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Dredging transforms the seafloor and enhances functional diversity in urban seascapes

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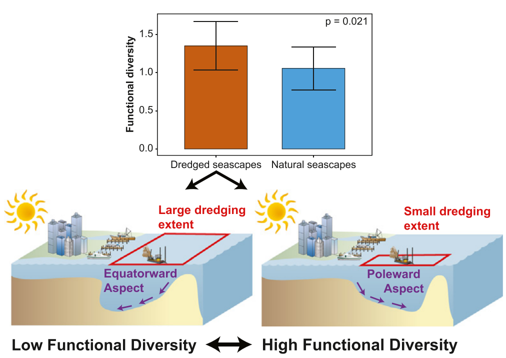
HIGHLIGHTS

- We investigated the functional consequences of dredging and terrain modification.
- Dredging reshapes the seafloor and can promote functional diversity.
- Functional diversity is elevated in small poleward facing dredged channels.
- Regulating the size and aspect of artificial channels can reduce dredging impacts.
- Carefully designed dredging programs can have functional benefits in estuaries.

GRAPHICAL ABSTRACT



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ABSTRACT

Landscape modification alters the condition of ecosystems and the complexity of terrain, with consequences for animal assemblages and ecosystem functioning. In coastal seascapes, dredging is routine practice for extracting sediments and maintaining navigation channels worldwide. Dredging modifies processes and assemblages by favouring species with wide trophic niches, diverse habitat requirements and tolerances to dredge-related eutrophication and sedimentation. Dredging also transforms the three-dimensional features of the seafloor, but the functional consequences of these terrain changes remain unclear. We investigated the effects of terrain modification on the functional diversity of fish assemblages in natural and dredged estuaries to examine whether dredging programs could be optimised to minimise impacts on ecological functioning. Fish assemblages were surveyed with baited remote underwater video stations and variation in functional niche space was described using species traits to calculate metrics that index functional diversity. Terrain variation was quantified with nine complementary surface metrics including depth, aspect, curvature, slope and roughness extracted from sonar-derived bathymetry maps. Functional diversity was, surprisingly, higher in dredged estuaries, which supported more generalist species with wider functional niches, and from lower trophic levels, than natural estuaries. These positive effects of dredging on functional diversity were, however, spatially restricted and were linked to both the area and orientation of terrain modification. Functional diversity was highest in urban estuaries where dredged channels were small (i.e. <1% of the estuary), and where channel slopes were orientated towards the poles (i.e. 171–189°), promoting both terrain variation and light penetration in urban estuaries. Our findings highlight previously unrecognised functional consequences of terrain modification that can easily be

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incorporated into dredging programs. We demonstrate that restricting the spatial extent of dredging operations and the orientation of dredged channel slopes, wherever this is practical, could help to limit impacts on ecosystem functioning and productivity in urban seascapes.

1. Introduction

Landscape transformation is ubiquitous in most biomes and is associated with widespread declines in the abundance and fitness of populations, and the condition and functioning of ecosystems (Hadley and Betts, 2012; Mitchell et al., 2015). Coasts in particular have become hotspots for landscape and seascape modification through intensive urbanisation due to the large human population that concentrate in cities by the seaside or near major ports (Bulleri and Chapman, 2010; Bishop et al., 2017). Urban coastlines are characterised by an abundance of armoured shorelines and artificial habitats, and modified estuaries are dredged intensively to improve their navigability and extract materials for construction (Heery et al., 2017; Todd et al., 2019). These major physical disturbances fragment natural ecosystems, which are also widely replaced with hard impervious surfaces, change bathymetry and hydrodynamics, modify run-off and the delivery of nutrients, sediments and pollutants into estuaries, and often leads to significant reductions in water and habitat quality (Erftemeijer and Lewis, 2006; Bishop et al., 2017; Wenger et al., 2017). The impacts of shoreline hardening, habitat loss and poor water quality have been documented for many urban estuaries, and are linked to declines in biodiversity, ecosystem functioning and food-web complexity (Dafforn et al., 2015; Malerba et al., 2019). Intensive dredging operations (e.g. sediment extraction) also remove habitat, fragment seascapes, and modify the three-dimensional structure of the seafloor, with negative effects on the abundance and diversity of a variety of functionally important taxa (e.g. dolphins, fish, macro-invertebrates, seabirds) (Todd et al., 2014; Fraser et al., 2017; Borland et al., 2022). The functional consequences of terrain modification are, however, rarely considered, and it is not known whether dredging programs can be spatially optimised to negate the adverse impacts on ecological functioning and ecosystem health in urban seascapes (Borland et al., 2021).

Seafloor dredging modifies the distribution of species and the composition of assemblages, and can also shape the physiological, behavioural and morphological traits of species, with potential consequences for the provision of ecosystem services and ecological functions (Todd et al., 2014; Zou et al., 2019; Borland et al., 2022). These impacts typically result from the effects of a diversity of stressors that accompany dredging projects, including declines in water and sediment quality (i.e. increased suspended sediments and nutrients), reduced light availability (i.e. for benthic photosynthetic organisms) and altered hydrodynamic processes (i.e. currents, circulation, residency) (Jones et al., 2016; Fraser et al., 2017; Wenger et al., 2017; Martelo et al., 2019; Callaway et al., 2020). These stressors interact to reduce diversity and increase dominance in assemblages by favouring generalist species with broad environmental tolerances and wide trophic niches (Meng et al., 2020; Bolam et al., 2021; Pledger et al., 2021). By selecting for species and phenotypes that are resistant to the effects of sedimentation, eutrophication and pollution, and altering the properties of trophic niche space, dredging operations can also modify functional diversity (i.e. variation in physiological, morphological and behavioural traits), and have led to declines in the functional attributes of bacteria and invertebrate assemblages in modified estuaries (Barrio Froján et al., 2011; Cooper et al., 2011; Störmer et al., 2013). The functional implications of dredging activities (e.g. sediment extraction) are, however, poorly understood for most mobile taxa (e.g. fish, turtles, seabirds) that perform important ecological roles in coastal ecosystems (Cooper et al., 2011; Störmer et al., 2013).

Dredging projects are conducted to modify the bathymetry of the seafloor, and to transform the complexity and morphology of terrain features, but changes to these three-dimensional attributes of estuarine seascapes have consequences for the distribution of biodiversity and ecosystem functioning (Borland et al., 2021; De Clippele et al., 2021; Borland et al., 2022). This is because high-relief and topographically complex terrain features (e.g. reefs, pinnacles, ledges) support a diversity of ecological niches and provide important feeding, sheltering and breeding habitats for many resident and migratory species (Wedding et al., 2019; Pygas et al., 2020). Variation in seafloor terrain can shape food-web dynamics, and modify ecosystem health and productivity, by altering the availability of light for photosynthetic organisms, and reducing the intensity of exposure to physical disturbances (e.g. tidal currents, waves, wind) (Pirtle et al., 2017; Stamoulis et al., 2018). Changes to terrain complexity can also alter the spatial distribution of predator-prey interactions, with cascading effects on a range of ecological functions (Henry et al., 2013; Barbini et al., 2018; Aarflot et al., 2020; Sutton et al., 2020). For example, variation in seafloor terrain is linked to changes in perceived predation risk in coral reef seascapes, and this alters patterns of habitat selection and the distribution of herbivory by a diversity of herbivorous fishes, which forage at different rates and in locations of differing terrain complexity when predators are present (Catano et al., 2015). The abundance of a diversity of species from a range of trophic levels (e.g. invertebrates, fish, cetaceans) is positively correlated with terrain complexity in many marine seascapes (e.g. coral and rocky reefs, continental shelves, the deep sea) (Bouchet et al., 2015; Pygas et al., 2020; Borland et al., 2021). Effects of terrain variation on ecosystem processes (e.g. herbivory, predation, primary production), and the spatial distribution of some functional groups, have also been reported in coral reef and deep sea seascapes (Catano et al., 2015; Ferrari et al., 2018; Mangan et al., 2020; De Clippele et al., 2021). The functional significance of terrain changes has, however, not been examined in coastal seascapes.

Estuaries support diverse fish assemblages that perform important ecological roles in coastal seascapes (e.g. herbivory, scavenging, predation) (Braga et al., 2012; Goodridge Gaines et al., 2020; Henderson et al., 2020b). The spatial distribution of these species and the ecological functions they perform are sensitive to the impacts of landscape modification, and can change in response to habitat fragmentation, shoreline armouring and the construction of artificial structures (Heery et al., 2017; Olds et al., 2018; Macura et al., 2019). Estuarine seascapes also contain major shipping ports and are subjected to frequent and widespread terrain modification from dredging operations, which remove rough and soft substrates from the seafloor (e.g. rocky bars and reefs, sand and mud flats), and create deep, steep-sided channels (Wenger et al., 2017; Borland et al., 2022). Dredging activity is typically associated with declines in the diversity of estuarine fish assemblages, which is a consequence of changes in the distributions of many fish species (Bilkovic, 2011; de Jong et al., 2014; Barletta et al., 2016). It can, however, also have positive effects on the abundance and biomass of generalist omnivores and scavengers (e.g. catfishes, Ariidae), which rapidly colonise dredged channels and outcompete other specialist predators (e.g. grunts, Sciaenidae) (Bilkovic, 2011; Barletta et al., 2016). Variation in the relief and complexity of seafloor terrain features also shapes the distribution, abundance and diversity of fish from a variety of trophic groups (Purkis et al., 2008; Pittman et al., 2009; Catano et al., 2015; Ferrari et al., 2018), but the possible functional effects of terrain transformation in dredged estuaries has not been examined (Borland et al., 2021). The primary objective of this study was to: (i) quantify the possible consequences of terrain modification from, and spatial extent of, dredging operations on functional diversity, and to inform the design of future dredging programs that minimise potential impacts on ecological functioning; and (ii) identify whether dredging modifies relationships between functional diversity and terrain features in natural and dredged seascapes. We mapped the bathymetry of dredged channels and estuarine seascapes, and the spatial extent of dredging operations, to test for the first time globally, for the effects of terrain variability in natural and dredged seascapes on four complementary measures of functional trait space (i.e. functional diversity, richness, evenness and dispersion), examine the functional consequences of variation in the spatial extent and context of dredging works in modified estuaries and identify the functional traits that explain assemblage-level responses to dredging.

2. Materials and methods

2.1. Study location

We surveyed fish assemblages from 29 estuaries (21 natural; 8 dredged) in Queensland, extending over 1000 km of eastern Australia, from Water Park Creek (22°57′S, 150°47′E) in the north to Currumbin Creek (28°07′S, 153°29′E) in the south (Fig. 1). The focal estuaries support abundant and diverse terrain features (e.g. subtidal rock-bars, intertidal sand-bars, tidal channels) and encompass a gradient in the spatial extent of seafloor modification by dredging (i.e. dredged channel size = 6–40% of the sampled extent of the estuary; e.g. low: Maroochy River; moderate: Burnett River; high: Brisbane River) (Hossain et al., 2004; Skilleter et al., 2006; Gilby et al., 2018; Henderson et al., 2019), and were therefore ideal seascapes for examining the possible effects of terrain modification on functional diversity (Fig. 1, Table S1).

2.2. Fish surveys

Fish assemblages were surveyed using Baited Remote Underwater Video Stations (BRUVS) that are a standard method for sampling fish assemblages in coastal and marine seascapes and are commonly used in studies that aim to calculate the functional diversity of fish assemblages (Coleman et al., 2015; Henderson et al., 2020a). BRUVS were constructed with a GoPro Hero 5 camera mounted on a 5 kg weight, that was connected to a PVC pole holding a bait bag extending 1 m from the camera (Olds et al., 2018). The bait bags were filled with 500 g of Pilchards (*Sardinops sagax*), which is used as a standard attractant to survey fish in most marine ecosystems (Harvey et al., 2007; Wraith et al., 2013). We standardised BRUVS deployments for salinity and the size of each estuary by deploying 10 BRUVS (i.e. $n = 290$) from the mouth of each estuary, up to the point in which salinity reached 30 psu (i.e. the marine extent of the estuary), with a minimum separation of 250 m to ensure independent sampling (Gilby et al., 2017). To account for the possible confounding effects of time, season, tide, water quality and seascape context, BRUVS were deployed: (1) for 1 h; (2) on one occasion per estuary during the austral winter (i.e. temporal variation was not a focus of this study); (3) over soft sediments at high tide (±2 h); and (4) 30 m away from intertidal mangroves and in 2 m of water (Olds et al., 2018; Henderson et al., 2020b). Fish abundance, diversity and assemblage composition were calculated from BRUVS footage once the disturbed suspended sediment had settled using the standard MaxN statistic (Murphy and Jenkins, 2010; Gladstone et al., 2012).

2.3. Mapping seafloor terrain and dredging

To investigate whether, and how, terrain modification by dredging impacts the functional diversity of estuarine fish assemblages, high resolution (≤1 m) bathymetry maps were created for each sampled estuary using an acoustic sounder (Lowrance HDS 7 - Gen 3). Bathymetry and benthic composition (i.e. backscatter: roughness and hardness) maps were creating by recording depth soundings of along-shore and cross-shore terrain variation on overlapping latitudinal and longitudinal transects conducted at a

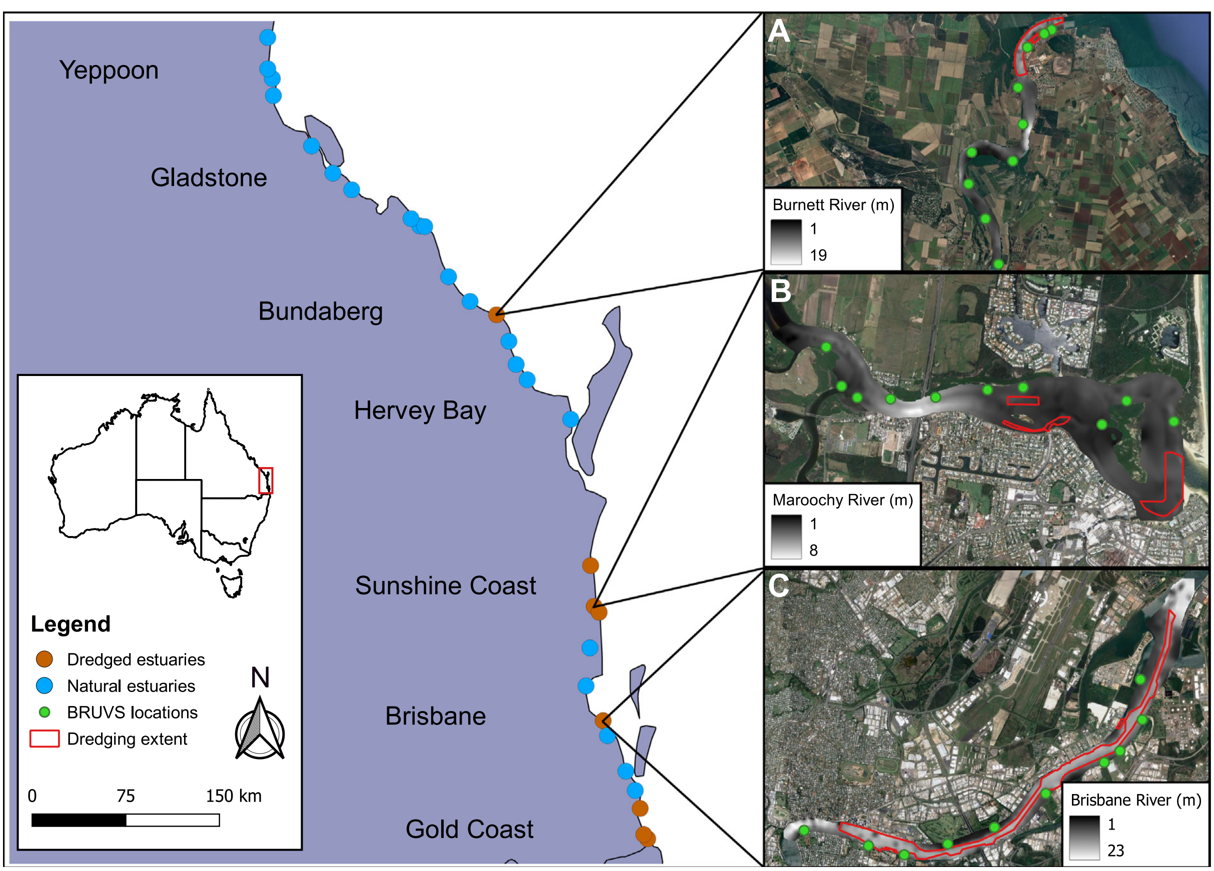

Fig. 1. Distribution of natural (blue circles) and dredged (brown circles) estuaries in Queensland, eastern Australia. Insets illustrate variation in seafloor terrain and the spatial extent and aspect of dredged channels in a: moderately dredged estuary with transformed terrain features (A); minimally dredged estuary with a diversity of terrain features (B); and extensively dredged estuary with modified terrain features (C).

maximum speed of 8 km/h^{-1}. To account for tidal variation, sonar files were corrected to highest astronomical tide (HAT) using data collected by pressure sensors (INW Smart Sensor) placed in each estuary, and were exported as digital bathymetric models (DBMs) in ReefMaster 2.0, for GIS analysis (Young et al., 2010; Li et al., 2017). Terrain metrics were quantified from the DBMs to describe variation in seafloor terrain using the Benthic Terrain Modeller and Spatial Analyst packages in ArcMap (Walbridge et al., 2018). Nine terrain metrics that are consistent predictors of the effects of terrain on fish diversity and abundance in a range of marine seascapes were used to quantify variation in terrain: seafloor relief (i.e. average depth), seafloor complexity (i.e. rugosity and slope), seafloor morphology (aspect: northness and eastness, plan curvature and profile curvature) and composition (i.e. backscatter: roughness and hardness) (Table 1) (Borland et al., 2021). These terrain metrics were averaged within 500 m buffers surrounding each sampling location, to match the daily home ranges of estuarine fishes, and the scale used in studies that have successfully linked variation in seascape patterning with the composition of fish assemblages, the performance of ecological functions, and the distribution of functional diversity in estuaries (Gilby et al., 2017; Olds et al., 2018; Henderson et al., 2020b; Borland et al., 2022).

Estuaries were categorised as either dredged or natural on the basis of their modification history, with data on dredging operations sourced from the Australian Government dredging permit database (https://apps.des.qld.gov.au/env-authorities/map/) (following Borland et al., 2022). The spatial extent of dredging operations was calculated in ArcMap from georeferenced dredging maps, and was corrected to the proportion of the sampled extent of each dredged estuary to standardise for variation in estuary size. Dredging permits facilitate annual dredging operations throughout the study area, but insufficient data are available to describe the frequency of these activities. Nonetheless, dredged channels are prominent features of estuaries, which persist in these seascapes in spite of slight variation in the frequency of sediment extraction (Borja et al., 2010). To examine whether the effects of terrain modification differed with variation in the spatial characteristics of dredging operations, we quantified the same nine terrain metrics, that were used to contrast dredged and natural estuaries, within the footprint of dredging operations in each estuary. We also calculated the percentage of urban shoreline within the sampled extent of each estuary in QGIS, to account for the possible confounding effects of urban land development and shoreline armouring (following Henderson et al., 2020b; Borland et al., 2022).

2.4. Calculating functional diversity

Functional diversity was indexed by obtaining data on the traits of all fish species identified in BRUVS footage using the *rfishbase* package in R (Boettiger et al., 2012). We used traits that correlate with variation in diet (i.e. functional group and trophic level), feeding ecology (i.e. head length, pre-orbital length and eye diameter), and body condition and morphology (i.e. body shape, length and depth), which describe how and where fish species forage, and the type of prey they can consume (Henderson et al., 2020a) (Tables S2 & S3). Data on fish traits and the composition of fish assemblages (extracted from BRUVS surveys) was then combined, using the *FD* and *fundiv* packages in R, to calculate four metrics that index different components of functional trait space (i.e. functional diversity, richness, evenness and dispersion) (Laliberté and Legendre, 2010; Gagic et al., 2015). Functional diversity (FD_{PG}) describes the diversity of occupied functional niches, and is calculated as the functional distance between all species in a dendrogram (Petchey and Gaston, 2002) (Fig. 2). Functional richness describes the overall fullness of functional trait space, and is calculated as the amount of functional trait space that is occupied by an assemblage (Mason et al., 2005). Functional evenness describes the fullness of different functional niches, and is calculated as the mean area of each occupied niche, weighted by species abundance (Mason et al., 2005). Functional dispersion describes the overall variability of functional trait space, and is calculated as the mean distance of each species from the centre of functional trait space, weighted by species abundance (Laliberté and Legendre, 2010).

Table 1
Description of terrain metrics derived from the digital bathymetric models (DBMs) in this study (see Borland et al., 2021 for more information).

Terrain metric	Description
Seafloor relief	
Average depth	Distance from the seafloor to sea level (metres)
Seafloor complexity	
Rugosity	Surface area to planar area ratio
Slope	Maximum change in elevation (degrees)
Seafloor composition	
Backscatter:	Reflectance and scattering of acoustic sonar
Roughness	Roughness of the seafloor (1 = least rough; 6 = most rough)
Hardness	Hardness of the seafloor (1 = least hard; 6 = most hard)
Seafloor morphology	
Plan curvature	Horizontal curvature of a feature: −1 = concave; 1 = convex
Profile curvature	Vertical curvature of a feature: −1 = concave; 1 = convex
Aspect:	The down-slope compass direction of a feature
Northness	Cos aspect: −1 = south orientation; 1 = north orientation
Eastness	Sin aspect: −1 = west orientation; 1 = east orientation

2.5. Statistical analysis

We examined the possible effects of terrain variation from dredging on functional diversity by testing for: (1) differences between dredged and natural estuaries; (2) variation in the consequences of terrain modification in dredged estuaries; (3) functional traits that explain assemblage-level responses to dredging; and (4) differences in the significance of terrain features between dredged and natural estuaries.

Generalised linear mixed models (GLMMs) were used to test for effects of modification (a fixed factor with two levels, natural or dredged) on: (1) terrain complexity (indexed as variation in seafloor depth, roughness, slope, curvature and aspect); and (2) functional diversity (indexed as functional diversity, richness, evenness and dispersion). All GLMMs used in this study were fitted using the *glmmTMB* package in R, and included estuary as a random factor (Brooks et al., 2017).

Generalised linear mixed models (GLMMs) were fitted with natural splines, with four of fewer polynomial functions, to test for effects of terrain variation on the spatial distribution of functional diversity (FD_{PG}) in dredged estuaries, using the *splines* package in R (Brooks et al., 2017; Geraci et al., 2021). These analyses focused on FD_{PG}, as this was the only measure of functional diversity that differed between dredged and natural estuaries, and tested for possible interactions between the spatial extent of dredging, latitude and variation in a suite of terrain metrics, including dredged channel depth, roughness, slope, plan curvature and aspect (northness and eastness). All variables were tested for co-linearity prior to analysis using Pearson's correlation coefficient (following Leitner et al., 2017; Rees et al., 2018), and consequently, rugosity (correlated with slope), profile curvature (correlated with plan curvature) and hardness (correlated with roughness) were removed from analyses ($r^2 \geq 0.7$). Models were compared using Akaike Information Criteria corrected for small sample sizes (AICc) using the *MuMIn* package in R, and best-fit models were those with the lowest AICc value. Quantitative interaction terms within best-fit models were visualised with contour plots using the *visreg* package in R (Breheny and Burchett, 2017).

TraitGLMs were then used to identify functional traits that were associated with assemblage-level responses to terrain modification, both between dredged and natural estuaries and within dredged estuaries, using the *mvabund* package in R (Tables S2 & S3) (Wang et al., 2012). TraitGLMs use a fourth-corner model to test for the interactive effects of species traits and environmental variables on multivariate abundance data. Best-fit traitGLM models were selected as those with the lowest Bayesian Information Criteria (BIC) using the LASSO penalty function, and the random effects of estuary were accounted for using the "block" function in *mvabund* (Wang et al., 2012; Rees et al., 2019).

GLMMs fitted with splines were then used to test for possible differences in the effects of terrain features on functional diversity (FD_{PG}) between

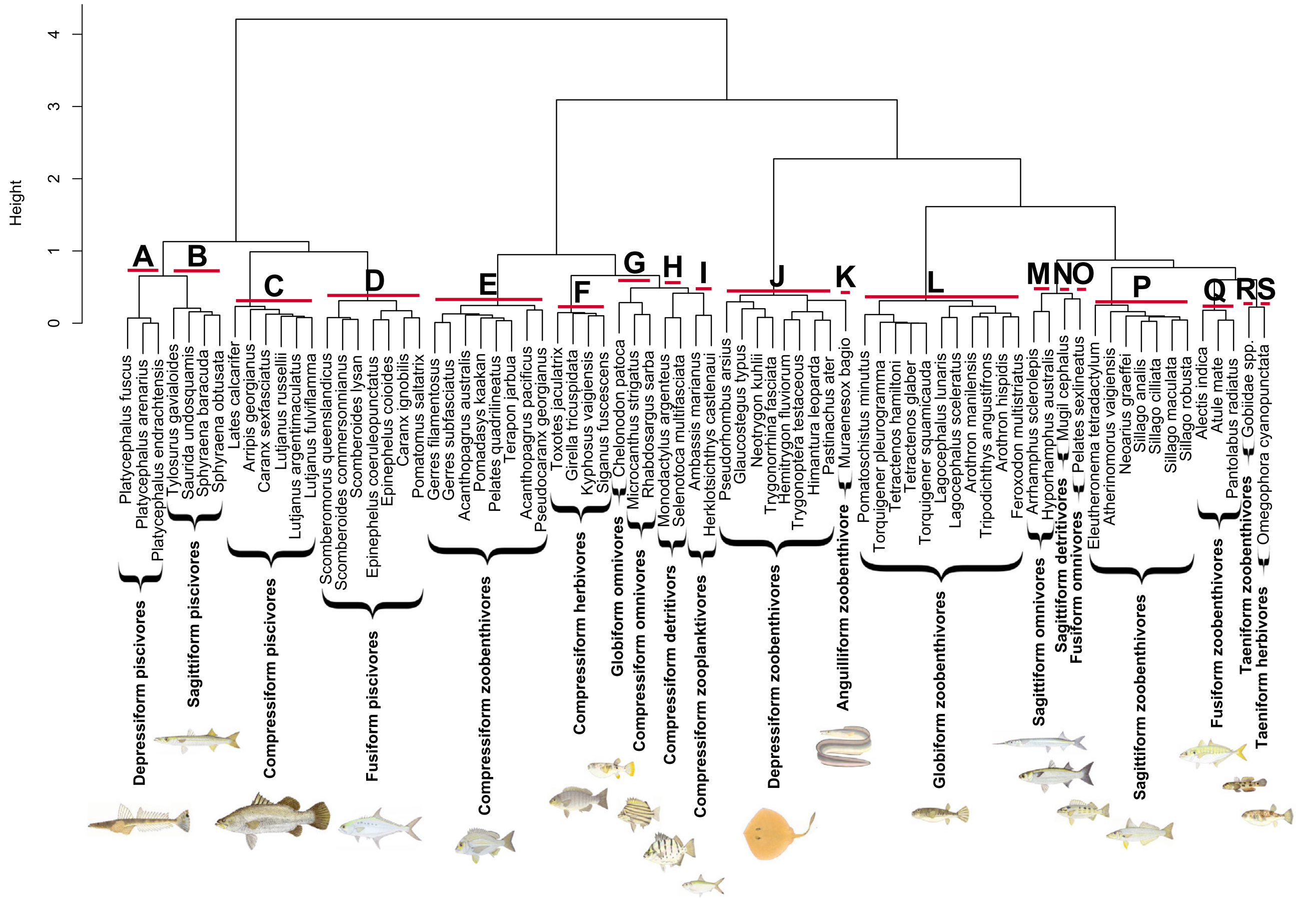

Fig. 2. Dendrogram used to calculate FD_{PG} illustrating differences in the functional traits of estuarine fish species. Letters and functional group names are assigned to groups of species that are separated from other groups by one or more divisions in the tree.

dredged and natural estuaries. These analyses tested for possible interactions between modification (a categorical variable with two levels, natural or dredged), latitude, percentage of urban shoreline, and variation in seafloor depth, roughness, slope, plan curvature and aspect (northness and eastness).

3. Results

3.1. Effects of dredging on seafloor terrain and functional diversity

Dredging substantially altered the terrain characteristics of modified estuaries, which were deeper (i.e. increased average depth), steeper (i.e. increased slope and plan curvature) and comprised of softer sediments (i.e. decreased roughness) then their natural counterparts (Table S4). The functional diversity (indexed by FD_{PG}) of fish assemblages also differed between dredged estuaries and natural systems and was highest in seascapes that were subjected to dredging (Fig. 3A, Table S5). Dredging did not, however, affect the functional richness, evenness or dispersion of fish assemblages (Fig. S1, Table S5).

Variation in ten functional traits of fishes was linked to assemblage-level responses to terrain modification (Fig. 4, Table S6). In contrast to natural estuaries, dredged seascapes contained: more species from low and mid-trophic levels (Fig. S2, Table S7); more zoobenthivores; more species with

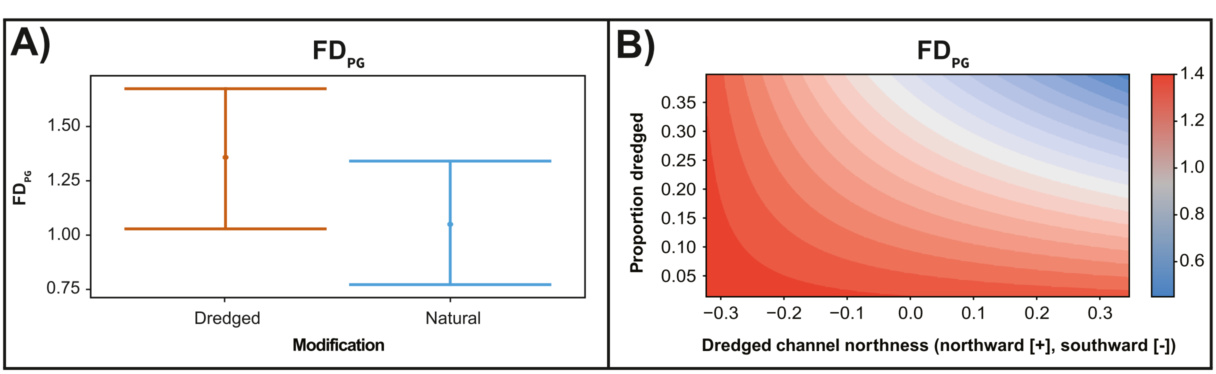

Fig. 3. Generalised linear mixed model (GLMM) illustrating the effects of modification (i.e. a categorical factor delineating either natural or dredged estuaries) on functional diversity in estuarine seascapes (A); and generalised linear mixed model (GLMM) illustrating the interactive effects of dredging extent (i.e. proportion dredged) and aspect (i.e. dredged channel northness) on functional diversity in dredged seascapes (B). See graphical abstract for a conceptual illustration of the effects of dredging extent and dredged channel northness on functional diversity in dredged seascapes.

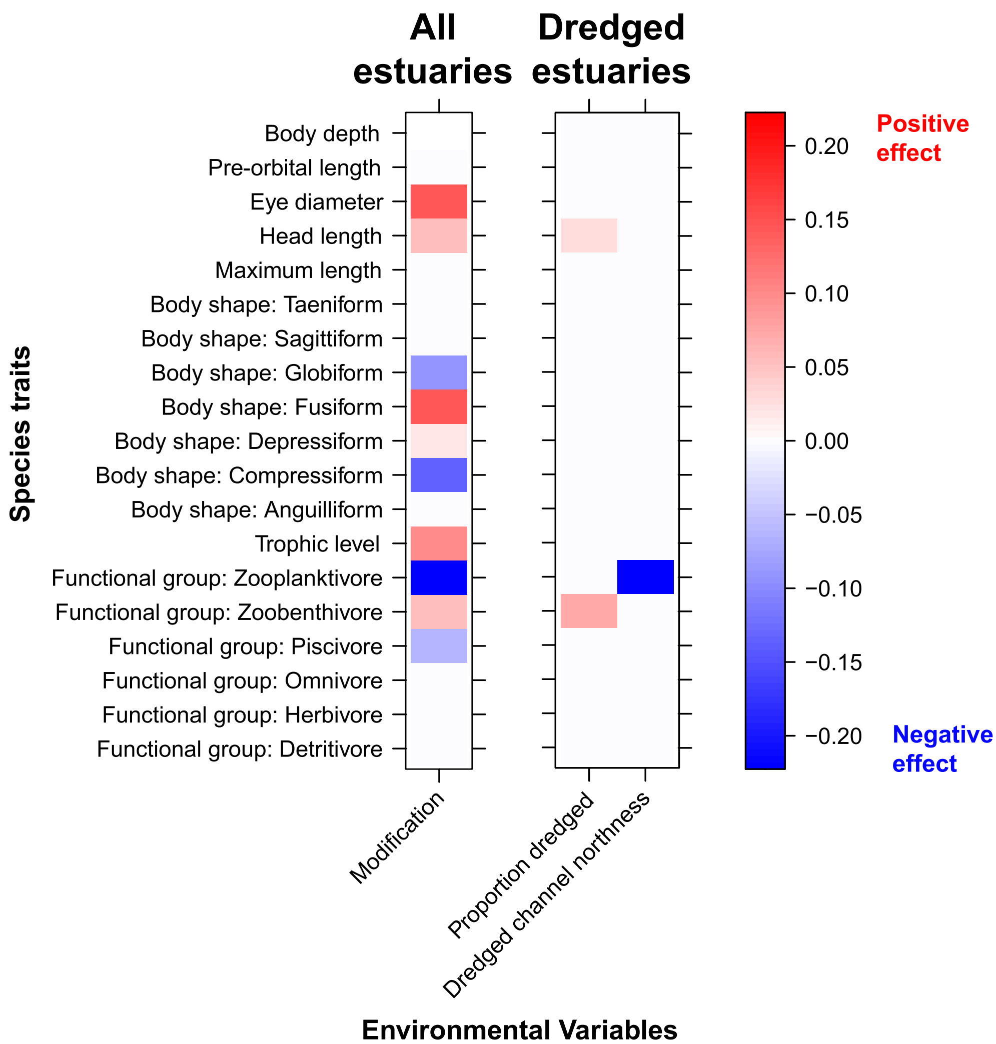

Fig. 4. TraitGLMs illustrating functional traits that were associated with assemblage-level responses to: modification (i.e. a categorical factor delineating either natural or dredged estuaries) in all estuaries; and dredging extent (i.e. proportion dredged) and channel orientation (dredged channel northness) in dredged estuaries.

fusiform or depressiform body shapes; more species with larger eyes and longer heads; fewer zooplanktivores and piscivores; and fewer species with globiform or compressiform body shapes (Fig. 4).

3.2. Effects of terrain on functional diversity in dredged estuaries

The functional diversity of fish assemblages in dredged estuaries was negatively correlated with the spatial extent of dredging (i.e. the proportion of each estuary that had been dredged) and also linked to the aspect of dredged channels (i.e. the orientation of channel slopes) (Fig. 3B, Table 2). Functional diversity was consistently highest in estuaries where the footprint of dredging operations was small, and at locations within these estuaries where the slope of dredged channels was orientated towards the south (Fig. 3B). Variation in the functional diversity of dredged estuaries was not, however, linked to changes in the depth, roughness, slope or curvature of seafloor terrain within dredged channels (Table 2).

The spatial extent of dredging operations and the orientation of dredged channels were correlated with three functional traits that explain assemblage-level responses to dredging and terrain transformation in modified seascapes (Fig. 4, Table S6). Estuaries that contained larger dredging extents (i.e. a larger proportion dredged) contained more zoobenthivores and species with longer heads, and estuaries with north-facing dredged channels (i.e. dredged channel northness) contained less zooplanktivores (Fig. 4).

3.3. Contrasting effects of terrain on functional diversity in dredged and natural estuaries

Terrain variation had contrasting effects on the functional diversity of fish assemblages in dredged and natural estuaries (Table 2). In dredged estuaries, functional diversity was highest where depths were either low or

Table 2
Summary of generalised linear mixed models (GLMMs) testing for effects of variation in the spatial extent (i.e. proportion of estuary dredged) and aspect (i.e. orientation of channel edges) of dredging footprints on functional diversity in dredged estuaries; and correlations between functional diversity, modification (i.e. a categorical factor delineating either natural or dredged estuaries) and seafloor terrain in all estuaries.Values in bold indicate statistical significance (p < 0.05).

Functional diversity	χ^2	*p*-Value
Dredged estuaries		
FD_{PG}		
Proportion dredged × dredged channel northness	7.761	**0.021**
All estuaries		
FD_{PG}		
Average depth × modification	27.143	**<0.001**
Eastness × modification	15.144	**0.004**
Slope × modification	9.545	**0.049**
Plan curvature	8.360	**0.004**

moderate, terrain features were orientated towards the poles (i.e. moderate eastness) and channel edges were steep (i.e. slope was high) (Fig. 5, Table 2). By contrast, in natural estuaries functional diversity was highest where depths were either low-moderate or high, terrain features were orientated towards the west (i.e. low aspect) and channel edges were gentle (i.e. slope was low) (Fig. 5, Table 2). The effects of plan curvature were consistent across both dredged and natural estuaries, with functional diversity always being highest near convex terrain features (Fig. 5, Table 2).

4. Discussion

Landscape modification leads to the fragmentation, replacement, and removal of natural habitats and three-dimensional terrain features, and this can result in declines in biodiversity and ecosystem functioning (Mayer-Pinto et al., 2018; Malerba et al., 2019). Our findings demonstrate that dredging operations can also modify functional diversity, and suggest that the functional consequences of dredging are likely determined by the spatial characteristics and footprint of terrain modification in urban estuaries. Functional diversity was highest in dredged estuaries, which supported more species with generalist traits (i.e. longer heads and larger eye diameters) and wide dietary niches (i.e. zoobenthivores), and were characterised by taxa from lower trophic levels, compared to their natural counterparts. The functional diversity of fish assemblages in dredged estuaries was, however, also linked to the spatial extent and orientation of dredging works, and was higher in locations with small southward facing dredged channels. There was also a sharp contrast in relationships between functional diversity and seafloor terrain in dredged and natural estuaries. Dredging transforms the terrain of modified estuaries by reducing the roughness and hardness (i.e. backscatter) of the seafloor, and by creating deeper channels with steeply sloping sides, and these human-modified terrain features provide valuable habitat for numerous species and can become hotspots for functional diversity in these highly modified seascapes (Madricardo et al., 2019; Eidam et al., 2020; Borland et al., 2022). These results concur with the findings of previous research highlighting the impacts of landscape transformation on functional diversity (Villéger et al., 2010; Henderson et al., 2020a), and the significance of seafloor terrain features for biodiversity (Pygas et al., 2020; Borland et al., 2021). Our findings suggest that the functional consequences of dredging can be reduced, and potentially enhanced, simply by reducing the extent of dredging operations and concentrating efforts on the poleward side of estuaries.

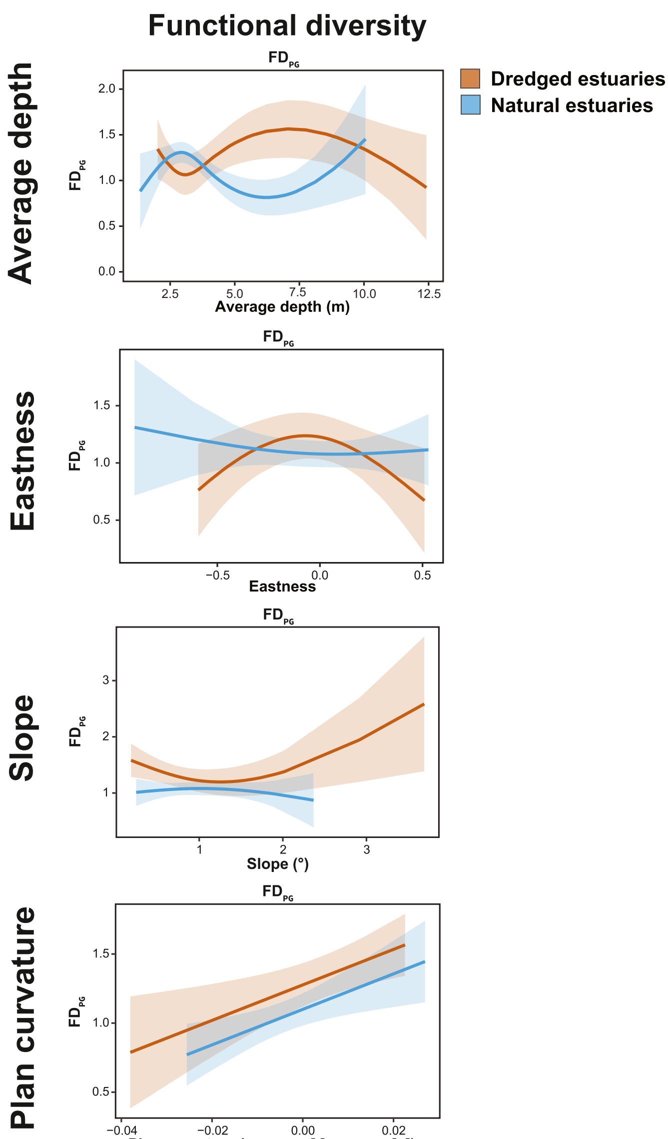

Fig. 5. Generalised linear mixed models (GLMMs) illustrating best-fit models testing for effects of modification and seafloor terrain on the distribution of functional diversity in natural and dredged seascapes.

It is widely accepted that dredging is associated with changes in ecosystem functioning, assemblage composition and species distributions in coastal seascapes (Todd et al., 2014; Fraser et al., 2017; Wenger et al., 2017; Borland et al., 2022). This occurs when a diversity of specialist species are replaced by generalists with high plasticity in their diets and patterns of habitat use, with cascading consequences for functional diversity and ecosystem health (Pezy et al., 2017; Bolam et al., 2021). Our results show that functional diversity was highest in estuaries that were subjected to dredging activity. These findings concur with the results of recent research reporting positive effects of perturbation (e.g. shoreline armouring, agricultural land transformation, water quality decline) on functional traits, and the performance of ecological functions, in estuaries (Olds et al., 2018; Teichert et al., 2018a; Teichert et al., 2018b; Henderson et al., 2020a). They are, however, also in contrast to the findings of several studies reporting negative effects of dredging on the functional diversity of bacteria and benthic invertebrates (Cooper et al., 2008; Wan Hussin et al., 2012; Störmer et al., 2013; Bolam, 2014). This juxtaposition appears to relate to the scale of research on functional diversity, the type of dredging impacts examined and the ecology of the focal animal assemblages. Our results suggest that larger functional effects might be expected from larger dredging projects and possibly from sediment extraction and terrain reprofiling rather than from elevated turbidity or spoil disposal works. Dredging creates deep channels with steep sloping sides (Madricardo et al., 2019; Eidam et al., 2020), and our findings indicate that these artificial features increase terrain relief and complexity in modified estuaries with direct benefits for a diversity of fishes that are similar to those that have been reported on reefs and in the deep sea (Pittman et al., 2009; Rees et al., 2018; Stamoulis et al., 2018). The consequences of this terrain modification are, however, not universally positive because dredging also increases the depth and changes the concavity in highly modified estuaries (Leuven et al., 2018; Madricardo et al., 2019), with negative effects on functional diversity in intensively dredged estuaries. It is likely that large-scale dredging activities affect the functional traits of assemblages by reducing niche diversity, and selecting for species with broad environmental tolerances, generalist traits (e.g. longer heads) and diets (e.g. zoobenthivores) which capitalise on an abundance of soft-sediment invertebrate prey in the absence of many natural competitors and predators (Bilkovic, 2011; Barletta et al., 2016; Rehitha et al., 2017; Piló et al., 2019). The functional consequences of dredging, therefore, appear to vary depending on the physiological, behavioural and morphological traits of animal assemblages, and this suggests that adaptive dredging plans which seek to maintain terrain complexity and heterogeneity and promote functional diversity, might be needed to limit potential impacts on ecosystem functioning in urban seascapes.

Dredging modifies the health and functioning of ecosystems, and food-web dynamics, by modifying the density and availability of primary producers that support coastal food-chains (Erftemeijer et al., 2012; de Jonge and Schückel, 2019). This occurs through the direct removal or burial of photosynthetic organisms, and the indirect effects of increased channel depth and turbidity on benthic light availability (Erftemeijer and Lewis, 2006; Ewa-Oboho et al., 2008; Pineda et al., 2016; Thomson and Manoylov, 2019). Our findings show that functional diversity was correlated with the aspect of dredging, and was highest in seascapes that contained southward facing dredged channels. The compass orientation (i.e. aspect) of terrain features determines the duration and intensity of light availability for photosynthetic organisms (Bouchet et al., 2015; Borland et al., 2021), and terrain features that face the equator typically experience light at greater intensities and for longer durations, with significant consequences for primary productivity and food-web complexity (Bennie et al., 2008; Gutiérrez-Jurado and Vivoni, 2013). Decreased light availability through shading has negative impacts on primary production from subtidal vegetation and microorganisms, and can limit the amount of carbon that is transferred through food-webs by microbial decomposition within seascapes that are already impacted by high turbidity (Underwood and Kromkamp, 1999; Hyndes et al., 2014; Abrantes et al., 2015; Jänes et al., 2020). Consequently, shaded channels typically support a lower abundance and diversity of prey for fish from most functional groups (e.g. plankton for zooplanktivores) (Fontanarrosa et al., 2010; Lorda and Lafferty, 2012; Pollard and Hodgson, 2016; Oh et al., 2019). It is, therefore, likely that functional diversity might have been highest over southward facing dredged channels because, in the southern hemisphere, these terrain features block less solar radiation than their northward facing counterparts, and the increased light availability promotes primary productivity and prey diversity, with flow-on effects to fish assemblages in turbid estuaries (Cussioli et al., 2019; Mangan et al., 2020). We suggest that the impacts of aspect on functional diversity could be minimised by concentrating dredging operations to the poleward side of estuaries, where the potential negative effects of steep terrain on light availability might be reduced.

Variation in the functional diversity of fish assemblages was correlated with the dominance of generalist zoobenthivores in dredged estuaries. These species likely dominated these seascapes because they are relatively free of their natural predators, and because their generalist diets, traits and habitat requirements allow them to take advantage of newly created niches, abundant foraging opportunities and reduced competition, provided by the increased seafloor complexity (i.e. slope), in shallow regions of urban seascapes (Pérez-Ruzafa et al., 2006; Henderson et al., 2020a). Whilst functional diversity was highest in dredged seascapes, these estuaries also supported fewer piscivores, which occupy higher trophic levels in estuarine seascapes. The abundance of many piscivores is strongly linked to the presence of hard substrates with high seafloor complexity (Morton and Gladstone, 2014; Bradley et al., 2017). Dredging removes structurally complex habitat and rough terrain features (e.g. rock bars and rocky reefs), and these processes are also associated with significant declines in water clarity (Wilber and Clarke, 2001; Todd et al., 2014). This likely means that dredging activity removes suitable habitat for piscivorous fishes and reduces their visual foraging efficiency, which can have fundamental consequences for food-web dynamics in modified estuaries (Rosenblatt et al., 2013; Wenger et al., 2017). Some piscivorous fish species (e.g. snappers and groupers) also use estuarine ecosystems, like seagrass meadows and mangrove forests, as nurseries and move out of coastal seascapes as their resource requirements change with growth, recruiting into adult populations in offshore habitats (e.g. coral and rocky reefs) (Abrantes et al., 2015; Baker et al., 2019). Declines in the diversity and abundance of piscivores in dredged seascapes might, therefore, also impact the productivity, health and functioning of both estuaries and their key connections with other habitats in coastal seascapes (Erftemeijer et al., 2012; Pollock et al., 2014).

5. Conclusion

The results of this study provide the first empirical evidence that the transformation of three-dimensional terrain features is associated with widespread changes in the amount, and spatial distribution, of functional diversity in natural and dredged seascapes. This study demonstrates that functional diversity can be higher in dredged estuaries than in their natural counterparts, where it is strongly associated with the relief, complexity, morphology and composition of terrain features in estuarine seascapes. Intense seafloor modification, however, altered the ecological value of these terrain features, and changed the relationship between functional diversity and seafloor terrain complexity. Changes to the functional ecology of urban estuaries were also correlated with the spatial characteristics of dredged channels, and functional diversity was highest when dredged channels were smaller and had slopes that were orientated towards the south. The influence of dredged channel size and orientation on functional diversity was consistent across all estuaries, despite considerable variation in their latitudinal distribution and some clustering towards the southern extent of our study area. These results suggest that small-scale seafloor modification (i.e. dredged channel size $\leq$ 1% of the marine extent of the estuary) might enhance terrain variation (i.e. increase the diversity of distinct terrain features) and promote the diversity of prey for generalist species with high habitat and dietary plasticity, but that these potential positive effects deteriorate with increased dredging activity (i.e. dredged channel size $\geq$ 1% of the marine extent of the estuary). Furthermore, it is possible that concentrating dredging efforts on the poleward side of estuaries to maintain channel aspects that do not impede light penetration (i.e. northness values ≤ -0.1 [i.e. ~171–189°] in the southern hemisphere, and values ≥ 0.1 [i.e. ~351–9°] in the northern hemisphere) might help to minimise the consequences of dredging activity on the functional ecology of estuarine seascapes. Small-scale seafloor modification might enhance terrain variation and promote the diversity of prey for generalist species with high habitat and dietary plasticity, but these potential positive effects deteriorate with increased dredging activity. These findings have wide implications for coastal management and urban planning in coastal seascapes, because the functional consequences of dredging operations can be severe but are rarely considered in marine spatial planning. These underappreciated impacts can also be minimised simply by limiting the footprint of dredging operations, and by concentrating terrain modification works along the poleward side of estuarine channels, whenever this is practical.

CRediT authorship contribution statement

Hayden P. Borland: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Ben L. Gilby**: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Christopher J. Henderson**: Data curation, Investigation, Methodology, Project administration, Writing – review & editing. **Rod M. Connolly**: Conceptualization, Funding acquisition, Writing – review & editing. **Bob Gorissen**: Investigation, Writing – review & editing. **Nicholas L. Ortodossi**: Investigation, Writing – review & editing. **Ashley J. Rummell**: Formal analysis, Writing – review & editing. **Simon J. Pittman**: Conceptualization, Writing – review & editing. **Marcus Sheaves**: Conceptualization, Funding acquisition, Writing – review & editing. **Andrew D. Olds**: Conceptualization, Funding acquisition, Formal analysis, Investigation, Methodology, Project administration, Resources, 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.

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Appendix A. Supplementary data

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References

Aarflot, J.M., Dalpadado, P., Fiksen, Y., 2020. Foraging success in planktivorous fish increases with topographic blockage of prey distributions. Mar. Ecol. Prog. Ser. 644, 129–142. https://doi.org/10.3354/meps13343.

Abrantes, K.G., Barnett, A., Baker, R., Sheaves, M., 2015. Habitat-specific food webs and trophic interactions supporting coastal-dependent fishery species: an Australian case study. Rev. Fish Biol. Fish. 25, 337–363. https://doi.org/10.1007/s11160-015-9385-y.

Baker, R., Barnett, A., Bradley, M., Abrantes, K., Sheaves, M., 2019. Contrasting seascape use by a coastal fish assemblage: a multi-methods approach. Estuar. Coasts 42, 292–307. https://doi.org/10.1007/s12237-018-0455-y.

Barbini, S.A., Sabadin, D.E., Lucifora, L.O., 2018. Comparative analysis of feeding habits and dietary niche breadth in skates: the importance of body size, snout length, and depth. Rev. Fish Biol. Fish. 28, 625–636. https://doi.org/10.1007/s11160-018-9522-5.

Barletta, M., Cysneiros, F.J., Lima, A.R., 2016. Effects of dredging operations on the demersal fish fauna of a South American tropical-subtropical transition estuary. J. Fish Biol. 89, 890–920. https://doi.org/10.1111/jfb.12999.

Barrio Froján, C.R.S., Cooper, K.M., Bremner, J., Defew, E.C., Wan Hussin, W.M.R., Paterson, D.M., 2011. Assessing the recovery of functional diversity after sustained sediment screening at an aggregate dredging site in the North Sea. Estuar. Coast. Shelf Sci. 92, 358–366. https://doi.org/10.1016/j.ecss.2011.01.006.

Bennie, J., Huntley, B., Wiltshire, A., Hill, M.O., Baxter, R., 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. Ecol. Model. 216, 47–59. https://doi.org/10.1016/j.ecolmodel.2008.04.010.

Bilkovic, D.M., 2011. Response of tidal creek fish communities to dredging and coastal development pressures in a shallow-water estuary. Estuar. Coasts 34, 129–147. https://doi.org/10.1007/s12237-010-9334-x.

Bishop, M.J., Mayer-Pinto, M., Airoldi, L., Firth, L.B., Morris, R.L., Loke, L.H.L., Hawkins, S.J., Naylor, L.A., Coleman, R.A., Chee, S.Y., Dafforn, K.A., 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. J. Exp. Mar. Biol. Ecol. 492, 7–30. https://doi.org/10.1016/j.jembe.2017.01.021.

Boettiger, C., Lang, D.T., Wainwright, P.C., 2012. rfishbase: Exploring, Manipulating and Visualizing FishBase Data From R. 81, pp. 2030–2039. https://doi.org/10.1111/j.1095-8649.2012.03464.x.

Bolam, S.G., 2014. Macrofaunal recovery following the intertidal recharge of dredged material: a comparison of structural and functional approaches. Mar. Environ. Res. 97, 15–29. https://doi.org/10.1016/j.marenvres.2014.01.008.

Bolam, S.G., McIlwaine, P., Garcia, C., 2021. Marine macrofaunal traits responses to dredged material disposal. Mar. Pollut. Bull. 168, 112412. https://doi.org/10.1016/j.marpolbul.2021.112412.

Borja, Á., Dauer, D.M., Elliott, M., Simenstad, C.A., 2010. Medium- and long-term recovery of estuarine and coastal ecosystems: patterns, rates and restoration effectiveness. Estuar. Coasts 33, 1249–1260. https://doi.org/10.1007/s12237-010-9347-5.

Borland, H.P., Gilby, B.L., Henderson, C.J., Connolly, R.M., Gorissen, B., Ortodossi, N.L., Rummell, A.J., Pittman, S.J., Sheaves, M., Olds, A.D., 2022. Dredging fundamentally reshapes the ecological significance of 3D terrain features for fish in estuarine seascapes. Landsc. Ecol. https://doi.org/10.1007/s10980-021-01394-5.

Borland, H.P., Gilby, B.L., Henderson, C.J., Leon, J.X., Schlacher, T.A., Connolly, R.M., Pittman, S.J., Sheaves, M., Olds, A.D., 2021. The influence of seafloor terrain on fish and fisheries: a global synthesis. Fish Fish. 22, 707–734. https://doi.org/10.1111/faf.12546.

Bouchet, P.J., Meeuwig, J.J., Salgado Kent, C.P., Letessier, T.B., Jenner, C.K., 2015. Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions. Biol. Rev. 90, 699–728. https://doi.org/10.1111/brv.12130.

Bradley, M., Baker, R., Sheaves, M., 2017. Hidden components in tropical seascapes: deep-estuary habitats support unique fish assemblages. Estuar. Coasts 40, 1195–1206. https://doi.org/10.1007/s12237-016-0192-z.

Braga, R.R., Bornatowski, H., Vitule, J.R.S., 2012. Feeding ecology of fishes: an overview of worldwide publications. Rev. Fish Biol. Fish. 22, 915–929. https://doi.org/10.1007/s11160-012-9273-7.

Breheny, P., Burchett, W.J.R.J., 2017. Visualization of regression models using visreg. R J. 9, 56–71.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 400. https://doi.org/10.3929/ethz-b-000240890.

Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. J. Appl. Ecol. 47, 26–35. https://doi.org/10.1111/j.1365-2664.2009.01751.x.

Callaway, R., Fairley, I., Horrillo-Caraballo, J., 2020. Natural dynamics overshadow anthropogenic impact on marine fauna at an urbanised coastal embayment. Sci. Total Environ. 716. https://doi.org/10.1016/j.scitotenv.2020.137009.

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2015. Reefscapes of fear: predation risk and reef hetero-geneity interact to shape herbivore foraging behaviour. J. Anim. Ecol. 85, 146–156. https://doi.org/10.1111/1365-2656.12440.

Coleman, M.A., Bates, A.E., Stuart-Smith, R.D., Malcolm, H.A., Harasti, D., Jordan, A., Knott, N.A., Edgar, G.J., Kelaher, B.P., 2015. Functional traits reveal early responses in marine reserves following protection from fishing. Divers. Distrib. 21, 876–887. https://doi.org/10.1111/ddi.12309.

Cooper, K.M., Barrio Froján, C.R.S., Defew, E., Curtis, M., Fleddum, A., Brooks, L., Paterson, D.M., 2008. Assessment of ecosystem function following marine aggregate dredging. J. Exp. Mar. Biol. Ecol. 366, 82–91. https://doi.org/10.1016/j.jembe.2008.07.011.

Cooper, K.M., Curtis, M., Wan Hussin, W.M.R., Barrio Froján, C.R.S., Defew, E.C., Nye, V., Paterson, D.M., 2011. Implications of dredging induced changes in sediment particle size composition for the structure and function of marine benthic macrofaunal communities. Mar. Pollut. Bull. 62, 2087–2094. https://doi.org/10.1016/j.marpolbul.2011.07.021.

Cussioli, M.C., Bryan, K.R., Pilditch, C.A., de Lange, W.P., Bischof, K., 2019. Light penetration in a temperate meso-tidal lagoon: implications for seagrass growth and dredging in Tauranga Harbour, New Zealand. Ocean Coast. Manag. 174, 25–37. https://doi.org/10.1016/j.ocecoaman.2019.01.014.

Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L., 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. Front. Ecol. Environ. 13, 82–90. https://doi.org/10.1890/140050.

De Clippele, L.H., Rovelli, L., Ramiro-Sánchez, B., Kazanidis, G., Vad, J., Turner, S., Glud, R.N., Roberts, J.M., 2021. Mapping cold-water coral biomass: an approach to derive ecosystem functions. Coral Reefs 40, 215–231. https://doi.org/10.1007/s00338-020-02030-5.

de Jong, M.F., Baptist, M.J., van Hal, R., de Boois, I.J., Lindeboom, H.J., Hoekstra, P., 2014. Impact on demersal fish of a large-scale and deep sand extraction site with ecosystem-based landscaped sandbars. Estuar. Coast. Shelf Sci. 146, 83–94. https://doi.org/10.1016/j.ecss.2014.05.029.

de Jonge, V.N., Schückel, U., 2019. Exploring effects of dredging and organic waste on the functioning and the quantitative biomass structure of the Ems estuary food web by applying input method balancing in ecological network analysis. Ocean Coast. Manag. 174, 38–55. https://doi.org/10.1016/j.ocecoaman.2019.03.013.

Eidam, E.F., Sutherland, D.A., Ralston, D.K., Dye, B., Conroy, T., Schmitt, J., Ruggiero, P., Wood, J., 2020. Impacts of 150 years of shoreline and bathymetric change in the Coos Estuary, Oregon, USA. Estuar. Coasts https://doi.org/10.1007/s12237-020-00732-1.

Erftemeijer, P.L., Lewis III, R.R., 2006. Environmental impacts of dredging on seagrasses: a review. Mar. Pollut. Bull. 52, 1553–1572. https://doi.org/10.1016/j.marpolbul.2006.09.006.

Erftemeijer, P.L.A., Riegl, B., Hoeksema, B.W., Todd, P.A., 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. Mar. Pollut. Bull. 64, 1737–1765. https://doi.org/10.1016/j.marpolbul.2012.05.008.

Ewa-Oboho, I., Oladimeji, O., Asuquo, F.E., 2008. Effect of dredging on benthic-pelagic production in the mouth of Cross River estuary (off the Gulf of Guinea), S. E.Nigeria. Indian J. Mar. Sci. 37, 291–297.

Ferrari, R., Malcolm, H.A., Byrne, M., Friedman, A., Williams, S.B., Schultz, A., Jordan, A.R., Figueira, W.F., 2018. Habitat structural complexity metrics improve predictions of fish abundance and distribution. Ecography 41, 1077–1091. https://doi.org/10.1111/ecog.02580.

Fontanarrosa, M.S., Chaparro, G., de Tezanos Pinto, P., Rodriguez, P., O'Farrell, I., 2010. Zooplankton response to shading effects of free-floating plants in shallow warm temperate lakes: a field mesocosm experiment. Hydrobiologia 646, 231–242. https://doi.org/10.1007/s10750-010-0183-1.

Fraser, M.W., Short, J., Kendrick, G., McLean, D., Keesing, J., Byrne, M., Caley, M.J., Clarke, D., Davis, A.R., Erftemeijer, P.L.A., Field, S., Gustin-Craig, S., Huisman, J., Keough, M., Lavery, P.S., Masini, R., McMahon, K., Mengersen, K., Rasheed, M., Statton, J., Stoddart, J., Wu, P., 2017. Effects of dredging on critical ecological processes for marine invertebrates, seagrasses and macroalgae, and the potential for management with environmental windows using Western Australia as a case study. Ecol. Indic. 78, 229–242. https://doi.org/10.1016/j.ecolind.2017.03.026.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional Identity and Diversity of Animals Predict Ecosystem Functioning Better Than Species-based Indices. 282, p. 20142620. https://doi.org/10.1098/rspb.2014.2620.

Geraci, M.L., Colloca, F., Di Maio, F., Falsone, F., Fiorentino, F., Sardo, G., Scannella, D., Gancitano, V., Vitale, S., 2021. How is artificial lighting affecting the catches in deep water rose shrimp trawl fishery of the Central Mediterranean Sea? Ocean Coast. Manag. 215, 105970. https://doi.org/10.1016/j.ocecoaman.2021.105970.

Gilby, B.L., Olds, A.D., Connolly, R.M., Maxwell, P.S., Henderson, C.J., Schlacher, T.A., 2018. Seagrass meadows shape fish assemblages across estuarine seascapes. Mar. Ecol. Prog. Ser. 588, 179–189. https://doi.org/10.3354/meps12394.

Gilby, B.L., Olds, A.D., Yabsley, N.A., Connolly, R.M., Maxwell, P.S., Schlacher, T.A., 2017. Enhancing the performance of marine reserves in estuaries: just add water. Biol. Conserv. 210, 1–7. https://doi.org/10.1016/j.biocon.2017.03.027.

Gladstone, W., Lindfield, S., Coleman, M., Kelaher, B., 2012. Optimisation of baited remote underwater video sampling designs for estuarine fish assemblages. J. Exp. Mar. Biol. Ecol. 429, 28–35. https://doi.org/10.1016/j.jembe.2012.06.013.

Goodridge Gaines, L.A., Olds, A.D., Henderson, C.J., Connolly, R.M., Schlacher, T.A., Jones, T.R., Gilby, B.L., 2020. Linking ecosystem condition and landscape context in the conservation of ecosystem multifunctionality. Biol. Conserv. 243, 108479. https://doi.org/10.1016/j.biocon.2020.108479.

Gutiérrez-Jurado, H.A., Vivoni, E.R., 2013. Ecogeomorphic expressions of an aspect-controlled semiarid basin: II. Topographic and vegetation controls on solar irradiance. Ecohydrology 6, 24–37. https://doi.org/10.1002/eco.1263.

Hadley, A.S., Betts, M.G., 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. Biol. Rev. 87, 526–544. https://doi.org/10.1111/j.1469-185X.2011.00205.x.

Harvey, E.S., Cappo, M., Butler, J.J., Hall, N., Kendrick, G.A., 2007. Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Mar. Ecol. Prog. Ser. 350, 245–254. https://doi.org/10.3354/meps07192.

Heery, E.C., Bishop, M.J., Critchley, L.P., Bugnot, A.B., Airoldi, L., Mayer-Pinto, M., Sheehan, E.V., Coleman, R.A., Loke, L.H.L., Johnston, E.L., Komyakova, V., Morris, R.L., Strain, E.M.A., Naylor, L.A., Dafforn, K.A., 2017. Identifying the consequences of ocean sprawl for sedimentary habitats. J. Exp. Mar. Biol. Ecol. 492, 31–48. https://doi.org/10.1016/j.jembe.2017.01.020.

Henderson, C.J., Gilby, B., Schlacher, T.A., Connolly, R., Sheaves, M., Flint, N., Borland, H.P., Olds, A.D., 2019. Contrasting effects of mangroves and armoured shorelines on fish assemblages in tropical estuarine seascapes. ICES J. Mar. Sci. 76, 1052–1061. https://doi.org/10.1093/icesjms/fsz007.

Henderson, C.J., Gilby, B., Schlacher, T.A., Connolly, R.M., Sheaves, M., Maxwell, P.S., Flint, N., Borland, H.P., Martin, T.S.H., Gorissen, B., Olds, A.D., 2020a. Landscape transformation alters functional diversity in coastal seascapes. Ecography 43, 138–148. https://doi.org/10.1111/ecog.04504.

Henderson, C.J., Gilby, B.L., Schlacher, T.A., Connolly, R.M., Sheaves, M., Maxwell, P.S., Flint, N., Borland, H.P., Martin, T.S.H., Olds, A.D., 2020b. Low redundancy and complementarity shape ecosystem functioning in a low-diversity ecosystem. J. Anim. Ecol. 89, 784–794. https://doi.org/10.1111/1365-2656.13148.

Henry, L.A., Moreno Navas, J., Roberts, J.M., 2013. Multi-scale interactions between local hydrography, seabed topography, and community assembly on cold-water coral reefs. Biogeosciences 10, 2737–2746. https://doi.org/10.5194/bg-10-2737-2013.

Hossain, S., Eyre, B.D., McKee, L.J., 2004. Impacts of dredging on dry season suspended sediment concentration in the Brisbane River estuary, Queensland, Australia. Estuar. Coast. Shelf Sci. 61, 539–545. https://doi.org/10.1016/j.ecss.2004.06.017.

Hyndes, G.A., Nagelkerken, I., McLeod, R.J., Connolly, R.M., Lavery, P.S., Vanderklift, M.A., 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. Biol. Rev. 89, 232–254. https://doi.org/10.1111/brv.12055.

Jänes, H., Macreadie, P.I., Nicholson, E., Ierodiaconou, D., Reeves, S., Taylor, M.D., Carnell, P.E., 2020. Stable isotopes infer the value of Australia's coastal vegetated ecosystems from fisheries. Fish Fish. 21, 80–90. https://doi.org/10.1111/faf.12416.

Jones, R., Bessell-Browne, P., Fisher, R., Klonowski, W., Slivkoff, M., 2016. Assessing the impacts of sediments from dredging on corals. Mar. Pollut. Bull. 102, 9–29. https://doi.org/10.1016/j.marpolbul.2015.10.049.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1.

Leitner, A.B., Neuheimer, A.B., Donlon, E., Smith, C.R., Drazen, J.C., 2017. Environmental and bathymetric influences on abyssal bait-attending communities of the Clarion Clipperton Zone. Deep-Sea Res. I Oceanogr. Res. Pap. 125, 65–80. https://doi.org/10.1016/j.dsr.2017.04.017.

Leuven, J.R.F.W., Selaković, S., Kleinhans, M.G., 2018. Morphology of bar-built estuaries: empirical relation between planform shape and depth distribution. Earth Surf. Dyn. 6, 763–778. https://doi.org/10.5194/esurf-6-763-2018.

Li, D., Tang, C., Xia, C., Zhang, H., 2017. Acoustic mapping and classification of benthic habitat using unsupervised learning in artificial reef water. Estuar. Coast. Shelf Sci. 185, 11–21. https://doi.org/10.1016/j.ecss.2016.12.001.

Lorda, J., Lafferty, K.D., 2012. Shading decreases the abundance of the herbivorous California horn snail, Cerithidea californica. J. Exp. Mar. Biol. Ecol. 432–433, 148–155. https://doi.org/10.1016/j.jembe.2012.07.009.

Macura, B., Bystrom, P., Airoldi, L., Eriksson, B.K., Rudstam, L., Stottrup, J.G., 2019. Impact of structural habitat modifications in coastal temperate systems on fish recruitment: a systematic review. Environ. Evid. 8. https://doi.org/10.1186/s13750-019-0157-3.

Madricardo, F., Foglini, F., Campiani, E., Grande, V., Catenacci, E., Petrizzo, A., Kruss, A., Toso, C., Trincardi, F., 2019. Assessing the human footprint on the sea-floor of coastal systems: the case of the Venice lagoon,Italy. Sci. Rep. 9, 6615. https://doi.org/10.1038/s41598-019-43027-7.

Malerba, M.E., White, C.R., Marshall, D.J., 2019. The outsized trophic footprint of marine urbanization. Front. Ecol. Environ. 17, 400–406. https://doi.org/10.1002/fee.2074.

Mangan, S., Bryan, K.R., Thrush, S.F., Gladstone-Gallagher, R.V., Lohrer, A.M., Pilditch, C.A., 2020. Shady business: the darkening of estuaries constrains benthic ecosystem function. Mar. Ecol. Prog. Ser. 647, 33–48. https://doi.org/10.3354/meps13410.

Martelo, A.F., Trombetta, T.B., Lopes, B.V., Marques, W.C., Möller, O.O., 2019. Impacts of dredging on the hydromorphodynamics of the Patos Lagoon estuary, southern Brazil. Ocean Eng. 188. https://doi.org/10.1016/j.oceaneng.2019.106325.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x.

Mayer-Pinto, M., Cole, V.J., Johnston, E.L., Bugnot, A., Hurst, H., Airoldi, L., Glasby, T.M., Dafforn, K.A., 2018. Functional and structural responses to marine urbanisation. Environ. Res. Lett. 13. https://doi.org/10.1088/1748-9326/aa98a5.

Meng, X., Chen, J., Li, Z., Liu, Z., Jiang, X., Ge, Y., Cooper, K.M., Xie, Z., 2020. Degraded functional structure of macroinvertebrates caused by commercial sand dredging practices in a flood plain lake. Environ. Pollut. 263. https://doi.org/10.1016/j.envpol.2020.114415.

Mitchell, M.G.E., Suarez-Castro, A.F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K.J., Johansen, K., Rhodes, J.R., 2015. Reframing landscape fragmentation's effects on ecosystem services. Trends Ecol. Evol. 30, 190–198. https://doi.org/10.1016/j.tree.2015.01.011.

Morton, J.K., Gladstone, W., 2014. Changes in rocky reef fish assemblages throughout an estuary with a restricted inlet. Hydrobiologia 724, 235–253. https://doi.org/10.1007/s10750-013-1740-1.

Murphy, H.M., Jenkins, G.P., 2010. Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. Mar. Freshw. Res. 61, 236–252. https://doi.org/10.1071/MF09068.

Oh, H.J., Koo, B.J., Ryu, J.H., Lee, S., 2019. Spatial macrobenthos habitat on Ganghwa tidal flat, Korea: part I - spatial relationship between Potamocorbula laevis and spatial variables. J. Coast. Res. 90, 393–400. https://doi.org/10.2112/Si90-050.1.

Olds, A.D., Frohloff, B.A., Gilby, B.L., Connolly, R.M., Yabsley, N.A., Maxwell, P.S., Henderson, C.J., Schlacher, T.A., 2018. Urbanisation supplements ecosystem functioning in disturbed estuaries. Ecography 41, 2104–2113. https://doi.org/10.1111/ecog.03551.

Pérez-Ruzafa, A., García-Charton, J.A., Barcala, E., Marcos, C., 2006. Changes in benthic fish assemblages as a consequence of coastal works in a coastal lagoon: the Mar Menor (Spain, Western Mediterranean). Mar. Pollut. Bull. 53, 107–120. https://doi.org/10.1016/j.marpolbul.2005.09.014.

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411. https://doi.org/10.1046/j.1461-0248.2002.00339.x.

Pezy, J.-P., Raoux, A., Marmin, S., Balay, P., Niquil, N., Dauvin, J.-C., 2017. Before-after analysis of the trophic network of an experimental dumping site in the eastern part of the Bay of Seine (English Channel). Mar. Pollut. Bull. 118, 101–111. https://doi.org/10.1016/j.marpolbul.2017.02.042.

Piló, D., Carvalho, A.N., Pereira, F., Coelho, H.E., Gaspar, M.B., 2019. Evaluation of macrobenthic community responses to dredging through a multimetric approach: effective or apparent recovery? Ecol. Indic. 96, 656–668. https://doi.org/10.1016/j.ecolind.2018.08.064.

Pineda, M.C., Strehlow, B., Duckworth, A., Doyle, J., Jones, R., Webster, N.S., 2016. Effects of light attenuation on the sponge holobiont-implications for dredging management. Sci. Rep. 6. https://doi.org/10.1038/srep39038.

Pirtle, J.L., Shotwell, S.K., Zimmermann, M., Reid, J.A., Golden, N., 2017. Habitat suitability models for groundfish in the Gulf of Alaska. Deep-Sea Res. II Top. Stud. Oceanogr. 165, 303–321. https://doi.org/10.1016/j.dsr2.2017.12.005.

Pittman, S.J., Costa, B.M., Battista, T.A., 2009. Using lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. J. Coast. Res. 25, 27–38. https://doi.org/10.2112/si53-004.1.

Pledger, A.G., Brewin, P., Mathers, K.L., Phillips, J., Wood, P.J., Yu, D., 2021. The effects of water injection dredging on low-salinity estuarine ecosystems: implications for fish and macroinvertebrate communities. Ecol. Indic. 122, 107244. https://doi.org/10.1016/j.ecolind.2020.107244.

Pollard, M., Hodgson, A.N., 2016. Mytilus galloprovincialis (Mollusca: Bivalvia) in a warm-temperate South African estuarine embayment. Afr. J. Aquat. Sci. 41, 57–65. https://doi.org/10.2989/16085914.2015.1119670.

Pollock, F.J., Lamb, J.B., Field, S.N., Heron, S.F., Schaffelke, B., Shedrawi, G., Bourne, D.G., Willis, B.L., 2014. Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs. PLoS One 9, e102498. https://doi.org/10.1371/journal.pone.0102498.

Purkis, S.J., Graham, N.A.J., Riegl, B.M., 2008. Predictability of reef fish diversity and abundance using remote sensing data in Diego Garcia (Chagos Archipelago). Coral Reefs 27, 167–178. https://doi.org/10.1007/s00338-007-0306-y.

Pygas, D.R., Ferrari, R., Figueira, W.F., 2020. Review and meta-analysis of the importance of remotely sensed habitat structural complexity in marine ecology. Estuar. Coast. Shelf Sci. 235, 106468. https://doi.org/10.1016/j.ecss.2019.106468.

Rees, J.D., Kingsford, R.T., Letnic, M., 2019. Changes in desert avifauna associated with the functional extinction of a terrestrial top predator. Ecography 42, 67–76. https://doi.org/10.1111/ecog.03661.

Rees, M.J., Knott, N.A., Neilson, J., Linklater, M., Osterloh, I., Jordan, A., Davis, A.R., 2018. Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves. Biol. Conserv. 224, 100–110. https://doi.org/10.1016/j.biocon.2018.04.040.

Rehitha, T.V., Ullas, N., Vineetha, G., Benny, P.Y., Madhu, N.V., Revichandran, C., 2017. Impact of maintenance dredging on macrobenthic community structure of a tropical estuary. Ocean Coast. Manag. 144, 71–82. https://doi.org/10.1016/j.ocecoaman.2017.04.020.

Rosenblatt, A.E., Heithaus, M.R., Mather, M.E., Matich, P., Nifong, J.C., Ripple, W.J., Silliman, B.R., 2013. The roles of large top predators in coastal ecosystems: new insights from long term ecological research. Oceanography 26, 156–167. https://doi.org/10.5670/oceanog.2013.59.

Skilleter, G.A., Pryor, A., Miller, S., Cameron, B., 2006. Detecting the effects of physical disturbance on benthic assemblages in a subtropical estuary: a beyond BACI approach. J. Exp. Mar. Biol. Ecol. 338, 271–287. https://doi.org/10.1016/j.jembe.2006.06.016.

Stamoulis, K.A., Delevaux, J.M.S., Williams, I.D., Poti, M., Lecky, J., Costa, B., Kendall, M.S., Pittman, S.J., Donovan, M.K., Wedding, L.M., Friedlander, A.M., 2018. Seascape models reveal places to focus coastal fisheries management. Ecol. Appl. 28, 910–925. https://doi.org/10.1002/eap.1696.

Störmer, R., Wichels, A., Gerdts, G., 2013. Geo-Chip analysis reveals reduced functional diversity of the bacterial community at a dumping site for dredged Elbe sediment. Mar. Pollut. Bull. 77, 113–122. https://doi.org/10.1016/j.marpolbul.2013.10.022.

Sutton, G., Pichegru, L., Botha, J.A., Kouzani, A.Z., Adams, S., Bost, C.A., Arnould, J.P.Y., 2020. Multi-predator assemblages, dive type, bathymetry and sex influence foraging success and efficiency in African penguins. PeerJ 8, e9380. https://doi.org/10.7717/peerj.9380.

Teichert, N., Lepage, M., Chevillot, X., Lobry, J., 2018. Environmental drivers of taxonomic, functional and phylogenetic diversity (alpha, beta and gamma components) in estuarine fish communities. J. Biogeogr. 45, 406–417. https://doi.org/10.1111/jbi.13133.

Teichert, N., Lepage, M., Lobry, J., 2018. Beyond classic ecological assessment: the use of functional indices to indicate fish assemblages sensitivity to human disturbance in estuaries. Sci. Total Environ. 639, 465–475. https://doi.org/10.1016/j.scitotenv.2018.05.179.

Thomson, A.H., Manoylov, K.M., 2019. Algal community dynamics within the Savannah River Estuary, Georgia under anthropogenic stress. Estuar. Coasts 42, 1459–1474. https://doi.org/10.1007/s12237-019-00579-1.

Todd, P.A., Heery, E.C., Loke, L.H.L., Thurstan, R.H., Kotze, D.J., Swan, C., 2019. Towards an urban marine ecology: characterizing the drivers, patterns and processes of marine ecosystems in coastal cities. Oikos 128, 1215–1242. https://doi.org/10.1111/oik.05946.

Todd, V.L.G., Todd, I.B., Gardiner, J.C., Morrin, E.C.N., MacPherson, N.A., DiMarzio, N.A., Thomsen, F., 2014. A review of impacts of marine dredging activities on marine mammals. ICES J. Mar. Sci. 72, 328–340. https://doi.org/10.1093/icesjms/fsu187.

Underwood, G.J.C., Kromkamp, J., 1999. Primary production by phytoplankton and microphytobenthos in estuaries. In: Nedwell, D.B., Raffaelli, D.G. (Eds.), Advances in Ecological Research: Estuaries. Academic Press, Great Britain, pp. 93–139.

Villéger, S., Miranda, J.R., Hernández, D.F., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20, 1512–1522. https://doi.org/10.1890/09-1310.1.

Walbridge, S., Slocum, N., Pobuda, M., Wright, J.D., 2018. Unified geomorphological analysis workflows with Benthic Terrain Modeler. Geosciences 8, 94–117. https://doi.org/10.3390/geosciences8030094.

Wan Hussin, W.M.R., Cooper, K.M., Froján, C.R.S.B., Defew, E.C., Paterson, D.M., 2012. Impacts of physical disturbance on the recovery of a macrofaunal community: a comparative analysis using traditional and novel approaches. Ecol. Indic. 12, 37–45. https://doi.org/10.1016/j.ecolind.2011.03.016.

Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund– an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x.

Wedding, L.M., Jorgensen, S., Lepczyk, C.A., Friedlander, A.M., 2019. Remote sensing of three-dimensional coral reef structure enhances predictive modeling of fish assemblages. Remote Sens. Ecol. Conserv. 5, 150–159. https://doi.org/10.1002/rse2.115.

Wenger, A.S., Harvey, E., Wilson, S., Rawson, C., Newman, S.J., Clarke, D., Saunders, B.J., Browne, N., Travers, M.J., Mcilwain, J.L., Erftemeijer, P.L.A., Hobbs, J.-P.A., Mclean, D., Depczynski, M., Evans, R.D., 2017. A critical analysis of the direct effects of dredging on fish. Fish Fish. 18, 967–985. https://doi.org/10.1111/faf.12218.

Wilber, D.H., Clarke, D.G., 2001. Biological effects of suspended sediments: a review of suspended sediment impacts on fish and shellfish with relation to dredging activities in estuaries. N. Am. J. Fish Manag. 21, 855–875. https://doi.org/10.1577/1548-8675(2001)021<0855:Beossa>2.0.Co;2.

Wraith, J., Lynch, T., Minchinton, T.E., Broad, A., Davis, A.R., 2013. Bait type affects fish assemblages and feeding guilds observed at baited remote underwater video stations. Mar. Ecol. Prog. Ser. 477, 189–199. https://doi.org/10.3354/meps10137.

Young, M.A., Iampietro, P.J., Kvitek, R.G., Garza, C.D., 2010. Multivariate bathymetry-derived generalized linear model accurately predicts rockfish distribution on Cordell Bank, California, USA. Mar. Ecol. Prog. Ser. 415, 247–261. https://doi.org/10.3354/meps08760.

Zou, W., Tolonen, K.T., Zhu, G., Qin, B., Zhang, Y., Cao, Z., Kai, P., Cai, Y., Gong, Z., 2019. Catastrophic effects of sand mining on macroinvertebrates in a large shallow lake with implications for management. Sci. Total Environ. 695. https://doi.org/10.1016/j.scitotenv.2019.133706.