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TOPICAL REVIEW

Marine infrastructure support fewer producers and more filter feeders than natural habitats: a review and meta-analysis

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Abstract

Coastal infrastructure has reduced habitat complexity and altered light regimes compared to natural habitats, altering ecological communities and reducing overall biodiversity. Although, many studies have assessed effects of infrastructure on the overall biodiversity, these were often restricted in scope, by assessing only a particular type of infrastructure, such as coastal defence structures, or by focusing solely on diversity metrics. Therefore, we still have little knowledge on the functional impacts of infrastructure, in general, on coastal habitats. To address this knowledge gap, we conducted a systematic review and meta-analysis comparing the functional composition of natural and artificial marine habitats. We analysed a total of 68 publications from 26 countries, with data collected between 1995–2019. We found up to 60% more habitat-forming algae on natural habitats than on infrastructure at most tidal heights, but no differences were found when looking at all species of macro-algal, i.e. including non-habitat-formers. In contrast, we found more habitat-forming filter feeders, such as oysters and mussels, on subtidal vertical and floating structures, such as pylons and pontoons, respectively, than on natural habitats. Differences on the abundance of grazers varied with tidal height and/or the type of infrastructure. For example, in the subtidal, grazers were significantly more abundant on natural boulders than on infrastructure, while at low tidal heights, we found significantly less grazers on artificial floating structures and on vertical structures than on natural habitats. With coastal development on the rise, these differences have significant implications for productivity, energy and nutrient flow in coastal systems. Our findings highlight the importance of adopting a functional approach to have a more holistic understanding on the environmental impacts associated to marine urbanisation and thus better inform management and restoration efforts.

1. Introduction

The human population is predicted to exceed nine billion by 2050, with 68% of the population projected to live in urban areas (United Nations 2019). As this number grows, so does the pressure on ecosystems. Urbanisation leads to changes to ecosystems, due to changes in land use, increased disturbance, and the addition of infrastructure (Grimm *et al* 2008). These changes can promote non-native and invasive species (Lososová *et al* 2016, Santana Marques *et al* 2020), alter species composition and cause increased biotic homogenisation, which in turn can lead to functional homogenisation of systems (McKinney 2006). Urban sprawl and the resultant habitat loss, degradation and fragmentation are the leading cause of biodiversity decline globally (Dirzo and Raven 2003, Butchart *et al* 2010, Newbold *et al* 2015).

As global biodiversity declines, understanding the roles species play in ecosystem functioning will be crucial in maintaining and preserving key functions, and the services they underpin, into the future. Although there are links between the diversity of species and the diversity of ecosystem functions and processes within a system, these links are not always straightforward (Schulze and Mooney 1994, Grime 1997, Raffaelli 2006). Therefore, simply aggregating the total number of species in an ecosystem into a single measure of biodiversity often fails to reveal nuanced relationships between species and the functions they provide (Petchey and Gaston 2002). For example, the relative importance of species diversity or richness for ecosystem functioning may be overestimated if there is considerable overlap in the functional diversity of the assemblage (Bengtsson 1998). In some systems, comparatively rare organisms such as keystone species may contribute extensively to ecosystem function (Power *et al* 1996). Thus, species biodiversity or richness cannot be used as a singular measure of the health of an ecosystem, nor the impact of a stressor.

Ecological studies are increasingly using functional approaches to understand how changes in species and organismal traits influence ecosystem functioning (Laureto *et al* 2015). These functional diversity studies group different species or organisms based on shared trait/s, such as the height of a plant within the canopy, or morphology (e.g. vines vs grasses Harrison *et al* 2010). Other organisms may be grouped by the specific part of the habitat they occupy (e.g. in fish—pelagic vs benthic), body size, reproductive strategies (Ladds *et al* 2018) or feeding mode (Gerino *et al* 2003). Functional diversity has been used to understand and quantify the impacts of disturbances such as land-use change (Bengtsson *et al* 2000, Alberti 2010, Arnan *et al* 2018, Matuoka *et al* 2020, Hong *et al* 2022). The direct measurement of ecosystem function can be difficult, especially over large scales (Wessman and Asner 1998, terHorst and Munguia 2008). The use of proxies like functional groups can allow for understanding of potential functional changes over large scales (Lavorel and Garnier 2002, Gravel *et al* 2016, Hébert *et al* 2017). However, most studies to date have been done in terrestrial systems (Grace 1991, Tilman and Downing 1994, Grime 1997, Tilman *et al* 1997, Díaz and Cabido 2001, Hooper *et al* 2005, Naeem *et al* 2012, Hong *et al* 2022), and studies on function, and changes in function relating to human impacts and urbanisation are comparatively less prevalent in marine systems (Tait and Schiel 2011, Benkwitt *et al* 2020, Edwards *et al* 2020, Lam-Gordillo *et al* 2020).

The addition of infrastructure to marine ecosystems is one of the most common and obvious examples of urbanisation in coastal regions. Marine infrastructure includes multiple types of structures, built for diverse purposes such as coastal defence (e.g. seawalls and breakwaters), tourism and recreation (e.g. marinas and swimming enclosures), resource extraction (e.g. wind farms and oil rigs), and fisheries and aquaculture industry (Dafforn *et al* 2015). Infrastructure now occupy over 32 000 km^2 of the marine environment and this is predicted to grow by at least 23% to 39 400 km^2 by 2028 (Bugnot *et al* 2021). Marine built infrastructure differs from natural habitats (such as reefs or rocky shores) in several ways, including material and slope (Glasby 2000), light regime (Blockley 2007, Pardal-Souza *et al* 2017) and microhabitat availability (Loke *et al* 2017, Strain *et al* 2018, Waltham and Sheaves 2018), all of which can contribute to variations in species assemblages between habitat types (Bulleri and Chapman 2004, Moschella *et al* 2005, Chapman 2006). Marine infrastructure also tend to be more shaded or have altered light regimes compared to natural habitats (Glasby 1999, Pardal-Souza *et al* 2017, Trethewy *et al* 2023). This may have strong impacts on the type of colonising organisms, with functional consequences. For example, if producers are less abundant on infrastructure due to lower light availability, this may increase space availability for sessile, filter feeding animals to colonise, potentially leading to overall decreases in primary productivity and increases in filtration rates. In turn, this may also result in variations in other functional feeding groups, with potential ongoing impacts on the functions and services provided by marine infrastructure compared to natural habitats.

Most studies on the impact of marine infrastructure have focused on the consequences to marine biodiversity. In general, infrastructure support different and reduced biodiversity when compared to natural habitats (Chapman 2003, Bulleri and Chapman 2004, Moschella *et al* 2005, Mayer-Pinto *et al* 2018). In contrast, we know much less about their functional impacts (but see Mayer-Pinto *et al* 2018), and therefore the full extent of impacts of infrastructure on marine systems is largely unknown. Further, most studies have focused on impacts within localised sites. The one synthesis study by Gittman *et al* (2016) found reduced abundance and diversity of organisms (including flora, infauna, birds, nekton and epibiota) on seawalls compared to natural shores. This study, however, focused solely on coastal defence structures. Critically, they grouped all organisms living on the surface of the structure (including algae, barnacles, and gastropods) together as 'epibiota' and found no difference in epibiota abundance between natural and artificial habitats. Organisms colonising the hard surfaces of structures (epibiota) are extremely diverse, belonging to numerous taxonomic and functional groups including red, brown and green algae and several groups of invertebrates (Knott *et al* 2004, Schaefer

et al 2019, Bishop *et al* 2022). Thus, we still have very limited knowledge on how, and how much, infrastructure can alter functional diversity in the marine environment at large scales.

A straight forward initial step to assess ecosystem functions in different habitats consists on grouping organisms by feeding mode, which reflects the trophic position of species within an ecosystem and provides indication of energy and nutrient flows (Gerino *et al* 2003). Filter feeding organisms, for example, have critical impacts on aquatic ecosystems, with the potential to regulate both primary and secondary productivity through the consumption of plankton and their role in nutrient cycling in the water column (Gili and Coma 1998). Increased abundances of filter feeders on infrastructure can influence other trophic levels, with potentially less plankton available as food for other planktivorous organisms, or more food available to predators (Malerba *et al* 2019). Similarly, any changes in primary producers on infrastructure (compared to natural habitats) may also have significant functional consequences for global processes like carbon storage (Krause-Jensen *et al* 2018) or herbivory (Poore *et al* 2012).

Here, we performed a systematic review and meta-analysis aiming to investigate whether different marine infrastructure (e.g. seawalls, pontoons, or shipwrecks) support different functional groups of epibiota—based on feeding mode—compared to natural habitats. We compared across four tidal heights (high, mid, low, and subtidal) because different structures occupy different spaces within the marine environment and may therefore support an alternative suite of organisms. Abundances of habitat forming organisms such as kelps and oysters were also analysed individually, since these organisms underpin key functions such as filtration rates and primary productivity and support many other species. We also compared different sampling methods, and included studies over time and across multiple continents to examine latitudinal patterns. As infrastructure are typically more shaded, we hypothesised that they would support more filter feeders, since they are not dependent on light for photosynthesis, while less shaded natural habitats would support higher abundance of primary producers and, consequently, grazers. We also predicted that built infrastructure would support greater numbers of predators and detritivores, due to increased food (i.e. invertebrates) and space availability.

2. Methods

2.1. Systematic literature search
We systematically reviewed published studies on organisms colonising infrastructure and natural habitats, using a structured search through the online search engines *Scopus* and *ISI Web of Science* core

collections. The following search terms were used: seawall* OR 'artificial structure*' OR foreshore OR 'shoreline modification' OR 'rocky shore*' OR 'natural shore*' OR 'rocky reef' OR 'natural reef' OR 'artificial reef' OR 'coastal defence' OR 'shoreline hardening' OR 'novel habitat' OR 'modified habitat' OR pontoon* OR piling* OR marina* AND biodiversity OR community OR assemblage OR organism* OR invertebrat* OR alga* OR macroalga* OR kelp OR seaweed OR 'filter feeder*' OR tunicate* OR ascidia* OR oyster* OR mussel* OR epibiot* OR epifauna* OR 'sea squirt*' OR cunjevoi OR biofouling OR fouling OR grazer OR predator OR scavenger OR detritovore OR mollusc* OR gastropod* OR mobile OR sessile AND richness OR biomass OR diversity OR abundance OR density OR cover AND NOT fish* OR microb*. The initial search was done on 31 August 2021, and then repeated to uncover any new studies on 24 August 22. No time limit was applied to the searches.

The search returned 8868 results on *Web of Science*, and 4492 on *Scopus*. These were all imported to an Endnote library and duplicates removed, leaving 7750 unique publications (figure S1). Publications were then assessed at the title and abstract level, with 490 studies remaining, which were assessed at the whole publication level. We also examined the citation lists of relevant papers identified by this search to capture studies that were not included in the initial searches or that had been published in journals not indexed in the databases we searched. Seventy-one publications met the criteria to be included in the final analysis (figure S1).

2.2. Inclusion and exclusion criteria
Publications were only included in the analysis if they assessed the abundance of one or more species/taxa on both infrastructure and natural substrata and where means and errors could be extracted, either directly in tables or text, or from figures. Count, cover, and biomass data were all included.

While no doubt important to marine ecosystems, we excluded fish and microbes from the search and analysis to focus on epibiota, given they inhabit the hard surfaces of the habitats and are, therefore, likely to be directly affected by the addition of infrastructure.

We included studies done on both subtidal and intertidal habitats, from any location and year. Publications that solely investigated the impacts of eco-engineering or restoration efforts on abundance and diversity of organisms were not included, except when they presented data on unrestored natural and infrastructure.

While we initially included soft bottom natural habitats in our literature search and data extraction, these were excluded in the final analysis. Since built structures are exclusively being made from hard

materials (concrete, stone etc), direct comparisons on the epifauna colonising hard vs soft substrata were not considered logical.

2.3. Data extraction

From each publication, means, standard deviations (SDs) and sample sizes of species/taxa(s) abundance(s) were extracted. Errors were extracted from figures using WebPlotDigitizer (Rohatgi 2022). Errors reported as confidence intervals or standard errors were converted to SD. Comparisons between natural habitats and infrastructure within each study were done according to the experimental design. For example, some studies directly compared a single natural habitat site with a single infrastructure site, whereas other studies investigated multiple types of infrastructure and/or had sampled uneven numbers of natural sites vs sites of infrastructure. In these cases, all available combinations were done for effect size calculations. So, if a study compared three natural rocky reef sites, for instance, with one piling and one seawall site, then we obtained effect sizes for all combinations of sites, i.e. each rocky reef site with each piling and seawall site for a total of six effect sizes. To account for the non-independence of these observations, we used a variance–covariance (VCV) matrix (see details below).

We extracted data on time(s) and location(s) of data collection, including year, month, and site coordinates where available. We also extracted data for the type of built structure (e.g. seawall, pilings, breakwater) and natural (e.g. rocky shores, boulder fields etc) habitat, tidal height, sample method (cores, quadrats, transects), size of sample area, sampling type (targeted or whole assemblage). Tidal height was recorded as high, mid, low, or subtidal as reported by the publication. For the latter, we also extracted depth when it this information was available. Where a range of depths were reported, we calculated the median depth and used this information in the analyses.

We classified publications according to the sampling taxonomic approach. Publications that only assessed specific species or taxa were classified as 'targeted' publications, whereas publications on the whole communities/assemblages were classified as 'whole assemblage' publications. The author(s) and publication year of each study was recorded, with each study being assigned to a unique 'Publication ID' to account for the lack of independence arising from calculating multiple effect sizes from the same publication. If a single publication reported data from multiple organisms, infrastructure, or sites, then we recorded all the information. This means that some publications contribute considerably more data to the analyses. For example, if a publication reported abundances of mussels, oysters, and kelp, then this publication would contribute three effects to our analyses. In addition, a unique 'Survey ID' was assigned to account for sites being sampled at multiple timepoints within the same publication. Thus, if a publication reported the abundance of oysters at the same sites on three separate occasions, the first timepoint would be assigned 'Survey 01', the second 'Survey 02' and the third 'Survey 03'. Survey ID was unique among and within publications to use as a random effect in the models.

The taxonomic identity of organism(s) or group(s) sampled in each study was recorded as reported by authors. Organisms or groups were then classified into the following functional groups based on their feeding mode: producer, filter feeder, detritivore, grazer, scavenger, or predator. This grouping allows us to draw conclusions about ecosystem processes and functions, which would not be possible if we compared individual species as reported in each study. Feeding mode of species/taxa were identified according to the literature. If a single feeding mode could not be identified for a taxonomic group (e.g. for publications that reported abundances of a group such as 'isopods', which can include species of several feeding modes), then the associated effect sizes were not included in the functional group models. Species/taxa were also classified as either habitat formers or not. Habitat formers are key species that create biogenic three-dimensional habitat structures that facilitate the presence of other species and support biodiversity and may therefore contribute greater function than other species (see e.g. Mayer-Pinto *et al* 2020), so understanding if their abundance is impacted by the construction of marine infrastructure is critical. The following taxa were considered as habitat-formers: canopy forming algae (producers), oysters, mussels, hard corals, solitary ascidians, sponges, and reef-forming worms (filter feeders) (table S1). Similarly, we combined the different types of infrastructure into broad groups: defence structures (seawalls, break walls, groynes), floating structures (pontoons, floats), vertical structures (pilings and pillars), and other (shipwrecks, artificial reefs, undersea cables, wind turbines). These classifications were used as, not only these broad infrastructure groups support different species assemblages (Connell 2000, Heery *et al* 2018, Mayer-Pinto *et al* 2018) but also occupy different habitats/zones of the marine environment (e.g. while many coastal defence structures are intertidal, large sections of pilings tend to be subtidal). Natural habitats were also classified into broad groups: natural shore (rocky shores and intertidal reefs), natural reef, and boulders.

2.4. Statistical analyses

All statistical analyses were done using R and RStudio (R Core Team 2022). Effect sizes were calculated using the natural log-transformed response ratio (lnRR). In our study, a positive lnRR indicates a higher abundance in infrastructure relative to natural habitats.

The percentage cover data reported in the studies is prone to zero values, which prevents the calculation of lnRR. To overcome this, we added 0.01 to the percentage cover data of both the infrastructure (treatment) and natural (control) habitat when means were reported as zero. The value of 0.01 was chosen as it was the lowest percentage cover reported in the dataset. We arcsine square root-transformed the data, because the percentage cover data were bounded at 0 and 100. The SD of these data was calculated using equation 10 in Macartney *et al* (2022), where M is the group means,

$$\mathrm{var}\left(f(M)\right) = \frac{\mathrm{SD}^2}{4M(1-M)}.$$

For count and biomass means reported as zero, we added 0.5 to both the infrastructure and natural means (Yamamura 1999).

The sampling variance of our effect sizes was calculated using the 'all cases' method reported in Nakagawa *et al* (2023). Specifically, we first ran Geary's test to assess the normality assumption of our effect sizes. We then used the SDs reported in the studies that passed Geary's test to calculate the weighted average coefficient of variation (CV) between studies. This CV was then used to calculate all sampling variance estimates, whether they were originally missing or not.

Several publications used designs whereby either a single infrastructure site was compared to several natural habitat sites, or vice versa. To account for the non-independence of these observations, we created a VCV matrix where we correlated the errors ($r = 0.5$) of effect sizes that used the same control (natural) site as a comparator. We were only able to use one VCV matrix per model. Therefore, to account for the shared artificial sites, we divided the sample size of the observations by two when the infrastructure site means were repeated (e.g. one seawall site being compared to multiple natural rocky shore sites), thus reducing the weight of these effects in the model (Pottier *et al* 2021).

2.4.1. Meta-analyses and meta-regressions
We compared the abundance of functional groups on natural habitats and infrastructure using univariate meta-regressions using the *rma.mv* function in the R package 'metafor' (version 4.6–0) (Viechtbauer 2010). We first calculated the overall meta-analytic mean from all the effect sizes, without moderators.

Due to the known differences in assemblages at different tidal heights (Colman 1933, Peterson 1991, Kelaher *et al* 2003), the models were run individually for each tidal height (high, mid, low and subtidal). We initially ran a single moderator model for each tidal height with functional group as the moderator. For each subsequent model, we then fitted an interaction between functional group and

another moderator (infrastructure type, natural habitat, sampling type, sample method, infrastructure site latitude, natural site latitude and median depth) to address our hypotheses. Publication ID, and Survey ID were all included as random effects to account for the nonindependence arising from multiple effects being extracted from each survey and each publication. We also added an effect size-level random effect to partition the heterogeneity (Noble *et al* 2022).

In each case, estimates with fewer than two effect sizes were not included in the analysis. Models were also run for just habitat forming species (canopy forming algae, oysters, mussels, hard corals, solitary ascidians, sponges, and reef-forming worms) per tidal height, to investigate the effect of infrastructure on the abundance of habitat forming species. These models were run with the same random effects as above. Data was visualised using either orchard plots (for categorical moderators) or bubble plots (for continuous moderators) using the *orchard_plot* or *bubble_plot* functions from the orchaRd package (version 2.0) (Nakagawa *et al* 2023).

2.4.2. Heteroscedasticity
After running each model, we assessed the assumption of homogeneity of variance visually. We then ran models accounting for heteroscedasticity, by allowing the variance of the random effect explaining the most variation in the model to vary based on the levels of the moderator tested, using a heteroscedastic compound symmetric structure. We compared the small-sample Akaike information criterion (AICc) of meta-regressions modelling heteroscedasticity or assuming homogeneity of variance, and the estimates from the best fitting model was used—i.e. the model with the lower AICc value. I^2 values were also calculated for each model per tidal height to partition the total heterogeneity of each model.

2.4.3. Sensitivity analyses
We performed leave-one-out analyses by iteratively removing one study at a time on the four main models (each tidal height with no moderators). This allows us to see the impact of each study on the overall result.

2.4.4. Publication bias
We checked for publication bias using Egger's meta-regressions, where we fitted standard error or variance as moderators (Nakagawa *et al* 2022). We also visually assessed publication bias using funnel plots. Publication bias is the phenomena whereby studies with statistically significant results are more likely to be published than studies without. This may skew the meta-analytic outcome if specific types of data are over-represented in the data-set (Nakagawa *et al* 2022).

3. Results

3.1. Systematic review summary

Data from 68 publications and 5024 individual effect sizes were used in the final analysis. Data were collected over 24 years, from 1995 to 2019. Publications included data from 26 countries (figure S3).

Most data (∼50% of publications) were from research on defence structures such as seawalls and breakwaters, followed by other structures (shipwrecks, artificial reefs etc), vertical structures (e.g. pilings) and floating structures, such as pontoons (figure S4(a)).

Data spanned the intertidal and subtidal environments, with 37 publications (∼50%) comparing subtidal habitats and the remaining done in the intertidal zone (figure S4(b)). Note that some publications compared more than one tidal height so were included in multiple models. A total of 41 publications collected data from the whole assemblage at their sites, while 27 only collected data from individual groups or species (figure S4(c)).

Overall, 23 publications reported abundances of mobile organisms and 60 reported abundances of sessile organisms (both algae and sessile animals). In total, 594 different taxa were reported (this includes individual species and broader groups such as 'foliose algae'). Data was mostly from filter feeders, followed by producers, grazers, predators, and finally detritivores (figure S4(d)). Filter feeders were dominated by barnacles and oysters. Producers were made up of various algae, including turfing and encrusting forms, as well as large foliose macroalgae. Grazers were mostly gastropods, while detritivores were mostly amphipods. Finally, predators were a diverse group, consisting of gastropods, flatworms, starfish, and other organisms.

3.2. Abundances of different functional groups

3.2.1. Producers

There was between 40%–62% more habitat-forming algae (i.e. large, canopy forming macroalgae) on natural habitats than on infrastructure at the mid-low-tidal heights as well as on the subtidal zone (lnRR(mid) = -0.5113; 95% CI = -0.9984, -0.0242; lnRR(low) = -0.9756; 95% CI = -1.8824, -0.0687; lnRR(sub) = -0.8175; 95% CI = -1.4038, -0.2311; figures 2(a)–(c)).

Our primary aim was to compare abundances of epibiota on infrastructure vs natural habitats. When considering at macro-algae generally (i.e. including non-habitat forming algae), there were no statistically significant differences in their abundances between infrastructure and natural habitats at high or mid-tidal levels for any of the moderators tested (figures S5(b) and (c)).

At low tidal and subtidal heights, total abundance of all producers was 43% greater on natural habitats than on infrastructure (lnRR(low) = -0.5691;

95% CI = -1.1257, -0.0124; figure 1(c); lnRR(sub) = -0.4350; 95% CI = -0.7439, -0.1262; figure S5(d)). At low tidal heights, this was mainly driven by patterns on defence structures (e.g. seawalls and breakwaters), where algae were significantly less abundant when compared to natural shores (lnRR(defence structures) = -0.5691; 95% CI = -1.1257, -0.0124; figure 1(c)). At subtidal zones, however, we found reduced abundance of algae on vertical structures (e.g. pilings) and other structures (e.g. shipwrecks, wind turbines) compared to natural habitats (lnRR(vertical structures) = -0.6535; 95% CI = -1.2438, -0.0633; lnRR (other structures) = -0.8228; 95% CI = -1.3375, -0.3081; figure 1(d)).

3.2.2. Filter feeders

In general, filter feeder abundance was not statistically different between infrastructure and natural habitats (figures S5(b)–(e)). However, there was evidence for differences depending on the type of structure at subtidal depths. In particular, subtidal filter feeders were 105% more abundant on floating structures (e.g. jetties) and 76% more abundant on vertical structures (e.g. pilings) than on natural habitats (lnRR(floating structures) = 0.7185; 95% CI = 0.1733, 1.2637; lnRR(vertical structures) = 0.5704; 95% CI = 0.0199, 1.1210; figure 1(d)), but 87% less abundant on artificial defence structures such as seawalls when compared to natural habitats (lnRR = -0.6264; 95% CI = -1.1149, -0.1378).

When examining habitat forming filter feeders (e.g. oysters and mussels), these were 217% more abundant on built infrastructure than on natural habitats at the low-tidal height (lnRR = 1.1538; 95% CI = 0.3764, 1.9312; figure 2(b)). No statistically significant differences for this group were found at the other tidal heights.

3.2.3. Grazers

There were no significant differences in grazer abundance between natural habitat and built infrastructure at high tidal height. Although grazers tended to be more abundant on natural habitats than infrastructure at mid and low tide levels, these differences were not statistically significant. There was, however, a strong difference at the subtidal height, where grazers were significantly more abundant on natural boulders than on infrastructure, in general (lnRR = -2.7648; 95% CI = -4.3777, -1.1519). There were strong patterns when considering grazer abundance in the different types of infrastructure. Specifically, grazers at low tide were almost 98% less abundant on artificial floating structures (lnRR = -4.0450; 95% CI = -5.5142, -2.5759; figure 1(c)) and on vertical structures than on natural habitats (lnRR = -2.8934; 95% CI = -4.2906, -1.4963; figure 1(d)).
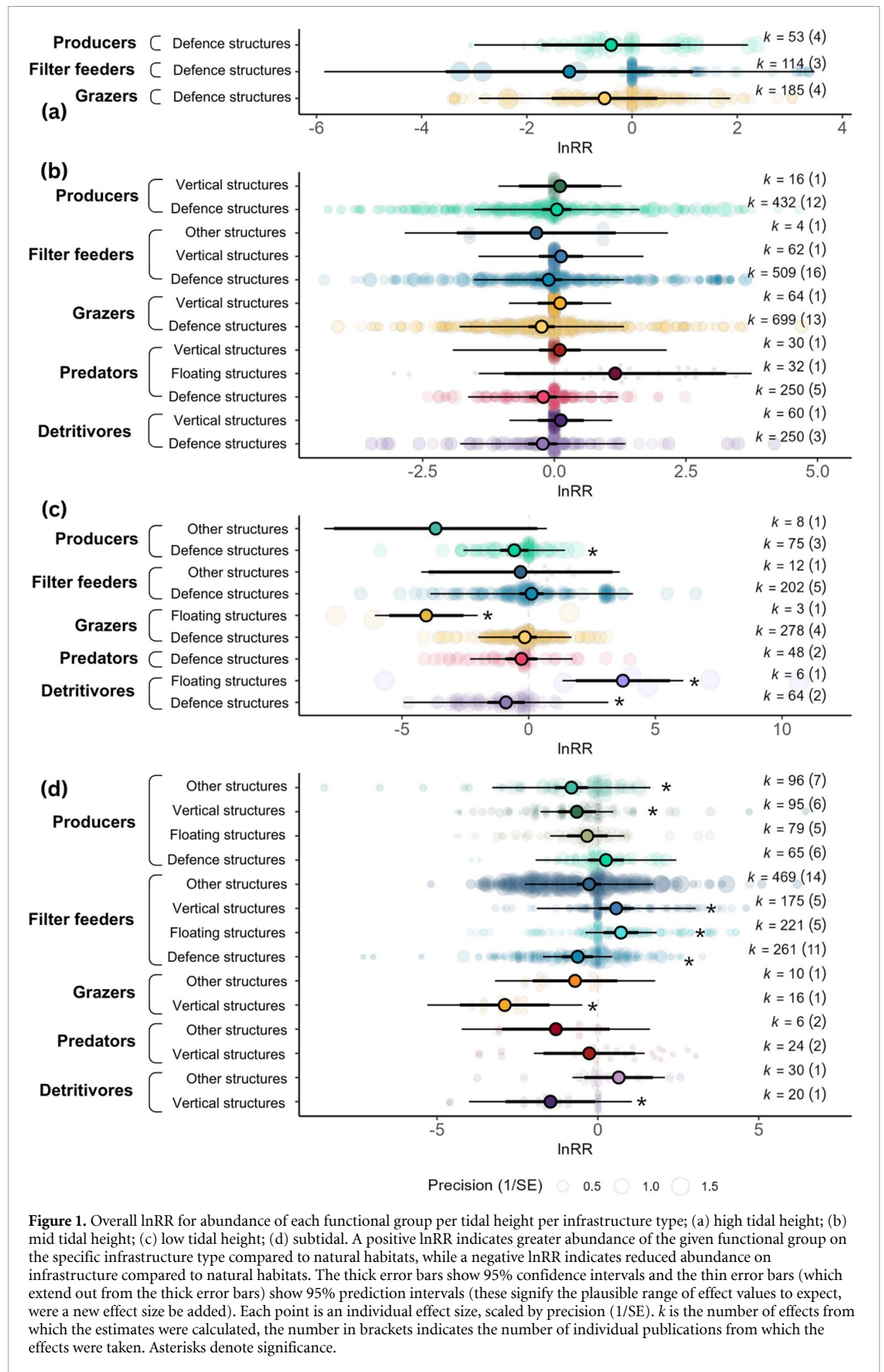
Figure 1. Overall lnRR for abundance of each functional group per tidal height per infrastructure type; (a) high tidal height; (b) mid tidal height; (c) low tidal height; (d) subtidal. A positive lnRR indicates greater abundance of the given functional group on the specific infrastructure type compared to natural habitats, while a negative lnRR indicates reduced abundance on infrastructure compared to natural habitats. The thick error bars show 95% confidence intervals and the thin error bars (which extend out from the thick error bars) show 95% prediction intervals (these signify the plausible range of effect values to expect, were a new effect size be added). Each point is an individual effect size, scaled by precision (1/SE). k is the number of effects from which the estimates were calculated, the number in brackets indicates the number of individual publications from which the effects were taken. Asterisks denote significance.

Figure 2. Overall lnRR for abundance of habitat forming organisms per tidal height; (a) mid tidal height; (b) low tidal height; (c) sub tidal height. No differences were found at the high tidal height. A positive lnRR indicates greater abundance of habitat forming organism (producers or filter feeders) on infrastructure (all types combined) compared to natural habitats, while a negative lnRR indicates reduced abundance on infrastructure compared to natural habitats. Thick error bars are 95% confidence intervals, the thin error bars extending out from the thick error bars show 95% prediction intervals (the plausible range of effect values to expect, were a new publication to be added). Each point is an individual effect size, scaled by precision (1/SE). *k* is the number of effects from which the estimates were calculated, the number in brackets indicates the number of individual publications from which the effects were taken. Asterisks denote significance.

3.2.4. Predators

Differences in predator abundance between natural habitats and built infrastructure were only found at the subtidal level; where this group were significantly more abundant on natural boulders than comparative infrastructure by 96% (lnRR = −3.3426; 95% CI = −6.1373, −0.5480). There were no statistically significant differences at the mid or low tidal levels, and no reviewed publication recorded predator presence at the high tidal level.

3.2.5. Detritivores

No statistically significant difference was found at mid tidal height for detritivores as a whole group, and no publications recorded detritivores at the high tidal level. At the low tidal height, detritivores were significantly less abundant on artificial defence structures like seawalls, but more abundant on floating structures like pontoons, than on natural habitats (lnRR(defence structures) = −0.8983; 95% CI = −1.6428, −0.1538; lnRR(floating structures) = 3.7170; 95% CI = 1.8546, 5.5794; figure 1(c)). Subtidal detritivores were significantly more abundant on natural habitats than on

vertical structures like pilings (lnRR(vertical structures) = −1.47313; 95% CI = 2.86767, −0.07858; figure 1(d)).

3.3. Sampling type and method

There was no evidence for sampling type (targeted vs whole assemblage sampling) or method (transects, cores, quadrats etc) affecting the abundances of different functional groups recorded. However, there were exceptions. For example, at the mid-tidal level, less predators were recorded on infrastructure than on natural habitats when using quadrats compared to cores or scrapings (lnRR = −0.2785; 95% CI = −0.5556, −0.0014; figure 3(a)). Grazers were also significantly less abundant on infrastructure when publications surveyed whole assemblages (lnRR = −0.2902; 95% CI = −0.5566, −0.0237; figure 3(d)), but no statistically significant differences were found when publications specifically targeted grazing organisms (lnRR = 0.3945; 95% CI = −0.4058, 1.1949; figure 3(c)).

Subtidal predators were more abundant on natural habitats than on infrastructure when they were sampled with quadrats (lnRR = −2.2567; 95% CI = −3.6501, −0.8633; figure 3(b)), but
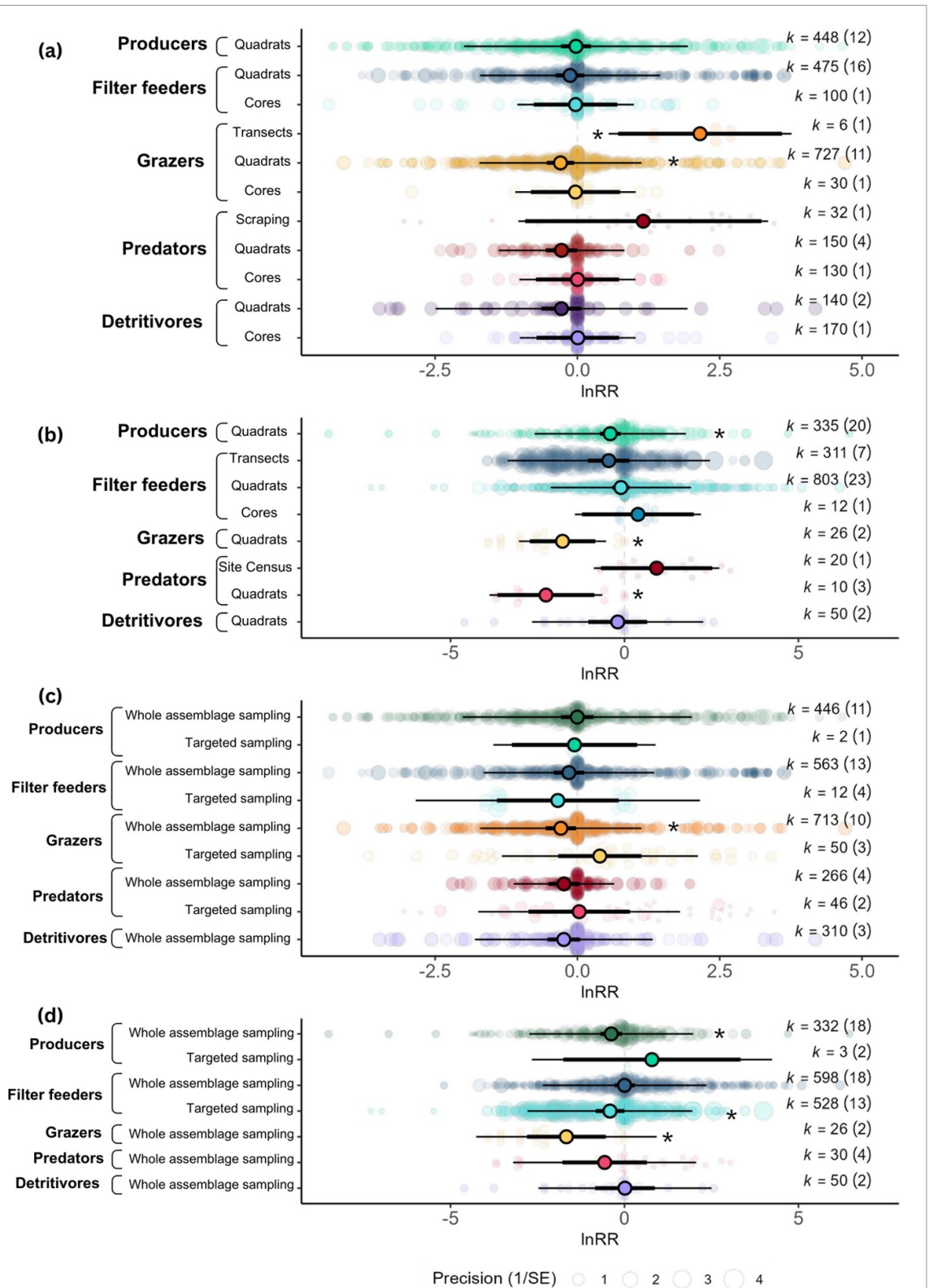
Figure 3. Overall lnRR for each functional group per tidal height per sampling method and sampling type; (a) mid tidal height sampling method; (b) subtidal sampling method; (c) mid tidal height sampling type; (d) subtidal sampling type. No differences were found for high or low tidal heights. A positive lnRR indicates greater abundance of the given functional group on infrastructure (all infrastructure types) compared to natural habitats, while a negative lnRR indicates reduced abundance on infrastructure compared to natural habitats. Thick error bars are 95% confidence intervals, the thin error bars extending out from the thick error bars show 95% prediction intervals (the plausible range of effect values to expect, were a new publication to be added). Each point is an individual effect size, scaled by precision (1/SE). *k* is the number of effects from which the estimates were calculated, the number in brackets indicates the number of individual publications from which the effects were taken. Asterisks denote significance.

Figure 4. Overall lnRR for each functional group per tidal height by site latitude; (a) mid tidal height; (b) low tidal height. No differences were found for the high or subtidal height. A positive lnRR indicates greater abundance on infrastructure compared to natural habitats, while a negative lnRR indicates reduced abundance on infrastructure compared to natural habitats. Asterisks indicate significance.
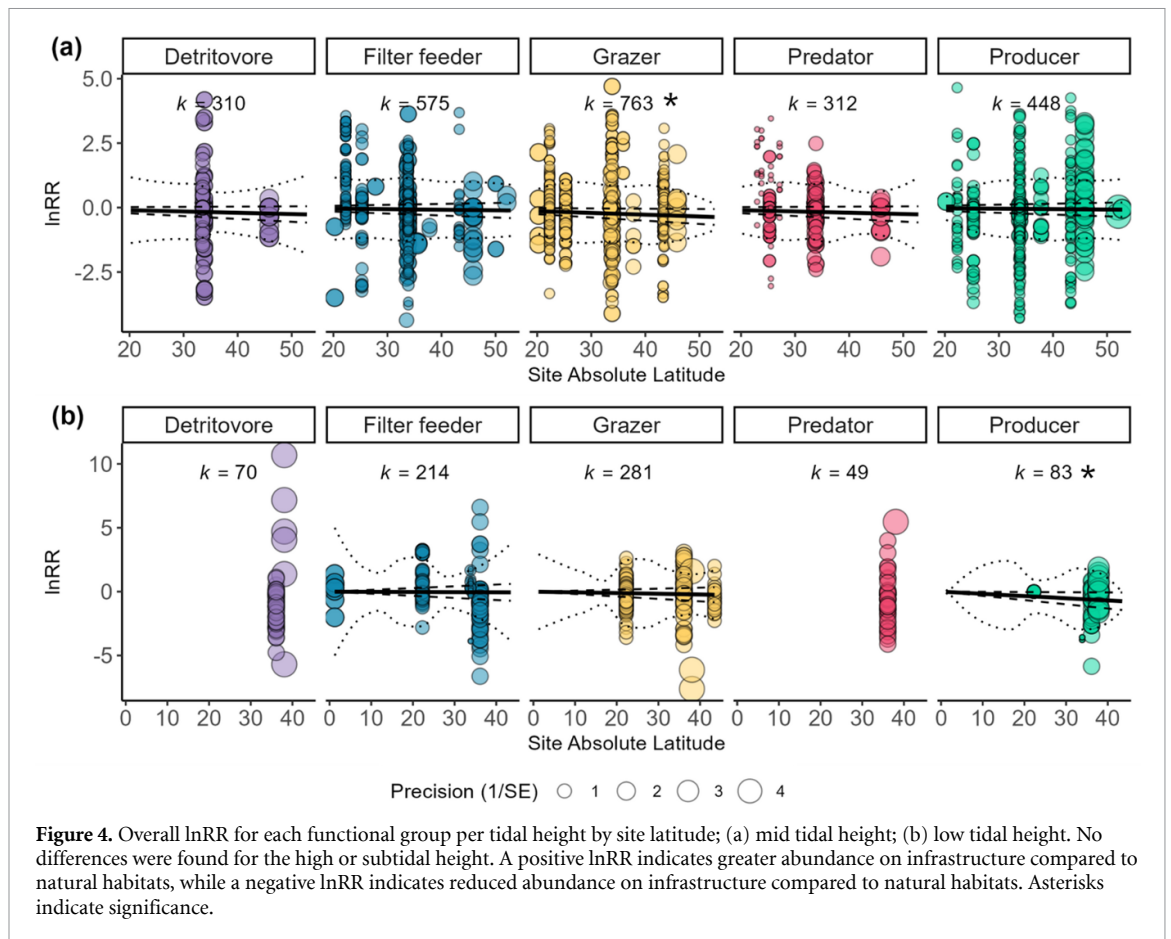
no statistically significant difference was found when publications used a site census method (counting organisms within the entire study area) (lnRR = 0.9233; 95% CI = −0.7442, 2.5908; figure 3(b)). Subtidal filter feeders were recorded as more abundant on natural habitats than infrastructure in publications specifically targeting filter feeders (lnRR = −0.4167; 95% CI = −0.8292, −0.0041; figure 3(d)), but no statistically significant difference was found when filter feeders were recorded in surveys of the whole assemblage (lnRR = 0.0033; 95% CI = −0.2876, 0.2942; figure 3(d)). The opposite pattern was found for subtidal algae, as significantly less algae was recorded on infrastructure than natural habitats in whole assemblage surveys (lnRR = −0.3803; 95% CI = −0.6964, −0.0642; figure 4(d)), but when algae was targeted specifically, no statistically significant difference was found (lnRR = 0.7890; 95% CI = −1.7581, 3.3361; figure 3(d)).
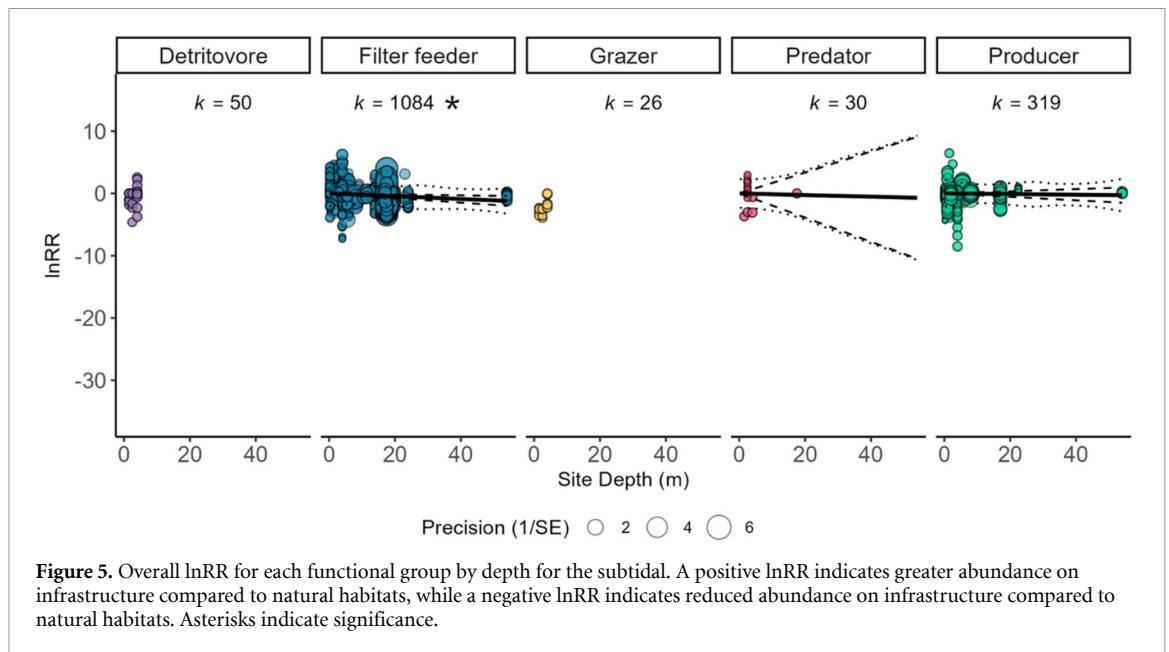
3.4. Latitudinal patterns

Models examining latitudinal patterns revealed significant decreases in epibiota abundance on infrastructure with latitude. i.e. the difference in abundances of the groups between infrastructure and natural habitat were most pronounced at higher latitudes. In some cases, there was not enough variation between study

site latitudes for some functional groups (specifically: detritivores and predators at low tide). Therefore, we were unable to reliably estimate patterns, so these groups have been excluded from analysis.

At the mid tidal height, grazer abundance was greater on natural habitats than on infrastructure at higher latitudes (slope(mid) = −0.0069; 95% CI = −0.0127, −0.0011; figure 4(a)). The same pattern was found for and producers at the low tidal height slope (producers) = −0.0173, 95% CI = −0.0322, −0.0015; figure 4(b)). No other groups showed any patterns with latitude.

3.5. Site depth

When investigating the impact of depth on epibiotic abundance, models revealed that only the relative abundance of subtidal filter feeders on infrastructure compared to natural habitats significantly decreased with depth (slope(filter feeders) = −0.0222; 95% CI = −0.0368, −0.0076; figure 5). There was no statistical evidence for differences for the other groups. There was not sufficient variation in the study depths for grazers and detritivores (2.5 m total depth range across studies) and we are unable to reliably estimate patterns, so these groups have been excluded from analysis.

Figure 5. Overall lnRR for each functional group by depth for the subtidal. A positive lnRR indicates greater abundance on infrastructure compared to natural habitats, while a negative lnRR indicates reduced abundance on infrastructure compared to natural habitats. Asterisks indicate significance.

3.6. Sensitivity analyses and publication bias

There was evidence for significant heterogeneity in our models. In most cases, accounting for heteroscedastity improved the model fit, and those results are what have been reported here. The I^2 values calculated for each tidal height model highlighted that heterogeneity mostly came from differences between surveys (i.e. sampling the same sites over multiple timepoints) for the high tidal height, and from variation between effects for the low and subtidal levels. The variation was equal among all effects, publication, and survey for the mid tidal height. (table S7).

Leave-one-out analyses were performed to demonstrate the effect of removing one study on the models. Leave-one-out analyses were done on the larger models—each tidal height without moderators, it was found that the estimates changed very little, and trends remained the same (table S8).

4. Discussion

We found strong differences in the functional epibiotic groups that live on built infrastructure compared to natural habitats. This has clear implications for marine function, given the current footprint of these infrastructure and the rapid increase in marine construction globally (Bugnot *et al* 2021). However, patterns varied significantly with structure types and functional groups, suggesting that management and conservation efforts need to be tailored to the structure or target function in question.

There was a clear trend of decreased algal and grazer abundance on infrastructure compared to natural habitats, supporting our initial hypothesis. Overwater structures, such as pontoons and jetties, significantly alter light regimes through

increased shading, leading to reduced algal abundance (Blockley 2007), as observed here. We also found significantly less habitat-forming algae on infrastructure compared to natural habitats. This is of particular concern as overall decreases of these key organisms are not only expected to have functional consequences for the local habitat (see Mayer-Pinto *et al* 2020) but also to have cascading effects on associated organisms/communities, such as grazing invertebrates and fish (Airoldi *et al* 2008, Schiel and Lilley 2011). Although some of the organisms that often depend on habitat-forming macroalgae might be able to colonise other habitat-forming organisms such as ascidians or oysters (Yakovis *et al* 2008, Sellheim *et al* 2010), which were significantly more abundant on infrastructure, different habitat-forming species support distinct species and assemblages (Chemello and Milazzo 2002, Kochmann *et al* 2008, Marzinelli *et al* 2014, Cole *et al* 2018), so impacts are still likely to occur. Further, other functions provided specifically by algae, such as primary production or carbon-capture are expected to be affected by the proliferation of infrastructure. The loss of algae as a food source on infrastructure, when compared to natural habitats, may also contribute to the reduced grazer populations we observed. Additionally, increased wave action on structures like seawalls may also prevent grazers from attaching to the substrata (Kilar and McLachlan 1989, Pister 2009). Grazers, particularly grazing gastropods, rely heavily on microhabitats such as pools and crevices (Kohn and Leviten 1976, Beck 2000), which are notably absent on infrastructure. This lack of habitat complexity is a key factor driving the reduced abundance of grazers on such structures (Chapman 2003, 2006). Grazers play a crucial role in structuring ecosystems and can directly impact recruitment success of algae as well as sessile

animals (Underwood and Jernakoff 1981, Petraitis 1987). Reduced grazer abundance may therefore also be linked to the increased abundances of filter feeding organisms observed on infrastructure.

Our analysis revealed significantly more filter feeders on infrastructure than on natural habitats, although results were structure- and tidal height-specific. Filter feeders play key roles in marine systems, including capturing material suspended in the water column, resulting in changes in water clarity and phytoplankton availability (Prins and Escaravage 2005), and ultimately influencing nutrient cycling and food webs. For instance, increased consumption of plankton due to higher filter feeder abundance could limit the flow of energy through the ecosystem, potentially impacting higher trophic level species such as fish in pelagic food webs (Legendre 1990, Prins and Escaravage 2005). Alternatively, higher densities of filter feeders may also promote phytoplankton production by release of nutrients into the water columns, potentially enhancing productivity in these regions (Asmus and Asmus 1991, Nakamura and Kerciku 2000). Increased nutrients by way of deposition of faecal pellets from filter feeders may also have benefits for other benthic invertebrates living within or nearby to the filter feeders (Norkko *et al* 2001). Therefore, the shift between dominance of producers and filter feeders can have knock-on effects through several mechanisms in coastal areas where urbanisation is prevalent.

We initially hypothesised a greater abundance of mobile secondary consumers (predators and detritivores) on infrastructure compared to natural habitats due to the increased food resources (sessile invertebrates). A clear pattern did not emerge for these groups, with results varying with both tidal height and structure type. The predator and detritivore groups had the least amount of available data. These organisms also tend to be more mobile than grazing organisms, and thus are harder to detect in quadrat or transect type surveys, which made up most of the data analysed. The predator and detritivore groups were made up of a comparatively wider range of organisms than the other functional groups analysed here and included species from multiple taxa. For example, the predator group included both flatworms and sea stars, which likely have different prey types and habitat requirements. The lack of clear patterns for predators in this study may reflect this variation.

When comparing abundances of the groups between habitats across latitudes, we found that grazers (at mid and subtidal heights) and producers and detritovores (at low tidal height) were significantly more abundant on natural habitats than infrastructure at higher latitudes. The colder higher latitudes have reduced growth and recruitment (Brown 2014); thus it may be difficult for some organisms to colonise onto additional infrastructure. Bracewell

et al (2018) found that the effects of habitat complexity were most pronounced at higher latitudes, thus the lack of complexity on infrastructure compared to natural habitats may also be more critical for species to persist at higher latitudes.

We also considered how the method and type of sampling in each study may impact findings. Generally, the way in which studies were sampled revealed no differences in recorded abundances of the different functional groups, though grazers were found to be less abundant on infrastructure than on natural habitats when whole assemblages were surveyed. This may be because these organisms are often small and cryptic, making them difficult to find when they are not specifically targeted. Upon infrastructure that may also be more shaded, this difficulty may be more pronounced.

In this study, we compared the differences in abundance of functional groups of epibiota between infrastructure and natural hard substrata, as both types of habitats have hard surfaces. However, marine construction generally adds new hard substrata habitat to marine systems, rather than replacing it (Bulleri 2005). Therefore, although we found lower abundance of habitat-forming algae on infrastructure when compared to their natural counterparts, the net effect on their overall abundance is likely either positive, increased in abundance due to addition of hard substrata, or are negligible. Nevertheless, it is important to note that built infrastructure is significantly changing the coastal environment, creating novel assemblages and novel ecological dynamics to those on natural rocky shores. Importantly, structures are often built upon soft sediment habitats, which provide vastly different functions than hard substrata communities (Mumby *et al* 2008). Therefore, the potential losses of function provided by soft sediment communities, such as carbon storage (Song *et al* 2022), nutrient cycling (Levin *et al* 2001), denitrification (Fulweiler *et al* 2013), and habitat provisioning for numerous species (Snelgrove 1998) are arguably the more critical aspect of marine construction.

5. Conclusion

This study has provided an overview of the differences in epibiotic marine communities on natural habitats versus infrastructure and highlighted clear differences in abundances of key functional groups. Such shifts have important implications for key ecological processes including grazing and predation rates (Duffy 2003, Vergés *et al* 2014, Nowicki *et al* 2021), with expected consequences for ecosystem functions and the services they underpin (Hawkins *et al* 2009). Shifts in the dominance of primary producers and filter feeding organisms will alter the flow of nutrients within coastal marine ecosystems, while modified consumer abundance will alter the structure

of these systems through trophic cascades. Our results can also relate to the United Nations Sustainable Development Goals, particularly Goal 14 (Conserve and sustainably use the oceans, seas and marine resources for sustainable development) by highlighting the need for specific and targeted management of coastal urbanised marine ecosystems. We emphasise the need to consider functional diversity alongside biodiversity measures to comprehend the full range impacts of introducing infrastructure into marine environments. We highlight that the sustainable addition of marine infrastructure requires careful planning to preserve critical ecosystem processes such as nutrient cycling, carbon storage and habitat provisioning into the future. With the global acceleration of marine construction (Bugnot *et al* 2021), understanding the functional consequences of assemblage shifts is imperative.

Data availability statement

No new data were created or analysed in this study.

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