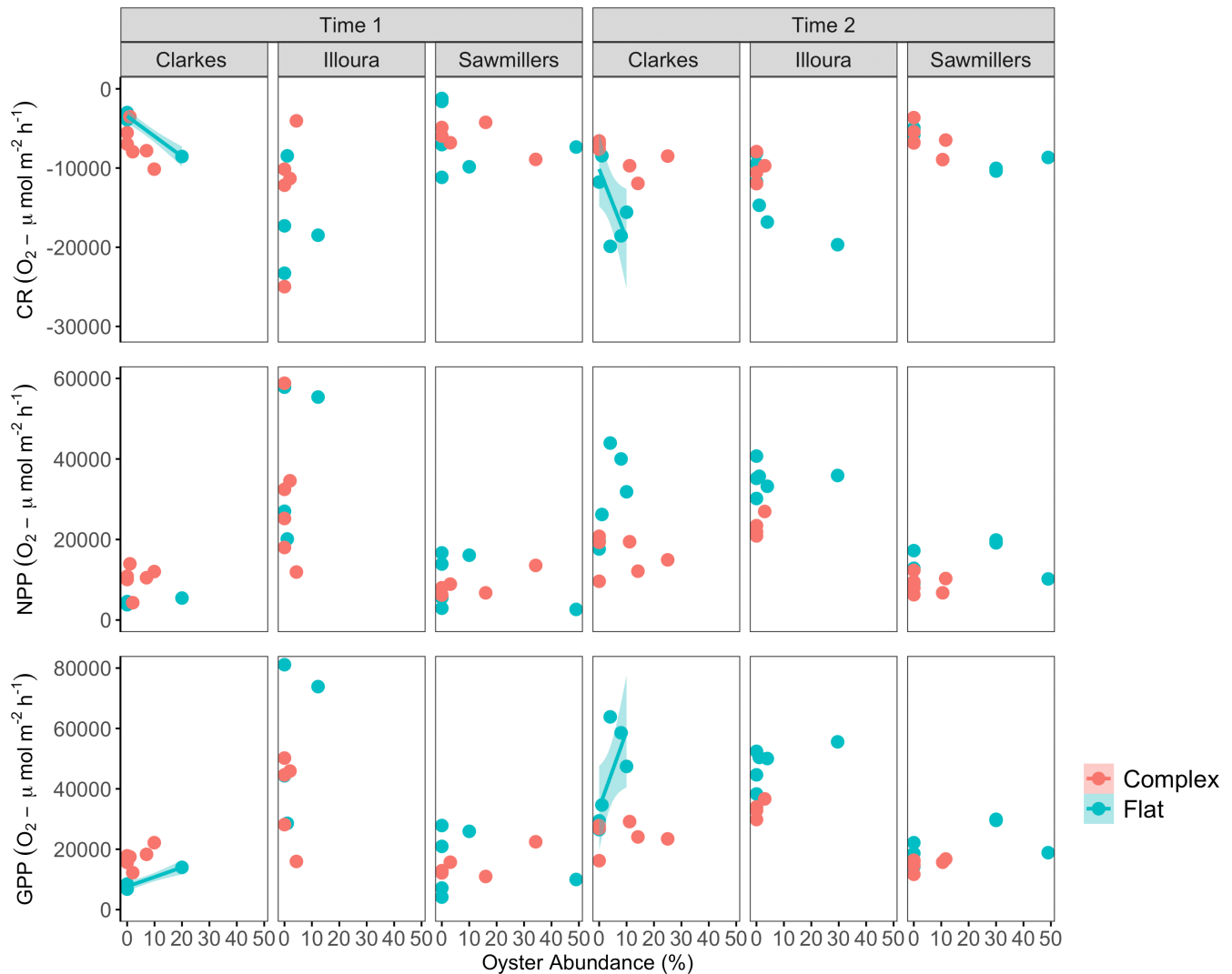


FIGURE 2 Relationship between oyster abundance (%) and rates of gross primary productivity (GPP), net primary productivity (NPP) and community respiration (CR) for complex and flat tiles, at each site and time. Lines are fitted values calculated from the generalised linear model (GLM) for each site (where $p < 0.05$), and shading represents a 95% confidence interval.

decreased respiration rates on complex tiles with increasing biogenic complexity when standardised per unit-area of tile. Importantly, effects of habitat complexity on the productivity and nutrient cycling of marine sessile communities were largely unrelated to diversity measures, such as richness or cover of key taxa and functional groups (e.g. primary producers). Our results show that, under certain conditions, there might be trade-offs between species richness and functional targets, as we found that if the aim is to maximise primary productivity on seawalls at the studied sites, flat surfaces are likely better than adding the physical or biogenic complexity types assessed here.

The greater number of sessile species on tiles with increased physical and biogenic complexity could be due to a few different factors. Our experiment does not allow us to unconfound increased surface area of the entire tile from other factors, even when results were standardised by sampling a set amount of 2D surface area, since we did not have tiles with different complexities and identical surface areas. However, other studies have found that the addition

of protective microhabitats to seawalls, similar to those offered by the crevices in complex tiles, can increase biodiversity, regardless of total surface area (Loke & Todd, 2016; Matias et al., 2010). Thus, it is likely that the increased richness here is the result of a combination of increased surface area and the addition of micro-habitats.

We hypothesised a positive relationship between realised richness (the number of species present at a place at a given time) and ecosystem function. This is supported by an overall trend showing that complex tiles acted as sinks of ammonia, compared to flat tiles, which mostly acted as sources of NH_4^+ . This supports our initial hypothesis that increased species richness would lead to a higher uptake of inorganic nutrients (i.e. being sinks of inorganic nutrients) (see e.g. Cardinale et al., 2011), given that complex tiles had greater species richness compared to flat tiles. However, contrary to the pattern we found for species richness, there was a trend of greater gross and net primary productivity and predominance of an autotrophic state (as evidenced by NDM, see Supporting Information) on flat tiles compared to complex tiles. In addition, unlike species

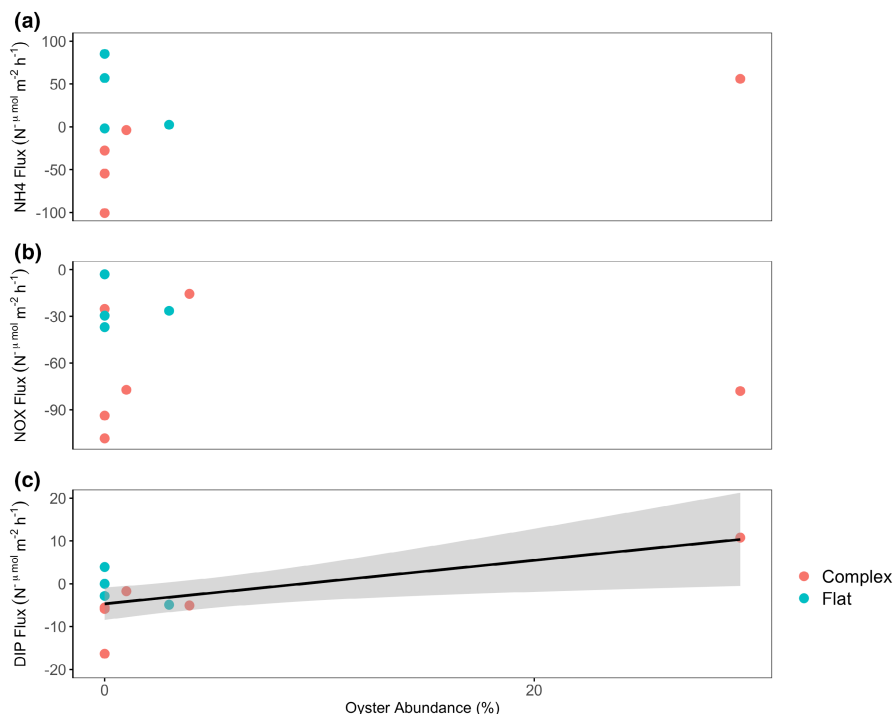


FIGURE 3 Mean (\pm SE, $n = 3$) net daily fluxes of ammonia (NH_4^+ ; a), nitrate + nitrite (NO_x ; b) and dissolved inorganic phosphorus (DIP; c) between the tiles and water column on complex and flat tiles with varying levels of biogenic complexity at Illoura, Time 2. Positive values represent a net flux out of the tile to the water column. A negative value represents a net uptake by the tile from the water column. Lines are fitted values calculated from the generalised linear model (GLM) for each site (where $p < 0.05$), and shading represents a 95% confidence interval.

richness, we found no effects of biogenic complexity on GPP or NPP. This supports the idea that the relationship between realised richness and ecosystem function is not straightforward (Hagan et al., 2021). This lack of apparent relationship between richness and function may have been a consequence of not quantifying biomass of the species present. It is, nevertheless, difficult to determine what is driving the productivity on flat tiles. We found that the cover of producers (macro-algae) decreased with increasing biogenic complexity (cover of oysters), which could be due to competition for space between these taxa. However, there were no overall effects of increasing biogenic complexity on GPP or NPP and, when we did find an effect, which was only at one site and time, GPP actually increased with biogenic complexity. Differences in the most abundant species of macro-algae do not seem to explain these results, as we found no significant effects of the cover of *Ulva* or *Corallina* when these were included in the models. There were, however, significant effects of both biogenic and physical complexity on the structure of assemblages (composition and relative abundance). Therefore, other, less abundant, algal species could be driving the observed results. Other explanatory factors for the observed overall higher productivity on flat tiles could be differences in abundances/composition of micro-algae present on tiles and/or the photosynthetic performance of individual algae caused by differences in light availability on tiles (e.g. Barranguet et al., 1998), neither of which were measured here. Moreover, lower cover of primary producers might also reduce competition of light and nutrients, fostering individual photosynthetic performance. Future studies should therefore build on the knowledge gained here to not only assess whole assemblages (i.e. mobile and sessile species), but also assess photosynthetic efficiency of primary producers, and potentially manipulate algal composition to understand the main factor(s) driving observed patterns.

Further investigation of micro-algae using methods such as DNA and RNA analyses could also provide greater taxonomic resolution and identify changes in functional genes to clarify drivers of the differences in productivity observed here.

It is important to also note that, unlike many studies that look at the relationship between diversity and ecosystem functioning, we did not assess biomass of organisms (including macroalgae). Instead, we quantified organisms using percentage cover, which is a limitation of the study. Results found here are, however, still relevant given that, in many cases, managers want to assess the efficacy of interventions without removing organisms. Our findings also provide an important baseline for future, more comprehensive studies, on how rehabilitation of urbanised habitats can influence diversity and ecosystem functioning using non-destructive sampling.

Contrary to our hypothesis, we found no effects of biogenic complexity on function, except at Clarke's Point on flat tiles, where we find a slight trend of efflux of ammonia and increased primary productivity with increasing biogenic complexity. These patterns can probably be due to bivalves, such as mussels and oysters, increasing the concentrations of bioavailable nitrogen (i.e. ammonia) and phosphorus in the water column through their excretion, which can then be assimilated by micro and macroalgae, increasing primary productivity (Bracken, 2004; Dame & Libes, 1993; Zwierschke et al., 2020).

We found significant differences in the functioning of tiles among sites and between times. Differences in the orientation, wave action and moisture at low tide due splash waves from boating activities of seawalls among sites could influence physical factors such as light, temperature and desiccation, which are known to affect productivity (Matta & Chapman, 1995). This is illustrated by greater maximum temperatures recorded at Clarke's point, which

had an eastern orientation and the lowest wave action, and might explain the differences observed at this site. Sawmillers Reserve, on the other hand, which had the smallest overall productivity rates, is mostly shaded by a large hill to the north and surrounding terrestrial vegetation (personal observation). Assemblages colonising these sites were also significantly different from each other. Again, without manipulating species composition and abundance it is not possible to identify which species is/are contributing to these patterns. Nevertheless, our results re-enforce the point that there is no one-size-fits-all approach, and interventions should consider the local environment and available species pool (Bishop et al., 2022; Strain et al., 2021). Also, it is important to note that assemblages assessed here were relatively young (7–8 months) and may not represent long term effects of increased physical or biogenic complexity as colonisation of benthic habitats may continue over several years (Butler & Connolly, 1999). Our results demonstrate important patterns of early differences in ecosystem functioning between physical and biogenic interventions. In addition, short-term effects of eco-engineering are often of interest to management bodies where early recruitment can influence longer-term patterns, particularly in temperate and polar ecosystems (Bracewell et al., 2017). We emphasise, however, the need for long-term experiments, so potential benefits and trade-offs can be fully assessed.

4.1 | Summary and recommendations to managers

We found, on average, that both physical and biogenic complexity independently increased the number of sessile species. We found weaker, or no, effects of complexity on the functioning of tiles' assemblages when considering total surface area of tiles. We did find, however, a trend of greater gross and net productivity on flat tiles, that is, with lower physical complexity, than complex tiles. We also found no significant effects of the percentage cover of particular taxa (e.g. coralline algae and *Ulva* spp.) or functional groups (e.g. primary producers) on tile productivity. These results suggest that habitat complexity likely mediated changes in functioning differently from changes in biological diversity. While we found no evidence of direct relationships between sessile species richness and percentage cover of sessile communities and functioning, this might be related to the fact that we used non-destructive sampling, considering only primary cover of sessile species. Mobile and microbial communities—not assessed here—are likely to affect ecosystem functioning, with potential idiosyncratic effects of key taxa, such as mobile grazers and micro-algae. Future experiments should incorporate assessments of multiple trophic links, including mobile assemblages and microbial biofilms as well as measurements of biomass of species/taxa so links between habitat complexity, diversity and functioning can be further elucidated. We did find strong effects of sites and time on the functional variables measured, corroborating previous studies that found that local environmental conditions can mediate effects of complexity on assemblages (e.g. Strain et al., 2021).

Our findings suggest that reconciliation approaches, such as eco-engineering, aiming to enhance the ecological value of degraded/artificial habitats through increases in habitat complexity might benefit from an approach where functional targets and associated services are explicitly considered. This study shows that, under some conditions, there is a trade-off between biodiversity and functional targets. For example, increasing complexity may support increases in the richness of sessile macro-species, but it may not support other desired functions, such as increased productivity. Therefore, clearly stating objectives and priorities of these interventions is essential to inform design. The lack of relationships found here between habitat complexity, biodiversity and functioning also show that functions cannot be inferred from biodiversity measures, but that direct measurements of the structural and functional components of the manipulated assemblages need to be readily integrated in management interventions in urbanised areas. Moreover, we observed variation between sites, emphasising the importance of pilot studies before interventions to inform designs appropriate for the area. We highlight that eco-engineering interventions should be applied with targeted outcomes for biodiversity and function, and conservation and/or restoration of natural, complex, habitats should always be priority (Firth et al., 2020).

AUTHOR CONTRIBUTIONS

Mariana Mayer-Pinto, Ana B. Bugnot, Emma L. Johnston, Laura Airoidi, Tim M. Glasby, Elisabeth M.A. Strain and Katherine A. Dafforn conceived the idea. Mariana Mayer-Pinto, Ana B. Bugnot, Emma L. Johnston, Laura Airoidi, Tim M. Glasby, Jaimie Potts, Peter Scanes and Katherine A. Dafforn designed the experiment. Mariana Mayer-Pinto, Ana B. Bugnot, Jaimie Potts, Peter Scanes, Shinjiro Ushijima, Elisabeth M.A. Strain and Katherine A. Dafforn collected the data. Mariana Mayer-Pinto analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

Mariana Mayer-Pinto is an Associate Editor of Journal of Applied Ecology but took no part in the peer review and decision-making processes for this paper. The authors declare no other conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via the Mendeley Data Repository <https://doi.org/10.17632/s5yvzkw4k3.1> (Mayer-Pinto et al., 2022).

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