Marine Environmental Research 198 (2024) 106498

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Influence of habitat features on the colonisation of native and non-indigenous species

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ARTICLE INFO

Original content: Australia_Metaanalysis (Original data)

Keywords:
Artificial structures
Colonisation
Eco-engineering
Non-indigenous species
Meta-analysis

ABSTRACT

Marine artificial structures provide substrates on which organisms can settle and grow. These structures facilitate establishment and spread of non-indigenous species, in part due to their distinct physical features (substrate material, movement, orientation) compared to natural habitat analogues such as rocky shores, and because following construction, they have abundant resources (space) for species to colonise. Despite the perceived importance of these habitat features, few studies have directly compared distributions of native and non-indigenous species or considered how functional identity and associated environmental preferences drive associations. We undertook a meta-analysis to investigate whether colonisation of native and non-indigenous species varies between artificial structures with features most closely resembling natural habitats (natural substrates, fixed structures, surfaces oriented upwards) and those least resembling natural habitats (artificial materials, floating structures, downfacing or vertical surfaces), or whether functional identity is the primary driver of differences. Analyses were done at global and more local (SE Australia) scales to investigate if patterns held regardless of scale. Our results suggest that functional group (i.e., algae, ascidians. barnacles, bryozoans, polychaetes) rather than species classification (i.e., native or non-indigenous) are the main drivers of differences in communities between different types of artificial structures. Specifically, there were differences in the abundance of ascidians, barnacles, and polychaetes between (1) upfacing and downfacing/vertical surfaces, and (2) floating and fixed substrates. When differences were detected, taxa were most abundant on features least resembling natural habitats. Results varied between global and SE Australian analyses, potentially due to reduced variability across studies in the SE Australian dataset. Thus, the functional group and associated preferences of the highest threat NIS in the area should be considered in design strategies (e.g., ecological engineering) to limit their establishment on newly built infrastructure.

1. Introduction

Non-indigenous species (NIS, or non-native species) are species introduced outside their natural historical or present range (Williamson and Griffiths, 1996). When these NIS survive, establish and proliferate in a new region they can have substantial negative environmental, economic and social impacts (Bax et al., 2003). Long distance translocations of marine species to new regions occur mainly via individuals attached to ships' hulls (i.e., fouling) or the ballast water of commercial ships (Jousson et al., 1998; McKindsey et al., 2007; Ruiz et al., 1997), though intentional aquaculture and aquarium translocations can also be significant contributors (Diana, 2009; Naylor et al., 2001). Upon arrival in a new region, marine artificial structures such as pilings, pontoons, seawalls, and breakwaters may provide habitat for marine NIS (Glasby

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https://doi.org/10.1016/j.marenvres.2024.106498
Received 28 November 2023; Received in revised form 21 March 2024; Accepted 7 April 2024

et al., 2007; Mineur et al., 2012) and can act as 'stepping stones' for the spread of NIS to surrounding habitats (Airoldi et al., 2015). Compared to natural hard substrates, artificial structures are often of lower native species diversity and abundance and higher NIS abundance (Mayer-Pinto et al., 2018; Colgan and Middelfart, 2011). As maritime trade, growing demand for coastal defences, and the growth in the blue economy lead to further construction of artificial structures (Bugnot et al., 2021; Sardain et al., 2019), NIS introductions, establishment and spread are likely to increase (Floerl et al., 2021).

Artificial structures are prone to NIS colonisation because they are often proximate to transport vectors (i.e., international vessels, in port facilities) that produce high propagule pressure; they have a high availability of bare space with few native competitors, when newly constructed or situated in contaminated estuaries, ports and marinas (Johnston et al., 2017); and they may be regularly disturbed through cleaning for inspection and maintenance (e.g., through water blasting, replacement of denso tape) (Bulleri and Chapman, 2010). The suitability of artificial structures for the establishment of NIS over native species may also reflect differences in substratum material (Dodds et al., 2022), movement (Dafforn et al., 2009; Glasby, 2001), orientation (Connell, 1999; Glasby and Connell, 2001) and/or complexity (Furchert, 2019) as compared to natural habitats, however, few studies have directly tested for these effects. Identifying the habitat features that influence NIS colonisation can inform designs of future marine structures to reduce NIS establishment in main areas of entry, such as ports and harbours.

Marine artificial structures are often constructed of materials (e.g. concrete, PVC) that do not naturally occur (Commissions, 2004; Dodds et al., 2022). These materials differ in microtexture, hardness, chemistry, wettability and colour/brightness compared to natural surfaces (Bulleri and Chapman, 2010; Loke and Todd, 2016) – influencing recruitment processes (settlement and post-settlement survival (Dodds et al., 2022), and hence community composition. For example, metal-leaching, can select NIS over native species due to greater environmental tolerances of NIS (Piola and Johnston, 2009).

Unlike natural substrata that are typically fixed or stationary, artificial structures may be fixed (e.g., jetty pilings) or floating (e.g., pontoons, boats) (Mineur et al., 2012). Whether a structure is fixed or floating can influence conditions such as inundation, light, and water movement, which determine the type of communities (or functional groups) that colonise these structures (Glasby, 1999; Glasby, 2001; Holloway and Connell, 2002, Perkol-Finkel et al., 2006). For example, structures that have good natural lighting may favour the establishment and growth of algae and other photosynthetic taxa, while those with high water movement may favour filter feeders such as mussels, though not serpulid polychaetes (Holloway and Connell, 2002). Unlike fixed structures, floating structures provide an isolated habitat with limited connection to benthos and an environment for NIS that is free from some benthic predators (Forrest et al., 2013), though not fish. Overall, floating artificial structures provide surfaces analogous to floating transport vectors (e.g., hulls of ships). Given that NIS are often transported on the hulls of vessels (Godwin, 2003; Gollasch, 2002), it is likely that artificial structures with physical properties similar to floating vectors will aid NIS colonisation to new areas.

Most artificial structures are either vertical (seawalls, side of pontoons, pylons) or oriented down (underside of pontoons). In contrast, natural reefs generally provide a greater intertidal area of gently sloping and of mainly upward-facing surfaces, with less overhangs or down-facing surfaces (Bulleri and Chapman, 2010). These differences in orientation can, by determining light and sedimentation have a profound impact on the recruitment of marine organisms, in particular algae and invertebrates (Miller and Etter, 2008; Airoldi, 2003; Irving and Connell, 2002).

Structural complexity is an important driver of marine biodiversity (McCoy and Bell, 1991; MacArthur and MacArthur, 1961; Tews et al., 2004), with natural hard substrates typically providing a diversity of microhabitats (e.g., rock pools and overhangs), which are absent on artificial structures (Bulleri and Chapman, 2010). These microhabitats can influence the composition of sessile communities by reducing competitive interactions and/or by providing refuge to inhabitants from predators and/or environmental stressors (Bros, 1987; Garrity, 1984; Scyphers and Powers, 2013; Underwood and McFadyen, 1983). In contrast, they may also assist in the recruitment success of NIS by enabling them to grow until reaching a size refuge (Young and Chia, 1984), and subsequently overcoming the biotic resistance of native communities (Dumont et al., 2011; Freestone et al., 2013; Simkanin et al., 2013; Gauff et al., 2023).

Understanding how differences in physical properties of artificial structures affect colonisation by marine biota is essential to building and/or retrofitting multifunctional structures that provide both human and environmental benefits, a field that is referred to as 'ecological engineering '(Bergen et al., 2001). Theory and practice are showing that standard artificial structures can be designed to deliver both their primary engineered purpose (e.g., coastal protection, vessel berthing), as well as habitat to a diverse range of species (Bishop et al., 2022; Strain et al., 2018; Vozzo et al., 2021; Chapman and Underwood, 2011). However, previous studies have generally considered overall biodiversity rather than quantifying the relative effect of eco-engineering marine infrastructure on native species versus NIS (for exceptions see Strain et al., 2018; Vozzo et al., 2021), or if differences are due to functional groups rather than invasive properties. Native species and NIS of the same functional group with similar functional traits (e.g., morphology) are likely to respond to similar environmental cues (Tamburri et al., 2008), and designs that prevent NIS from one functional group settling will likely prevent the settlement of native species of the same functional group as well. Therefore, to design infrastructure that promotes the diversity of native species while limiting the establishment of NIS, it is necessary to have a holistic understanding of the local species pool (both native and NIS) as well as priority NIS that could establish in the area, their taxonomic identity, and environmental preferences of constituent species, including NIS.

Here, we reviewed experimental studies to assess the effects of physico-chemical features of artificial structures (namely, materials, movement, orientation, and complexity) on the colonisation of native and non-indigenous species. Specifically, we used a meta-analysis to assess whether colonisation of native and non-indigenous species varies between artificial structures with features most closely resembling natural habitats (natural substrates, fixed structures, surfaces facing up, complex surfaces) and those least resembling natural habitats (artificial materials, floating structures, downfacing or vertical surfaces, flat surfaces). We hypothesised that native and non-indigenous species from the same functional group respond to changes in physical properties in the same way and that environmental preferences of different functional groups are primary divers of compositional differences in communities among different types of infrastructure, rather than their geographic origin and hence classification as native or non-indigenous. We conducted two meta-analyses using studies from across the globe and from within Australia, which were restricted to SE Australia, with most studies done in Sydney Harbour. This was done to test whether any patterns hold true regardless of scale.

2. Methods

2.1. Database search

A systematic search was conducted for peer-reviewed papers and reports, published between 1637 (earliest year within the database used) and 2023 (accessed December 22, 2023) that compared recruitment of marine organisms among substrates that differed in material, movement, orientation and complexity (hereafter referred to as 'features'). We conducted a Web of Science topic search using keywords associated with artificial structures and marine communities, along with keywords on materials, movement, orientation and complexity (Fig. S1).

The searches returned 5688, 847, 516, and 1447 results for materials, movement, orientation, and complexity, respectively. Theses and publications known to the authors but not returned in the search were also included. The title and abstract of each study were initially screened for relevance to our research questions (Fig. 1). The remaining subset of studies was then assessed for eligibility and selected for inclusion in the meta-analyses and qualitative review if they met the criteria below.

2.2. Criteria for inclusion

Studies selected for the meta-analysis included studies that compared the abundance (density or percentage cover) of marine organisms between.

(i) surfaces made of natural (groupings: rock, wood, biogenic) and artificial (groupings: clay, concrete, metal, polymer) substrates,
(ii) fixed and floating structures (not including rotating structures) where the vertical movement of floating structures was no more than the local tidal range,
(iii) surfaces oriented up versus downfacing and vertical orientations, and
(iv) a complex substrate (e.g., with microhabitats, with (micro) texture) and a flat control of the same material.

Studies selected for the meta-analysis were restricted to experimental field studies with experimental timeframes >1 week. Surveys were excluded to eliminate any potential bias due to the different ages of substrates. Similarly, studies where one feature was confounded by another feature were excluded. Only data at the species/genus level was included. Taxa were classified as non-indigenous (NIS), native (N), cryptogenic (C; those with unknown or unassigned origin), or unclear (U) (hybrid forms) (e.g., *Mytilus edulis complex*, see Ab Rahim et al., 2016) based on their classification in the study region (see Supplementary Material ‘Species_Status’). When there was a debate as to the taxon classification, the higher invasion classification was chosen (highest to lowest classification: NIS > C > U > N). Where the classification was not given, the taxon was classified based on other studies in the region and the expertise of the authors. However, only taxa that were categorised as native or non-indigenous were included.

This resulted in 5, 10 and 6 publications that satisfied the criteria for inclusion in our meta-analyses comparing substrate materials, orientation, and movement, respectively, with a subset of these used for analyses specific to Australia (Fig. 1, Table 1). As most studies from Australia were restricted to South-Eastern Australia (9 from NSW and a single study from South Australia), this dataset and analysis will be referred to as ‘SE Australia’ from hereon. There were insufficient data available to enable formal comparisons of different scales of complexity manipulations (e.g., microtexture, microhabitats).

Table 1
Number of studies, sites, experiments, and taxa included for each feature. N = native species, NIS = non-indigenous species.

Substrate	Global	SE Australia
Number of studies	5	NA
Number of sites	5	NA
Number of experiments	27	NA
Number of species	31 (4 N, 2 NIS)	NA
Orientation	**Global**	**SE Australia**
Number of studies	10	3
Number of sites	14	6
Number of experiments	55	17
Number of species	90 (62 N, 28 NIS)	22 (11 N, 11 NIS)
Movement	**Global**	**SE Australia**
Number of studies	6	4
Number of sites	12	7
Number of experiments	18	13
Number of species	51 (30N, 21 NIS)	44 (25N, 19 NIS)

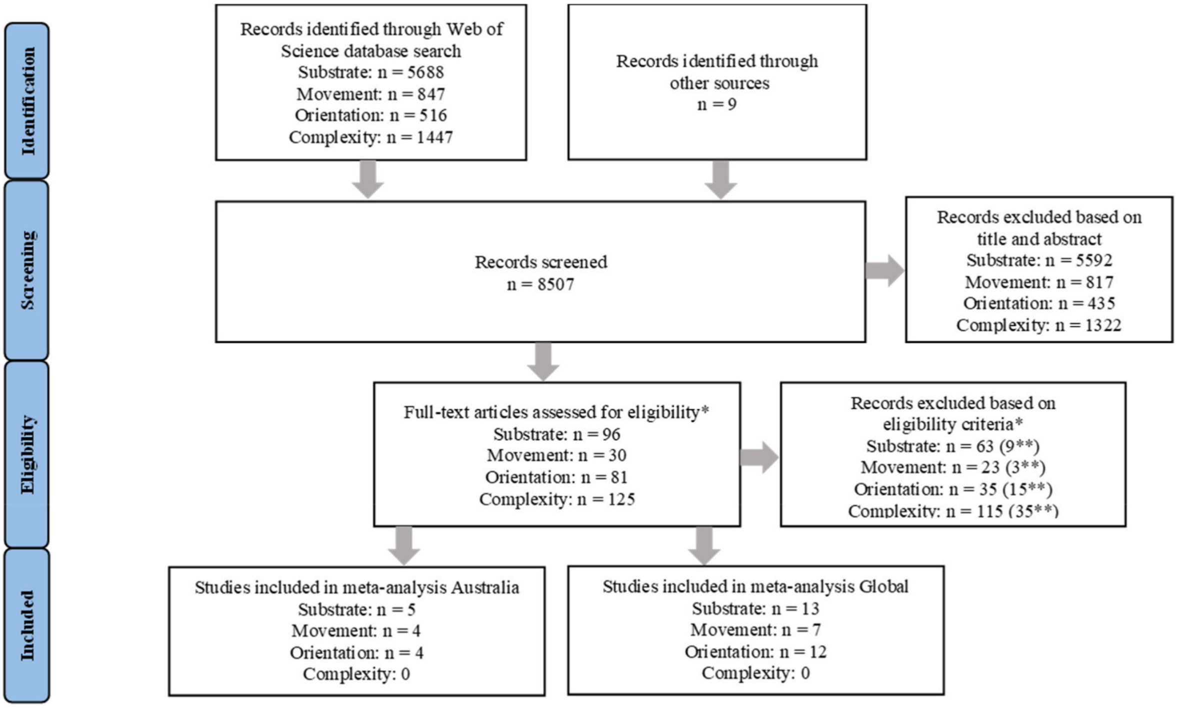

Fig. 1. Flow diagram for the identification of literature used in the meta-analysis and in the qualitative review. The automated process to remove duplicates did not identify all duplicates. Therefore, all records (including duplicates) were assessed, and this stage is omitted in the diagram. Reasons for exclusion of records at the eligibility stage are included in the Supplementary Material ‘Publication List’. N = Native species, NIS = Non-indigenous species.

2.3. Data extraction

From each publication we extracted the mean and standard deviation (SD) of abundance (count or cover) of each taxon, the taxon identity and classification (native or non-indigenous), the number of replicates, and experiment duration. If a publication reported multiple sites and/or time points, we recorded each comparison as a separate datapoint. Raw data or clarification was requested from authors where needed. Where necessary, data were mined from plots using GetData Graph Digitizer (version 2.26.0.20). Where SDs were not available, SDs were input from the fitted relationship between log (mean) and log (SD) for that dataset (after Van Rijkom et al., 1998). Features of artificial structures most closely resembling natural habitats (i.e., natural substrates, fixed surfaces, surfaces facing up) were used as controls, whereas characteristics most different to natural habitats (i.e., artificial substrates, floating surfaces, downfacing or vertical surfaces) were used as treatments. Effect sizes for each comparison between a treatment and a control were calculated for the abundance (abundance or cover) using natural logarithm of the ratio of means (ln RR; Hedges et al., 1999) with the *escalc* function from the R package 'metaphor' (Viechtbauer, 2010). For percent cover, arcsine-transformation data was used to calculate lnRR and the sampling variance to account for the non-normal distribution (data bounded by 0%–100%) (Jackson and White, 2018; Macartney et al., 2022). Therefore, positive effect sizes denote greater abundances on artificial than natural materials, greater abundances on floating than fixed surfaces, or greater abundances on downfacing/vertical surfaces than surfaces facing up, respectively. Zeros (no abundance, i.e., taxon absent on a control/treatment) were replaced with values slightly smaller with the lowest mean and standard deviations for both control and treatment to avoid taking natural logarithms of zero. This was done separately for density and percentage cover due to the different distributions. For studies where treatments shared a control material (or vice versa), we partitioned the sample size of the shared treatment/control evenly among the shared comparisons (Higgings et al., 2019). When features were tested interactively, or multiple shared controls/treatments were present, comparisons that had zero abundance for both the treatment and the control were deleted. In instances where an individual experiment provided data from multiple sampling points, we corrected for the resulting correlated sampling (error) variance (Noble et al., 2017) using variance–covariance matrices with a correlation coefficient of 0.5. To account for correlations that may arise due to evolutionary history and shared ecology (i.e., phylogenetic and non-phylogenetic species-level variances) (Lynch, 1991), we included taxonomic (species) and phylogenetic relatedness (a correlation matrix derived from a phylogenetic tree using the R package 'rotl' and Open Tree of Life data (Michonneau et al., 2016), with branch length computed using the compute.brlen() function in the R package 'ape' (Paradis et al., 2019) as random factors in the analysis (Cinar et al., 2022). When taxa were identified to genus level in one study and species level in another study, the genus level had to be used for all taxa to calculate this. When a species was not found in the database, a related species was used. Different materials (unless material was the physical characteristic of interest), movements (fixed and floating), orientations (facing up, facing down, vertical), sites, deployment times, or light treatments (shaded, unshaded) within a study were considered different 'experiments' unless an interactive effect was tested. The analysis was done for each dataset (Global, SE Australia) as described below.

2.4. Data analysis

A dummy variable using an interaction between feature (substrate, orientation, movement), functional group (algae, anthozoans, ascidians, barnacles, bivalves, bryozoans, polychaetes, poriferans) and classification (native (N) or non-indigenous (NIS)) was created and only levels of the three-way interaction that comprised of at least 3 experiments and 5 datapoints were kept. This dataset was used for analyses.

A multi-level meta-analytic model, including random effects, determined the overall mean effect sizes between natural and artificial materials, fixed and floating surfaces, and vertical and upfacing/downfacing surfaces. Random effects included the factors 'study', 'experiment' (experiments within a study), and 'duration' (for different sampling times within an experiment within a study) and an individual effect size identifier (unique per data row to estimate residual heterogeneity) to account for any other sources of variation. Parameter (abundance/percentage cover) was initially tested as a fixed factor, and was included as a random effect when significant (global analysis only). For global studies, five datapoints with large variances ($vi > 100$) were excluded as these were clear outliers. Variability between studies was investigated by testing the interaction between habitat feature, classification of the taxa, and functional group. High-level functional groups (algae, anthozoans, ascidians, barnacles, bivalves, bryozoans, hydrozoan, polychaetes, poriferans) were chosen and due to limited data at lower levels. Duration was not included as a variable in the model as there were insufficient datapoints for native and non-indigenous species within each feature. Marginal R^2 was used to quantify how much heterogeneity was explained by individual moderators and all moderators combined (Moatt et al., 2016; Nakagawa and Schielzeth, 2013). In all models, 'optim' was used as an optimizer (as per Nelder and Mead, 1965). Pairwise contrasts between moderator sublevels (for differences between native and non-indigenous species for each functional group) were conducted using general linear hypotheses via the function 'glht' in the 'multcomp' package (Hothorn et al., 2016). When pairwise comparisons identified no difference between native and non-indigenous species within a functional group within a feature, native and non-indigenous species were pooled and the model was re-run using an interaction of feature and functional group only. We visualized results using orchard plots in the R package 'orchaRd' (Nakagawa et al., 2021, 2023).

To assess whether our results were affected by publication bias, we visually inspected funnel plots of simple (no moderators) and multilevel (with significant moderators) models for asymmetry (Nakagawa and Santos, 2012) and ran Eggers regressions on the same models (Nakagawa et al., 2021). In no instance was asymmetry detected (Fig. S2, Table S1). Similarly, publication year was included as a moderator to test for time lag bias (Nakagawa and Santos, 2012) (Table 2).

3. Results

Studies included in the global analyses were from 12 countries (Fig. 2). Three studies, two from Australia and one from Chile (Dafforn et al., 2009, 2012a; Leclerc et al., 2020) directly compared native and non-indigenous cover/abundance. All studies were done in environments where artificial structures are common. Of the studies conducted in Australia, eight studies were conducted in Sydney Harbour (NSW), one in Port Kembla (NSW), and one in marinas in the St. Vincent Gulf and south of Adelaide (South Australia). Therefore, all studies from

Table 2
Level of heterogeneity (I^2), p-value, upper and lower confidence intervals (CI) for the simple model (no moderators), and QM statistic, heterogeneity (R2-marginal), and significance (p-value) for models with moderators for global studies.

Simple model	Estimate	SE	Lower CI	Upper CI	I2	p-value
No moderators	0.85	0.67	−0.46	2.16	99.99	0.2

Moderator(s)	**QM**	**R^2-marginal**	**p-value**
Feature*Functional group*Classification (F*T*C)	57.62	36.29	**<0.0001**
Functional group *Classification	37.68	29.86	**<0.0001**
Year	2.41	3.41	0.1205
F*T*C + Year	57.11	36.01	**<0.0001**

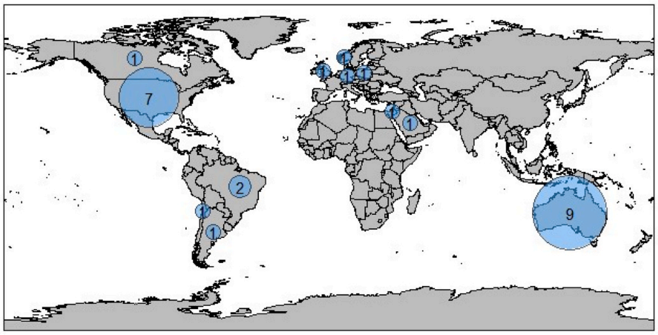

Fig. 2. Total number of studies included in the meta-analyses per country. The size of the circle is representative of the number of studies found in a country. For both meta-analyses, funnel plots and eggers regression indicated that no publication bias was present (Fig. S2, Table S1). Similarly, non-significant intercept for the model with publication year as a moderator demonstrated that our data were unaffected by time lag bias.

Australia were done in estuaries and bays characterised by an abundance of artificial structures and low to moderate wave conditions (Dafforn et al., 2012b; Lee, 2018).

3.1. Meta-analysis- global studies

The meta-analysis revealed that there was no difference in the overall abundance of colonisers (both native species and NIS pooled) between features of artificial structures most closely resembling natural habitats (i.e., natural substrates, fixed surfaces, surfaces oriented up) and those with features most different to natural habitats (i.e., artificial substrates, floating surfaces, downfacing or vertical surfaces) (Fig. 3, Table 2). The I^2 value was high (I^2: 99.99), indicating high levels of heterogeneity. Moderators identified sources of variability in abundance measures, explaining up to 58% of the variance (Table 2).

The interaction between feature, functional group and species classification was a significant moderator (Table 2, Fig. S3). However, pairwise comparisons revealed that there was no significant difference in abundance between native and non-indigenous species within the same functional group within each feature, except for ascidians (Table 3). Both native and non-indigenous ascidians showed greater abundances on vertical/downfacing surfaces compared to upfacing surfaces, though non-indigenous species showed a stronger response (Fig. S3).

Effects of features on functional groups were only found for ascidians, which were more abundant on vertical/downfacing surfaces than upfacing surfaces (Fig. 4).

3.2. Meta-analysis- SE Australian studies

The meta-analysis of SE Australian studies also found no difference in the overall abundance of colonisers (both native species and NIS pooled)

Table 3
Results of pairwise comparisons of native and non-indigenous species within each functional group and within each feature for global studies.

Feature-Functional group	Estimate	Standard Error	Statistic	p-value
Substrate-Bivalves	1.0998	1.6501	0.6665	0.9993
Orientation-Polychaetes	−0.9205	1.1298	−0.8148	0.9959
Orientation-Bryozoans	0.1659	0.5092	0.3258	1.0000
Orientation-Barnacles	1.1150	0.8471	1.3162	0.8798
Orientation-Ascidians	−1.8095	0.6347	−2.8508	**0.0453**
Orientation-Algae	−2.5850	1.1978	−2.1581	0.2782
Movement-Polychaetes	0.8555	1.2543	0.6820	0.9991
Movement -Bryozoans	0.6417	0.5784	1.1096	0.9576
Movement -Barnacles	0.1121	0.9723	0.1153	1.0000
Movement -Ascidians	0.8840	1.0520	0.8403	0.9947
Movement -Algae	−0.1724	0.8390	−0.2054	1.0000

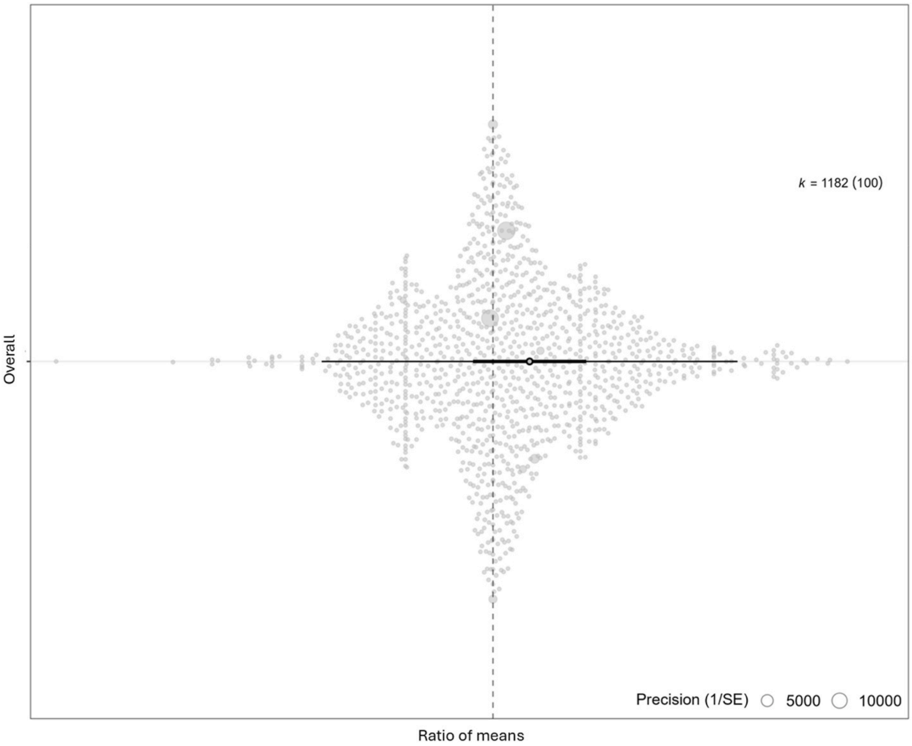

Fig. 3. Orchard plots showing the mean estimate, 95% confidence interval (bold line) and 95% prediction interval (fine line) for the simple model comparing abundances (counts, cover) of marine organisms on artificial structures with more natural (i.e., natural substrates, fixed surfaces, surfaces oriented up) and less natural (i.e., artificial substrates, floating surfaces, downfacing or vertical surfaces) features for global studies. "k" represents the number of data points. The number in brackets represents the number of experiments.

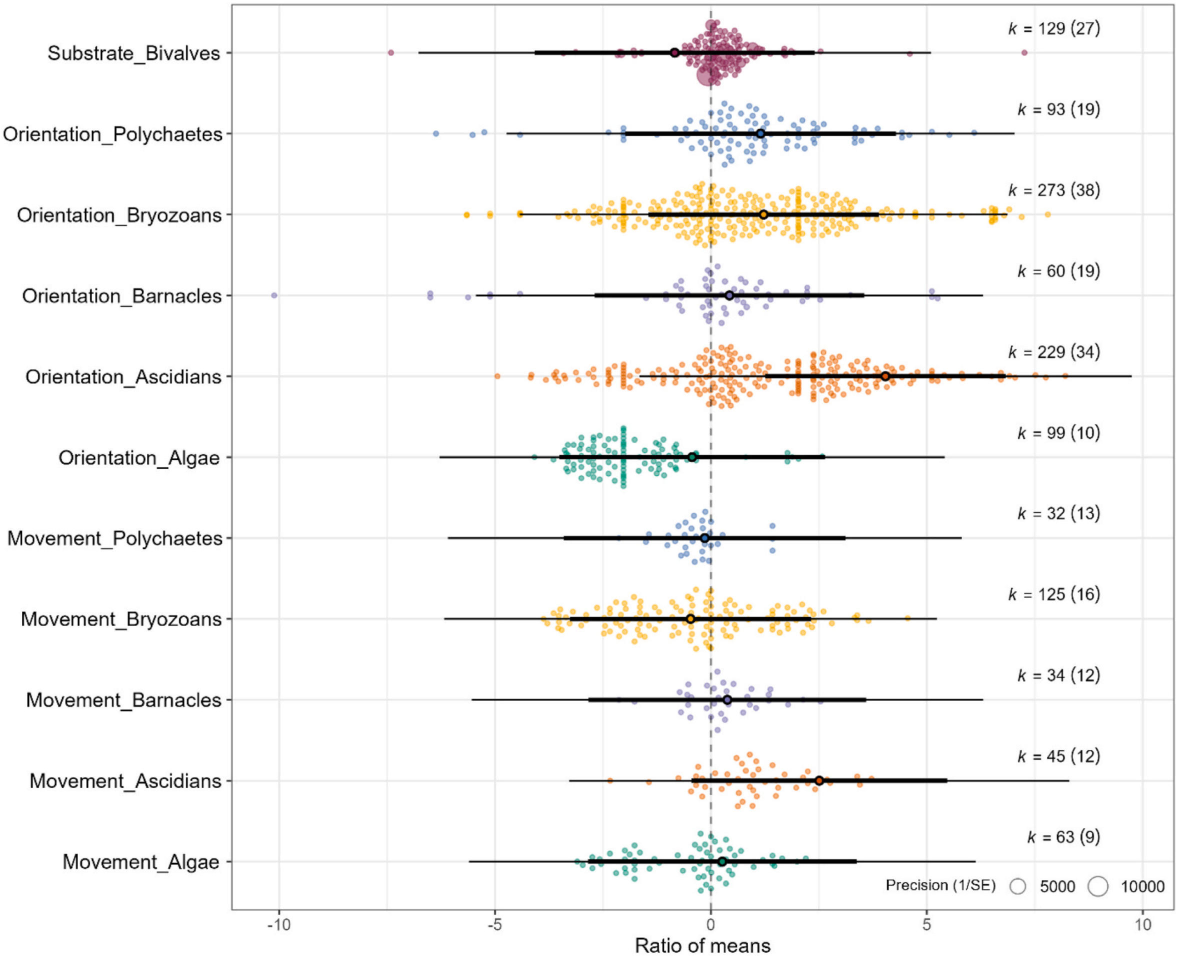

Fig. 4. Orchard plot showing the mean effect size (bordered circle), 95% confidence interval (bold line) and 95% prediction interval (fine line) for measures of abundance (abundance and percent cover) for different functional groups within each feature for global studies. Positive effect sizes denote greater abundances on structures most different to natural habitats. "k" represents the number of data points. The number in brackets represents the number of experiments.

between features of artificial structures most closely resembling natural habitats and those with features most different to natural habitats downfacing (Fig. 5, Table 4). In contrast to global studies, the I^2 value was low-medium (I^2: 34), indicating low to moderate levels of heterogeneity. Still, moderators identified sources of variability in abundance measures, explaining up to 40% of the variance (Table 4).

As for analyses of global studies, the interaction between feature, functional group and species classification was a significant moderator (Table 4, Fig. S4), but again, pairwise comparisons revealed no significant difference in abundance between native and non-indigenous species within the same functional group within each feature (Table 5).

Instead, there were effects of features (movement, orientation) that varied with functional group (Fig. 6, Supplementary Material 'Statistics'). Vertical/downfacing surfaces supported 72% more polychaetes than upfacing surfaces, but there was no difference in abundance for bryozoans. Responses to movement also varied between functional groups. Ascidians and barnacles were significantly more abundant (by 152% and 90%, respectively) on floating than fixed structures. No significant differences were found for other functional groups (algae, bryozoans, polychaetes).

4. Discussion

Increasing urbanisation of coastlines and expanding and increasingly connected transport networks are enhancing the risk of NIS introductions and establishment globally (Bugnot et al., 2021; Hulme, 2009). Preventative biosecurity management to inhibit NIS establishment and spread is considered the most cost-effective and efficient method to tackle invasive species (Department of Agriculture and Water Resources, 2015, Leung et al., 2002; Shannon et al., 2020; Simberloff et al., 2013). Our meta-analyses found there was no difference in the abundance of native and non-indigenous species between natural and artificial substrates collectively, or between surfaces facing up and those facing down or vertical surfaces, or fixed and floating structures, with a single exception in the global dataset (orientation-ascidians), though this was related to the strength of response. Rather we found that substrate features favoured certain functional groups, irrespective of whether they were native or non-indigenous taxa.

4.1. Artificial versus natural substrate

Substrate classification as 'artificial' or 'natural' could only be tested for a single functional group in the global analyses and was found to have little influence on their settlement. This may be because within these categories there is wide variation in the physico-chemical properties of individual materials which were more influential (Dodds et al., 2022). Artificial materials included concrete, metals and polymers – each of which may differentially influence colonists. Whereas concrete leaches calcium hydroxide that can serve as a settlement cue for calcifying organisms (Anderson, 1996; Bone et al., 2022), calcifying bivalves can be negatively influenced by metals, which may have negated positive effects of concrete. A further differentiation between different substrate materials as done in (Dodds et al., 2022) once more data becomes available could help disentangle these effects.

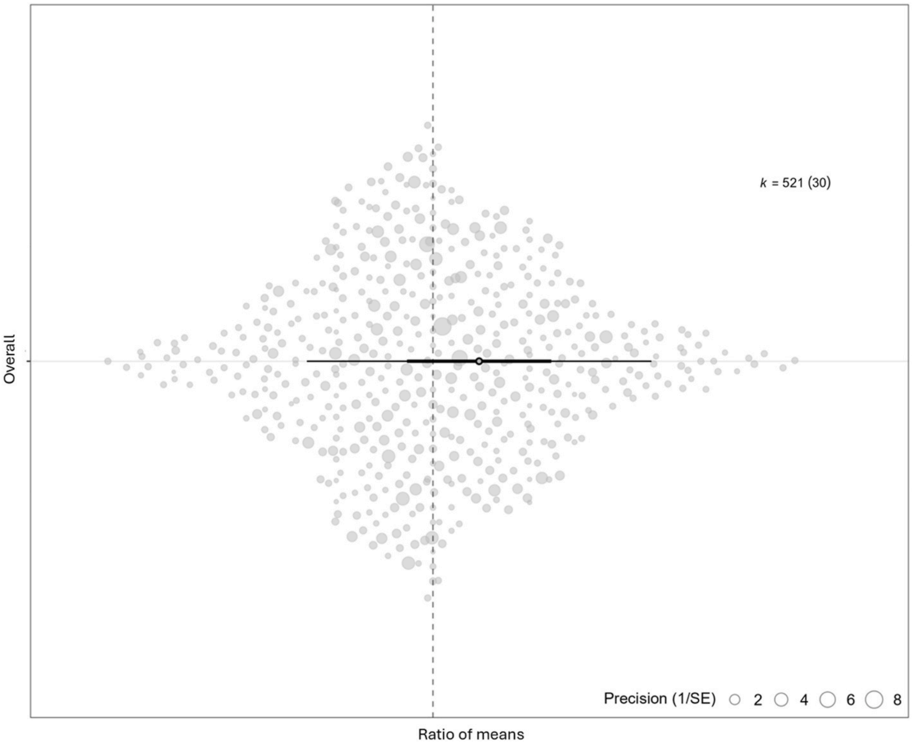

Fig. 5. Orchard plots showing the mean estimate, 95% confidence interval (bold line) and 95% prediction interval (fine line) for the simple model comparing abundances (counts, cover) of marine organisms on artificial structures with more natural (i.e., natural substrates, fixed surfaces, surfaces oriented up) and less natural (i.e., artificial substrates, floating surfaces, downfacing or vertical surfaces) features for SE Australian studies. “k” represents the number of data points. The number in brackets represents the number of experiments.

Table 4
Level of heterogeneity (I^2), p-value, upper and lower confidence intervals (CI) for the simple model (no moderators), and QM statistic, heterogeneity (R2-marginal), and significance (p-value) for models with moderators for SE Australian studies.

Simple model	Estimate	SE	Lower CI	Upper CI	I2	p-value
No moderators	0.36	0.28	−0.20	0.91	34.0	0.2

Moderator(s)	**QM**	**R^2-marginal**	**p-value**
Feature* Functional group*Classification (F*T*C)	29.91	26.74	**0.0079**
Functional group*Classification	39.76	35.84	**<0.0001**
Year	0.006	0.06	0.9366
(F*T*C) + Year	27.84	30.75	**0.0149**

Table 5
Results of pairwise comparisons of native and non-indigenous species within each functional group and within each feature for SE Australian studies.

Feature-Functional group	Estimate	Standard Error	Statistic	p-value
Orientation- Polychaetes	0.4390	0.3844	1.1420	0.8650
Orientation-Bryozoans	0.3489	0.2359	1.4791	0.6412
Movement- Polychaetes	0.1868	0.4731	0.3948	1.0000
Movement-Bryozoans	−0.0861	0.2865	−0.3003	1.0000
Movement- Barnacles	−0.1774	0.4567	−0.3885	1.0000
Movement- Ascidians	−0.1199	0.4925	−0.2434	1.0000
Movement-Algae	−0.0088	0.3048	−0.0290	1.0000

4.2. *Upfacing versus vertical/downfacing surfaces*

The effect of orientation showed varying responses. Algae tended to be more abundant on surfaces facing up than those facing down or in a vertical position, though this was not significant, whereas invertebrate groups either did not show different abundances between orientations or showed the opposite trend (polychaetes and bryozoans). These results likely reflect the differing environmental requirements of algae and invertebrates. Algae need light for photosynthesis so can be inhibited on shaded, downward-facing surfaces. Invertebrates, in turn can benefit from this release from competition with algae (Miller and Etter, 2008), displaying greater abundances on downward facing surfaces. Reduced levels of sedimentation on vertical and downfacing surfaces create conditions that may further enhance conditions for the recruitment of filter-feeding invertebrates (Irving and Connell, 2002), though some groups are able to adapt their behaviour to increased sediment load (e.g., ascidians actively expel suspended solids through their exhalant siphon) (Airoldi, 2003, Evans and Huntington, 1992). However, not all invertebrate groups differed in their abundance between orientations. This may be because not all functional groups or even species are equally as sensitive to orientation (Connell, 1999; Ushiama et al., 2016), or may have been caused by our methodological approach in in grouping vertical and downfacing surfaces together. When more studies are available in the future, distinguishing between these two orientations may further disentangle responses.

Most artificial structures are either vertical (seawalls, side of pontoons, pylons) or horizontal downward-facing (underside of pontoons) that receive less sunlight than natural upfacing surfaces. This increases the risk of NIS facilitation as many of the NIS globally are sessile invertebrates (Wasson et al., 2005; Williamson and Griffiths, 1996), which prefer poorly lit substrates (Miller and Etter, 2008). Changing the orientation of artificial structures to influence their colonisation by specific groups is however impractical. As light and sedimentation are the main factors associated with changes in orientation, these could be the focus of eco-engineering modifications. The light reaching overwater artificial structures may be enhanced by including light penetrating, gridded surfaces or by providing artificial lights (Blanton et al., 2002; Munsch et al., 2017). Sediment load may be reduced by

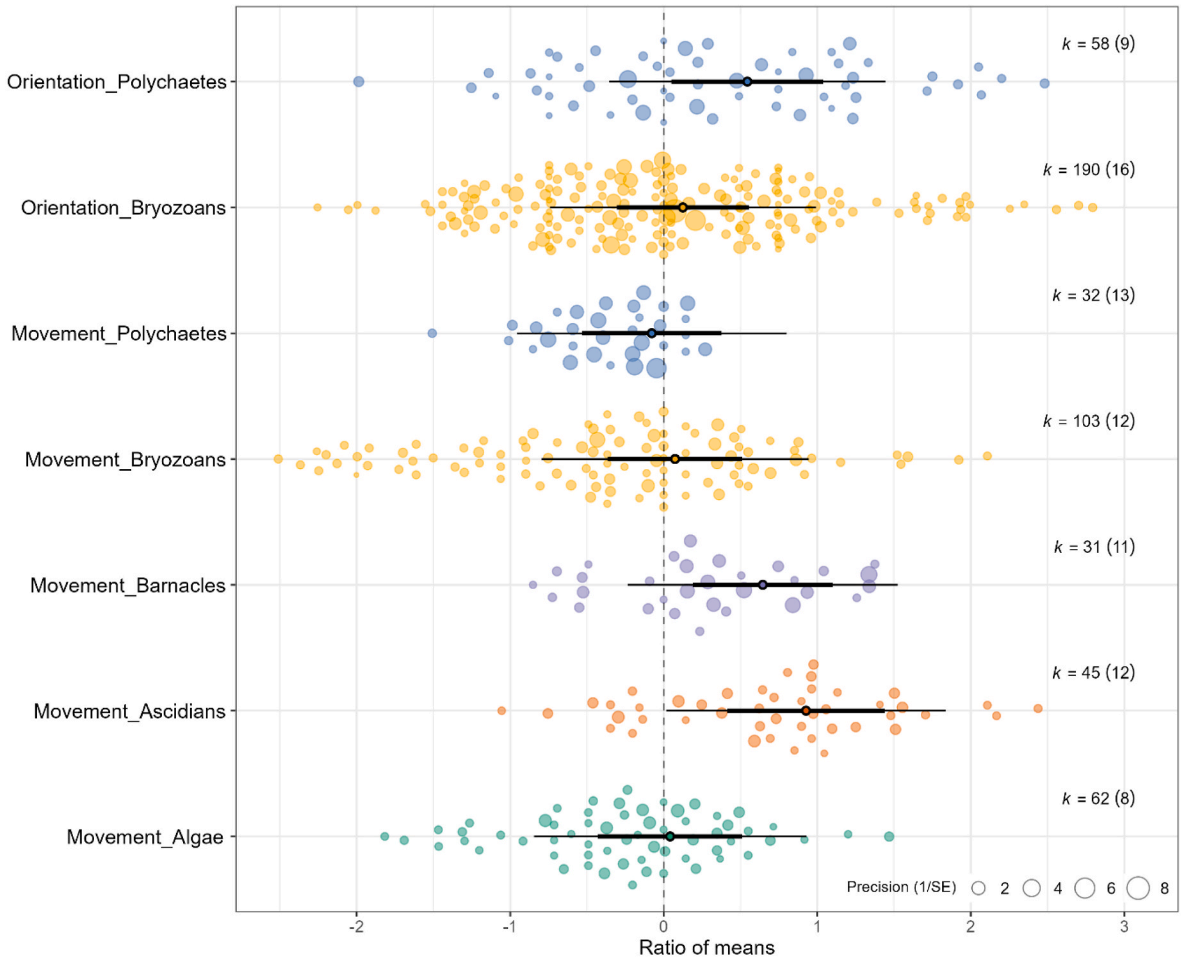

Fig. 6. Orchard plot showing the mean effect size (bordered circle), 95% confidence interval (bold line) and 95% prediction interval (fine line) for measures of abundance (abundance and percent cover) for different functional groups within each feature for SE Australian studies. Positive effect sizes denote greater abundances on structures most different to natural habitats. “k” represents the number of data points. The number in brackets represents the number of experiments.

preventing sediment runoff (e.g., through sediment traps). In areas where non-indigenous algae are present, other approaches, such as seeding artificial structures with native algae to reduce NIS colonisation, could be considered (Dafforn, 2017).

4.3. Fixed versus moving structures

The effect of movement on the abundance of functional groups was variable. Filter-feeding functional groups, where effects were found, generally benefited from increased water movement, which increases food availability and uptake (Eckman and Duggins, 1993). However, it is important to note that only one study used in this meta-analysis kept depth constant (Dafforn et al., 2009), and some of the differences, or lack thereof, may be explained by depth—stratified recruitment or light-related or hydrodynamic differences between structures (Holloway and Connell, 2002; Perkol-Finkel et al., 2008; Connell and Glasby, 1999). The lack of difference for some functional groups may be due to different responses towards movement by different species within the same functional group. For example, Dafforn et al. (2009) found that the barnacles *Amphibalanus variegatus* and *Megabalanus coccopoma* occupied more space on moving plates, whereas the barnacle *Balanus trigonus* was more abundant on fixed plates.

4.4. Global versus SE Australian studies

Results were somewhat variable between analyses using global studies and those using SE Australian studies only. For example, whereas ascidian and bivalves showed significant positive responses to movement in analyses for SE Australia, these effects were less pronounced and non-significant for global studies. Similarly, orientation had a significant effect on polychaetes in SE Australian studies, but only a trend was visible when using global studies.

Global studies were characterised by much greater variability than SE Australian studies (higher I^2), which could have been caused by the large spatial distance between study regions and therefore differences in environmental conditions. Similarly, numerous studies from the global dataset focussed on target species rather than entire communities, limiting the available data for the study. Both factors increase noise and therefore decrease the likelihood of detecting significant differences. However, the differences between global and SE Australian studies can also be a result of the smaller sample size, with only half the number of studies included in the SE Australian analyses compared to global analyses. Therefore, as more studies and data become available, analyses should be repeated to determine what caused these differences. Overall, it is important to note that the data included from Australian studies came from a very restricted geographical region (SE Australia), with 8/10 studies conducted in Sydney Harbour, and may therefore not reflect Australia more broadly. Australian analyses would benefit from better representation of studies from all geographical regions in Australia as they become available in the future. Nevertheless, the close proximity of study locations within SE Australian studies has likely made these analyses more robust, reducing effects of outliers and can thus provide important insights for management strategies within this region.

4.5. *Other considerations*

Overall, this study suggests that the success or failure of ecological engineering designs in preventing colonisation by NIS is likely driven by NIS present in the local environment, their shared characteristics (as represented by taxonomic or functional groupings) and their associated environmental tolerances/preferences. For example, in areas where sessile invertebrates are the dominant invaders (e.g., Sydney Harbour, Australia), eco-engineering designs that favour sessile invertebrate recruitment can facilitate NIS recruitment (Schaefer et al., 2023). Design options to limit NIS recruitment should therefore be chosen based on known responses to design factors of the NIS presenting the most risk to the area. However, this will have the caveat that native species of the same functional group may also be excluded and will not safeguard against future NIS establishment that may be from different taxa. Similarly, designs that promote the most common native species will likely attract NIS (with similar functional traits) of the same functional group as well due to similar environmental preferences, (Tamburri et al., 2008; Dodds et al., 2022), with NIS closely related to native species in the area being more likely to establish (McKnight et al., 2017). However, there is the risk that in urban areas, where contamination is high and NIS propagules and larvae are common (Johnston et al., 2017), eco-engineering designs will still favour NIS over native species. Duration could not be analysed in this study due to insufficient spread of datapoints for native and non-indigenous species within each feature. This factor is important in the determination of effects of features on the colonising biota, as early stages of community assembly may be dominated by opportunistic species (Hanlon et al., 2018), which are often non-indigenous, that may be outcompeted at later stages. Therefore, when more studies are available in the future, how the effects of features of infrastructure on native and non-indigenous species change over time should be investigated.

5. Conclusion

This meta-analysis assessed the effect of features of infrastructure designs on the abundance of NIS and native species. Overall, we found that ecological engineering designs can enhance or reduce the abundance of specific functional groups, which is linked to their environmental preferences. The meta-analyses revealed no difference in non-indigenous and native species abundance within the same functional group, indicating that effects found in studies could be reflective of the functional group of NIS abundant in the local environment. When considering ecological engineering in biosecurity management, such as in ports with high risk of NIS invasion, designs should consider the functional group of the highest threat NIS and modify physical properties of newly built infrastructure to incorporate cues that reduce their settlement. It is important to note that this may come at the risk of inadvertently reducing the abundance of native species within the same higher functional group as well. In ports with low risk of NIS invasion, increasing complexity and thus environmental niches should be prioritised.

CRediT authorship contribution statement

Nina Schaefer: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Melanie J. Bishop:** Writing – review & editing, Methodology. **Ana B. Bugnot:** Writing – review & editing, Methodology. **Cian Foster-Thorpe:** Writing – review & editing, Methodology. **Brett Herbert:** Writing – review & editing, Methodology. **Andrew S. Hoey:** Methodology, Writing – review & editing. **Mariana Mayer-Pinto:** Methodology, Writing – review & editing. **Shinichi Nakagawa:** Formal analysis, Methodology, Writing – review & editing. **Craig D.H. Sherman:** Methodology, Writing – review & editing. **Maria L. Vozzo:** Methodology, Writing – review & editing. **Katherine A. Dafforn:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

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

Data availability

I have shared the link to my data/code at the Attach File step Australia_Metaanalysis (Original data) (GitHub)

Acknowledgements

This project was funded through the Biosecurity Innovation Program by the Australian Department of Agriculture, Fisheries and Forestry.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106498.

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