


Seafloor Terrain Shapes the Three-dimensional Nursery Value of Mangrove and Seagrass Habitats

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ABSTRACT

Mangroves and seagrasses are important nurseries for many marine species, and this function is linked to the complexity and context of these habitats in coastal seascapes. It is also connected to bathymetric features that influence habitat availability, and the accessibility of refuge habitats, but the significance of terrain variation for nursery function is unknown. To test whether seafloor terrain influences nursery function, we surveyed fish assemblages from mangrove and seagrass habitats in 29 estuaries in eastern Australia with unbaited underwater cameras and quantified the surrounding three-dimensional terrain with a set of complementary surface metrics (that is, depth, aspect, curvature, slope, roughness) applied to sonar-derived bathymetric maps. Terrain metrics explained

variability in assemblages in both mangroves and seagrasses, with differing effects for the entire fish assemblage and nursery species composition, and between habitats. Higher depth, plan curvature (concavity or convexity) and roughness (backscatter) were negatively correlated with abundance and diversity in mangroves and positively linked to abundance and diversity in seagrass. Mangrove nursery species (6 species) were most abundant in forests adjacent to flats with concave holes, rough substrates and low-moderate depths, whereas seagrass nursery species (3 species) were most abundant in meadows adjacent to deep channels with soft mounds and ledges. These findings indicate that seafloor terrain influences nursery function and demonstrate contrasting effects of terrain variation in mangroves and seagrass. We suggest that incorporating three-dimensional terrain into coastal conservation and restoration plans could help to improve outcomes for fisheries management, but contrasting strategies might be needed for different nursery habitats.

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Key words: bathymetry; estuary; nursery; seafloor complexity; seascape ecology; terrain.

HIGHLIGHTS

- Fish assemblages in coastal nurseries are linked to seafloor terrain variation
- Distinct effects of terrain on nursery function in mangrove and seagrass habitats
- Nursery paradigms must consider the three-dimensional context of coastal habitats

INTRODUCTION

Landscapes consist of a mosaic of ecosystems that provide a diversity of habitat functions for mobile organisms (Nagelkerken and others 2015; Liqueste and others 2016). The ecological significance of many habitats is shaped by their capacity to provide these important functions, including food provision, protection from predators and safe reproduction sites, and is typically greatest in structurally complex ecosystems, as they support a diversity of ecological niches (Tews and others 2004; Borland and others 2021). The spatial distribution of ecosystems, and the habitat functions they confer, shape the diversity and distribution of species in most landscapes and can have pervasive effects on the growth and survival of juvenile animals (Baguette and Van Dyck 2007; Sheaves 2009). Habitats that support high densities of juveniles and facilitate elevated rates of growth and survival, and contribute disproportionately to the recruitment of juveniles into adult populations, are considered to function as ecological nurseries (Beck and others 2001; Barbier and others 2011; Whitfield and Patrick 2015). The importance of nursery habitats as foraging and refugia sites has been documented for the juveniles of a diversity of species in coastal seascapes, and positive effects of habitat size, complexity and context on nursery function have been widely documented (Nagelkerken and others 2008; Whitfield 2017; Bradley and others 2020). Nursery habitats occur in seascapes that are also characterised by a diversity of three-dimensional terrain features (for example, intertidal flats with high curvature, subtidal channels with steep slopes and rocky pinnacles with high rugosity), and these seafloor features likely modify the availability of nurseries and the accessibility of subtidal refuge habitats, but it is not clear how terrain variability affects nursery function (Nagelkerken and others 2015; Borland and others 2021).

The spatial distribution of animals in most landscapes is shaped by the composition (that is, substrate characteristics such as roughness and

hardness) and complexity (that is, topographic variation such as slope and rugosity) of terrain features (Simonson and others 2014; Pygas and others 2020). Animal abundance and diversity is positively correlated with terrain complexity in most seascapes, as the distribution of many species (for example, cetaceans, fish, turtles and crustaceans) is typically concentrated over complex bathymetric features (for example, reefs, pinnacles, seamounts and artificial structures) (Rex and others 2006; Pittman and others 2007b; Schlacher and others 2010; Rees and others 2014; Borland and others 2022a). Prominent terrain features often harbour diverse faunal assemblages because they support an abundance of food (for example, photosynthetic organisms and invertebrate prey species) (Cameron and others 2014; Rees and others 2018), provide settlement and sheltering sites (Sabatés and others 2007; Bejarano and others 2011) and offer refugia from various forms of disturbance (for example, hydrodynamic forces and fishing pressure) (Pittman and Brown 2011; Stamoulis and others 2018). These functions of complex terrain features are analogous to many of the services that are provided by nursery habitats (Sheaves and others 2015; Whitfield and Patrick 2015), and for this reason areas of high bathymetric relief are often viewed as enhanced nurseries in continental shelf and rocky reef seascapes (Giannoulaki and others 2011; Farmer and others 2017; Pirtle and others 2017). Seafloor terrain variation in coastal seascapes might also modify the ecological values of nursery habitats, like mangroves and seagrasses, but this concept has not been widely explored in studies of the nursery role hypothesis.

Coastal seascapes comprise a heterogeneous mix of many marine plant communities, including mangroves, seagrasses, algal beds, saltmarshes and tidal freshwater marshes, which provide nursery habitats for a diversity of estuarine and marine species (Sheaves and others 2015; Whitfield 2017). Many biotic (for example, food availability, predation risk and resource competition) and abiotic (for example, water quality, sediment characteristics and hydrodynamic conditions) factors combine to shape the ecological values of coastal ecosystems as nursery habitats, and many of these can be optimised in large habitat patches, which confer high structural complexity, and are also well connected to alternative habitats (Beck and others 2001; Baker and Sheaves 2005; Whitfield and Patrick 2015). Mangrove forests and seagrass meadows are prominent nursery habitats in many inshore seascapes, and these ecosystems are characterised by a diversity of structurally complex habitat features,

such as roots, rhizomes, stems, leaves and debris, which provide refuge from predators and frequently support an abundance of food (Nagelkerken and others 2000; Sheaves and others 2015). Many studies have identified the importance of connections between these ecosystems and neighbouring habitats, including coral reefs, oyster reefs and other nursery habitats, which also provide fish with suitable refuge sites, foraging areas and spawning grounds (Connolly and Hindell 2006; Pittman and others 2007a; Heck Jr and others 2008; Sheaves 2009; Hyndes and others 2014; Nagelkerken and others 2015). The ecological significance of mangroves and seagrasses as nursery habitats is also modified by tidal regimes, which determine the frequency and duration of their availability for aquatic organisms (Igulu and others 2014; Whitfield 2017). As tides recede from intertidal habitats, nursery species must move to alternative deeper habitats where they are typically more vulnerable to predators (Sheaves 2005; Unsworth and others 2009). Subtidal habitats with high structural complexity, such as rock-bars, pinnacles and channel edges, can provide supplementary habitats for nursery species at low tide, but there is no data to describe how changes in the bathymetric characteristics of these terrain features influence the ecological roles of nursery habitats across coastal seascapes (Dorenbosch and others 2004; Lugendo and others 2007; Alp and Pichon 2020; Bradley and others 2020).

Here, we investigated the importance of seafloor terrain variation for the ecological roles of mangrove and seagrass habitats that provide important nursery functions for a diversity of marine species in eastern Australia (Sheaves and others 2016; Hayes and others 2020). Terrain features in the subtidal zones of these seascapes can provide similar habitat functions to mangroves and seagrass for marine animals and might therefore serve as supplementary nursery habitats (Wedding and others 2008; Pittman and Brown 2011; Borland and others 2022a), but this hypothesis has not been tested with empirical data. Furthermore, many species use mangroves and seagrass habitats as juveniles (that is, nursery species), whilst other transient species (that is, non-nursery species) also occupy these ecosystems opportunistically (for example, during foraging and reproductive migrations) (Harborne and others 2017). The contrasting effects of seascape context and complexity on assemblages of nursery and non-nursery species are widely appreciated (Harborne and others 2016; Berkstrom and others 2020), but it is not known whether variation in seafloor terrain has consistent effects

on the composition of these species in nursery habitats. The primary aim of this research was to identify whether variation in the seafloor terrain of coastal seascapes affects the nursery function of intermittently available mangrove and seagrass habitats. Although it is well recognised that there are many measurable components of nursery function (for example, juvenile density, growth and survival), the intent of this study was to focus on the influence of seafloor terrain on particular aspects of this function: nursery species richness, abundance and composition (following Cheminée and others 2021; Dance and others 2021). The secondary objective of this research was to identify whether the composition of nursery species (that is, species with known juvenile-habitat associations in mangrove and seagrass nurseries) and the entire fish assemblage (that is, nursery and non-nursery species combined) respond to different terrain features in mangrove and seagrass nurseries. We predict that three-dimensional variation in seafloor terrain will have distinct effects on the composition, abundance and diversity of nursery species and that these effects will differ to the entire assemblage in mangrove and seagrass ecosystems and influence the value of these habitats as nurseries in coastal seascapes.

METHODS

Study Area

To investigate whether variation in seafloor terrain affects the ecological value of nursery habitats, fish assemblages were sampled from mangrove and seagrass habitats in 29 estuaries in eastern Australia (Figure S1). The focal estuaries support abundant mangrove forests and seagrass meadows and are characterised by substantial variation in the three-dimensional complexity of their terrain features, ranging from shallow sand-bar dominated estuaries (for example, Baffle Creek) to deeper estuaries with abundant subtidal rock bars (for example, Maroochy River) (Figure 1, Table S1) (Gilby and others 2018; Henderson and others 2019; Borland and others 2022a, b).

Fish Surveys

Fish assemblages from mangrove and seagrass habitats were surveyed using unbaited remote underwater video stations (RUVS), which were comprised of a high-definition GoPro camera mounted on a 3 kg weight (Gilby and others 2018; Henderson and others 2019). RUVS are widely used in ecological studies that examine the nursery

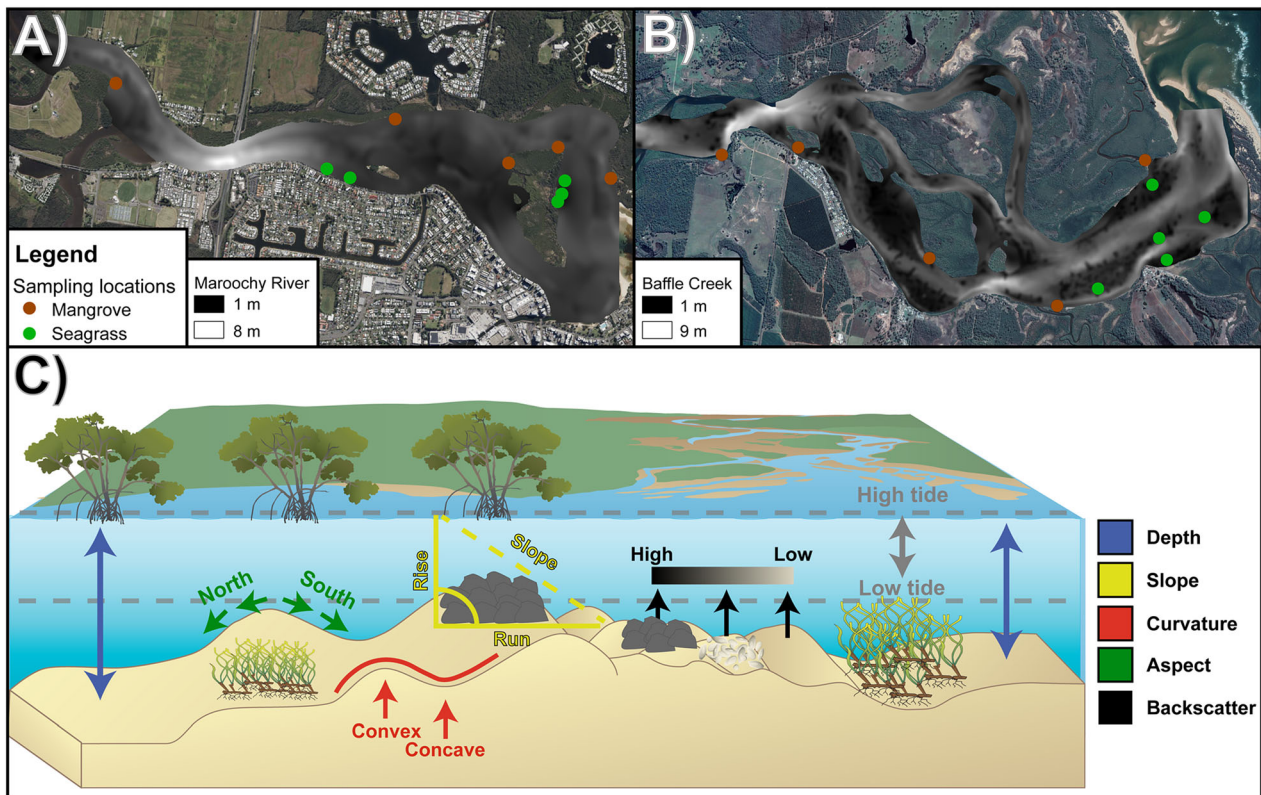


Figure 1. Estuaries demonstrating variation in the bathymetric context (that is, depth gradients measured as metres below HAT) of remote underwater video stations (RUVS) deployments in mangrove (brown circles) and seagrass (green circles) ecosystems (**A** and **B**); and a conceptual illustration of terrain metrics used to describe variation in seafloor relief (for example, depth), complexity (for example, slope), morphology (for example, curvature, aspect) and composition (for example, backscatter) in this study (**C**).

value of different ecosystems for fish because they efficiently sample fish species from all size classes (Leslie and others 2017; Parsons and others 2018), and the absence of bait minimises the likelihood of attracting species to the cameras from other ecosystems (Sheaves and others 2016; Bradley and others 2017). RUVS were deployed at 180 sites in mangrove and seagrass habitats across the 29 estuaries. Our intent was to survey five sites in each habitat in each estuary (following Gilby and others 2018; Henderson and others 2019; Swadling and others 2019), but this was not always possible because some estuaries did not support seagrass or contained patches that were simply too small to ensure independent sampling. To standardise all RUVS for time and account for the potential confounding effects of tide, depth, water quality and seascape context, they were deployed: (1) for 30 min; (2) within 2 h of high tide; (3) in water depths between one and two metres; (4) from the mouth of each estuary to the point at which salinity reaches 30 psu (Practical Salinity Units)

(that is, the marine extent of each estuary); and (5) in isolated mangrove and seagrass patches, which were separated by more than 500 m, but this was not always possible (90% efficiency) because of the scarcity of seagrass in some estuaries (Sheaves and others 2016; Brook and others 2018; Gilby and others 2018). RUVS were positioned over bare sediment parallel to mangroves and seagrass patches to capture species entering and exiting the nursery habitat (Henderson and others 2021). Data on fish abundance and diversity were obtained from video footage using the standard MaxN statistic (Ellis and Demartini 1995; Murphy and Jenkins 2010; Gladstone and others 2012). The MaxN was recorded for every species that swam within about 1 m of the camera to account for variable water clarity (following Gilby and others 2020). Fish were then categorised as nursery or non-nursery species based on their known utilisation of mangrove and seagrass habitats as juveniles (*sensu* Berkstrom and others 2020) (Table S2).

Table 1. Description of Terrain Metrics Derived from the Digital Bathymetric Models (DBMs) in This Study

Variable	Description
<i>Seafloor relief</i>	
Average depth	Distance from the seafloor to sea level (metres)
<i>Seafloor complexity</i>	
Rugosity	Surface area to planar area ratio
Slope	Maximum change in elevation (degrees)
<i>Seafloor morphology</i>	
Aspect:	Compass direction of a feature
Northness	Cos aspect: 1 = north orientation; -1 = south orientation
Eastness	Sin aspect: 1 = east orientation; -1 = west orientation
Plan curvature	Horizontal curvature of a feature: 1 = convex; -1 = concave orientation
Profile curvature	Vertical curvature of a feature: 1 = convex; -1 = concave
<i>Seafloor composition</i>	
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)

See Borland and others (2021) for more information.

Quantifying Seafloor Terrain

To describe the three-dimensional terrain features of estuarine seascapes, and test for effects of terrain variation on fish assemblages, high-resolution ($= 1 \text{ m}^{-1}$) digital bathymetric models (DBMs) were created for each estuary using sonar data obtained from surveys with an acoustic sounder (Lowrance HDS 7-Gen 3). The bathymetry and bottom composition (that is, backscatter: E1 hardness, E2 roughness) of each estuary were mapped by logging the along-shore and cross-shore variation in terrain features on overlapping latitudinal and longitudinal transects across the sampled extent of each estuary, which were traversed at a maximum speed of 8 km/h^{-1} . Sonar data were processed in ReefMaster 2.0, corrected to the highest astronomical tide (HAT) using tide data collected from pressure sensors (INW Smart Sensor) that were also deployed in each estuary (Young and others 2010; Li and others 2017; Borland and others 2022b). Terrain metrics were then quantified from DBMs to describe variation in the bathymetry surrounding the sampling sites in each estuary, using the Spatial Analyst and Benthic Terrain Modeler packages in ArcGIS (Walbridge and others 2018). Nine terrain metrics that are consistent predictors of the effects of terrain on fish assemblages in a diversity of marine seascapes were selected to describe variation in the: relief (that is, average depth), complexity (that is, slope and rugosity), morphology (that is, plan curvature; profile curvature; and aspect: northness and eastness) and composition (that is, backscatter: roughness and hardness) of

seafloor terrain (Figure 1, Table 1) (Borland and others 2021). All terrain metrics were indexed by quantifying their mean values within a 500-m buffer of each sampling location; this scale was chosen because it encompasses the daily home ranges of many estuarine fishes and has been widely used in other studies of fish-seascape relationships in the study area (Brook and others 2018; Henderson and others 2019; Borland and others 2022a).

Data Analysis

Multivariate generalised linear models (manyGLMs) were constructed in the *mvabund* package in *R* to test whether variation in seafloor terrain complexity shapes the composition of fish assemblages and the abundance and diversity of nursery species in mangrove and seagrass habitats (Wang and others 2012). These models also included latitude to account for the large geographical extent of the study area, and estuary as fixed effect because manyGLMs cannot incorporate random factors. Prior to analysis, terrain metrics were tested for collinearity using Pearson's correlation coefficient, and subsequently, eastness (correlated with northness), profile curvature (correlated with plan curvature), rugosity (correlated with slope) and hardness (correlated with roughness) were removed from analyses ($r^2 = \geq 0.7$). Best-fit models were selected using reverse stepwise simplification, based on Akaike Information Criterion (AIC). The "p.uni" function within the *mvabund* package was then used to identify indicator species that were

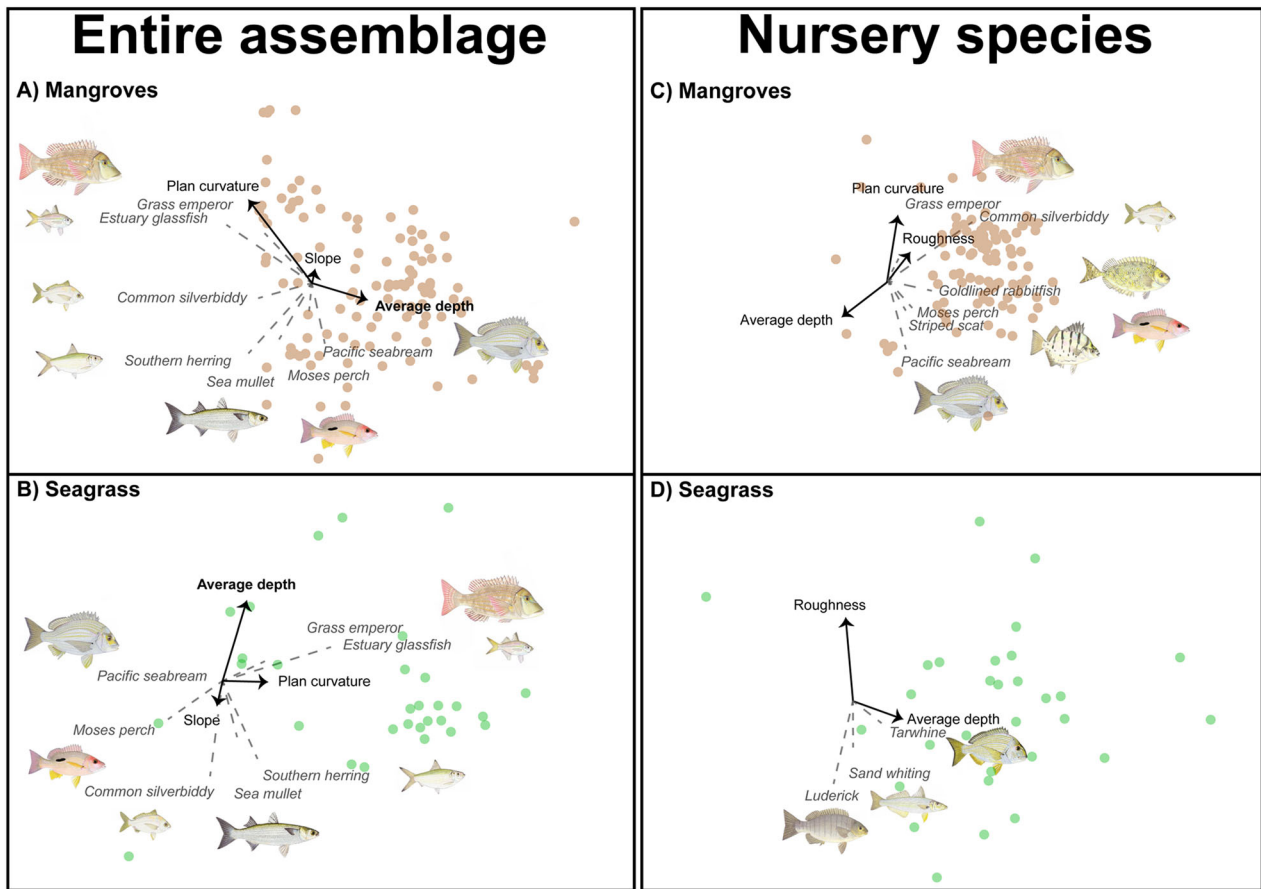


Figure 2. Non-metric multi-dimensional scaling ordinations (nMDS) illustrating the effects of seafloor terrain variation on the entire fish assemblage (that is, nursery and non-nursery species) in **A** mangrove and **B** seagrass habitats, and the effects of terrain changes on nursery species in **C** mangrove and **D** seagrass habitats. Black lines illustrate the correlation of significant terrain metrics with variation in assemblage composition (identified by manyGLM analysis); dotted lines illustrate correlations between indicator species and significant terrain metrics (identified by “p.uni” analysis); and text in bold illustrates significant interactions between terrain metrics and habitat (that is, a categorical factor delineating either mangrove or seagrass ecosystems).

correlated with significant factors within the best-fit manyGLM model. Non-metric multidimensional scaling ordinations (nMDS) were then used to visualise effects of significant factors identified by the manyGLM on the composition of fish assemblages and on the abundance and diversity of nursery species, in mangrove and seagrass habitats. Generalised linear mixed models (GLMMs) were then constructed using the *glmmTMB* package in *R* to further investigate, and illustrate, the effects of significant predictors identified by each manyGLM on fish abundance and species richness (Brooks and others 2017). GLMMs were fitted with natural splines, with three or fewer polynomial functions,

to encapsulate potential nonlinear effects of terrain using the *splines* package in *R*, and included estuary as a random factor (Brooks and others 2017; Geraci and others 2021). The relationship between significant indicator species (as identified by “p.uni” analyses) and variables from the best-fit manyGLMs were then plotted using the *predict.manyglm* function within the *mvabund* package in *R* (Wang and others 2012). Univariate and multivariate GLM(M)s were checked for normally distributed residuals, homogeneity of variance, outliers and over-dispersion and were fitted with negative binomial distributions, with log link functions.

Table 2. Summary of the Best-fit ManyGLM Testing for the Effects of Seafloor Terrain on the Entire Fish Assemblage (that is, Nursery and Non-nursery Species) in Mangrove and Seagrass Ecosystems

Variable	χ^2	<i>p</i>
Habitat x Average depth	27.7	0.043
Plan curvature	50.2	0.002
Slope	24.1	0.032
Estuary	654.9	0.005

Table 3. Summary of the Best-fit ManyGLMs Testing for the Effects of Seafloor Terrain Variation on the Composition of Nursery Species in Mangrove and Seagrass Ecosystems

Variable	χ^2	<i>p</i>
<i>Mangrove</i>		
Average depth	24.5	0.012
Plan curvature	39.8	0.002
Roughness	21.4	0.023
<i>Seagrass</i>		
Average depth	28.1	0.023
Roughness	150.4	0.001
Estuary	35.7	0.002

RESULTS

Effects of Seafloor Terrain on Fish Assemblages in Mangrove and Seagrass Habitats

The composition of fish assemblages in both mangroves and seagrass was associated with terrain features surrounding these habitats, but the nature of these correlations differed for the entire fish assemblage (that is, nursery and non-nursery species) versus the composition of nursery species (Figure 2, Tables 2 and 3). The composition of the entire fish assemblage varied between estuaries (8 species) and with changes in the plan curvature (5 species), slope (2 species) and depth (1 species) of terrain features, but the effects of depth differed between mangrove and seagrass habitats (Figures 2 and S2, Tables 2 and S3). By contrast, the composition of nursery species was linked to changes in plan curvature (5 species), roughness (2 species) and average depth (1 species) in mangroves and varied between estuaries (6 species) and with changes in roughness (2 species) and depth (1

species) in seagrass (Figures 2 and S3, Tables 3 and S4).

Effects of Seafloor Terrain on Nursery Species in Mangrove and Seagrass Habitats

The abundance and diversity of nursery species was highest at mangrove sites near terrain features with: low-moderate average depths (that is, 3 m), and either gradually (abundance) or sharply (diversity) declined at both lower and higher depths; high roughness (that is, 3.8), and gradually increased with increasing roughness; and low plan curvature (that is, -0.008), and sharply declined with increasing or decreasing plan curvature (Figure 3, Table 4). By contrast, the abundance and diversity of nursery species in seagrass was highest at sites near terrain features with: high average depths (that is, 4.1 m) and gradually increased with increasing depths; and low roughness (that is, 1.9) and sharply decreased with increasing roughness (Figure 3, Table 4).

In mangrove forests, variation in the depth, roughness and plan curvature of terrain features were linked to changes in the abundance of six nursery species (Figure 4, Table S4). The abundance of common silverbiddy (*Gerres subfasciatus*) sharply decreased with increasing depths and was highest at sites with low depths (that is, 1.3 m) (Figure 4, Table S4). The abundance of grass emperor (*Lethrinus laticaudis*) gradually decreased with increasing roughness, was highest at sites with low roughness (that is, 1.2) and were not present when roughness was low-moderate (that is, > 2) (Figure 4, Table S4). The abundance of common silverbiddy sharply increased with increasing roughness and was highest at sites with high roughness (that is, 3.8) (Figure 4, Table S4). The abundance of striped scat (*Selenotoca multifasciata*), goldlined rabbitfish (*Siganus lineatus*), moses perch (*Lutjanus russelli*) and pacific seabream (*Acanthopagrus pacificus*) sharply decreased with increasing plan curvature, were highest at sites with low plan curvature (that is, -0.02) and were not present when plan curvature was low-moderate (that is, > 0) (Figure 4, Table S4). The abundance of grass emperor sharply increased with increasing plan curvature, was highest at sites with high plan curvature (that is, 0.02) and was not present when plan curvature was moderate-high (that is, < 0.005) (Figure 4, Table S4).

In seagrass meadows, variation in the depth and roughness of terrain features were linked to changes in the abundance of three nursery species

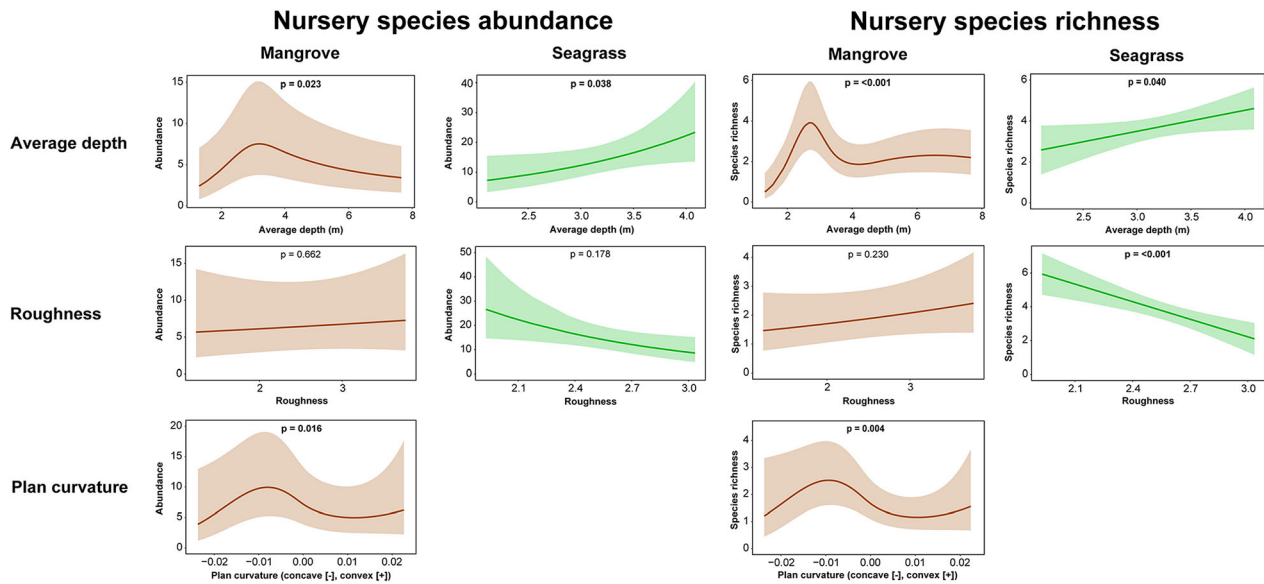


Figure 3. Generalised linear mixed models (GLMMs) illustrating the effects of average depth, roughness and plan curvature (that is, significant terrain features identified by manyGLM analyses) on the abundance and species richness of nursery species in mangrove and seagrass habitats.

(Figure 5, Table S4). The abundance of tarwhine (*Rhabdosargus sarba*) gradually increased with increasing depth, was highest at sites with greater depths (that is, 4.1 m) and were not present when depths were low-moderate (< 3.7 m) (Figure 5, Table S4). The abundance of luderick (*Girella tricuspidata*) and sand whiting (*Sillago ciliata*) decreased sharply with increasing roughness and were highest at sites with lower roughness (that is, 1.9) (Figure 5, Table S4).

DISCUSSION

Mangrove and seagrass ecosystems provide a variety of habitat functions for coastal organisms and are considered to be important nurseries for the juveniles of many species (Whitfield 2017; Lefcheck and others 2019), but these habitats are also located in diverse seascapes with variable bathymetry and changes in terrain complexity, which could mediate their roles as nurseries (Borland and others 2021). Our findings demonstrate, for the first time, that variation in the three-dimensional terrain features of coastal seascapes shapes the composition of fish assemblages in mangrove and seagrass nurseries. There was, however, a large diversity of responses, as the significance of terrain for fish assemblages differed between species that use mangrove and seagrass ecosystems as nurseries (that is, nursery species) and the entire fish

Table 4. Summary of Generalised Linear Mixed Models (GLMMs), Testing for the Effects of Terrain on the Abundance and Species Richness of Nursery Species in Mangrove and Seagrass Ecosystems

Variable	χ^2	p-value	R ²
<i>Mangrove</i>			
Fish abundance			
Average depth	9.6	0.023	0.73
Plan curvature	12.1	0.016	
Roughness	0.2	0.662	
Species richness			
Average depth	21.3	< 0.001	0.30
Plan curvature	12.4	0.004	
Roughness	1.4	0.230	
<i>Seagrass</i>			
Fish abundance			
Average depth	4.3	0.038	0.22
Roughness	5.5	0.178	
Species richness			
Average depth	4.2	0.040	0.26
Roughness	16.1	< 0.001	

Values in bold indicate statistical significance ($p < 0.05$)

assemblage (that is, nursery and non-nursery species), and between the different nursery habitats. Fish assemblages in both mangrove and seagrass habitats were affected by changes in the depth,

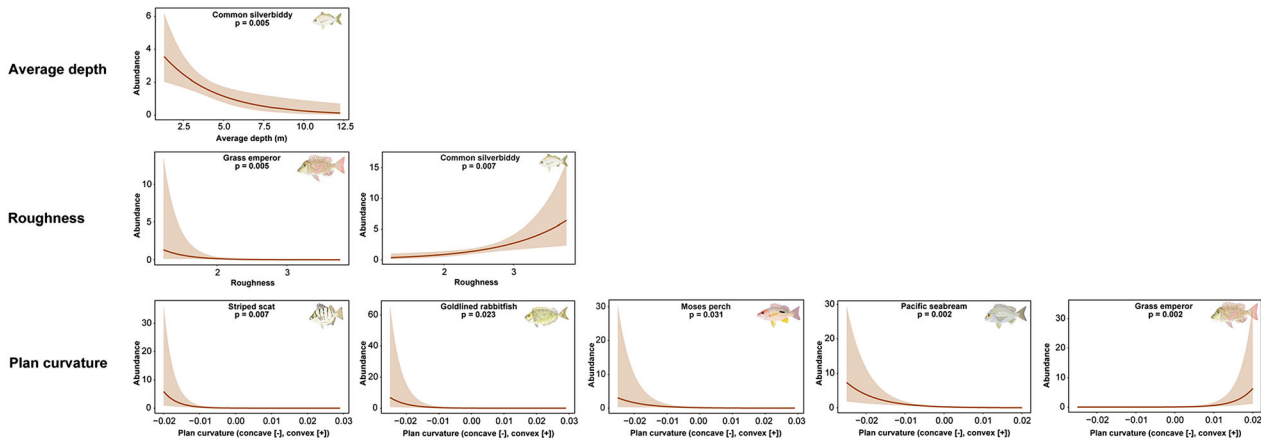


Figure 4. ManyGLM illustrating the effects of average depth, roughness and plan curvature (that is, significant factors in the best-fit model) on the abundance of indicator nursery species in mangroves.

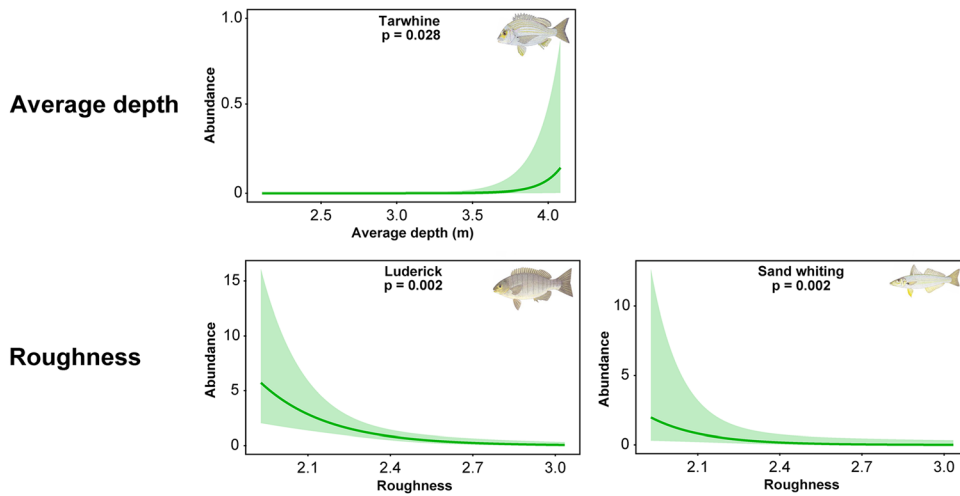


Figure 5. ManyGLM illustrating the effects of average depth and roughness (that is, significant factors in the best-fit model) on the abundance of indicator nursery species in seagrass.

plan curvature (that is, convexity or concavity) and slope of terrain features in the surrounding seascape. By contrast, nursery species were linked to the depth and roughness (that is, backscatter) of adjacent terrain features in both mangrove and seagrass habitats; and plan curvature in mangrove forests. The abundance and diversity of mangrove nursery species were highest in forests near rough terrain features with concave holes in shallow-moderate depths, whereas seagrass nursery species were most abundant and diverse in meadows near deep channels with soft sediment mounds and ledges. These findings align with previous research highlighting the importance of seafloor terrain for the distribution of fish species, composition of fish assemblages and provision of potential nursery habitats in deep reef and shelf seascapes (Farmer

and others 2017; Pirtle and others 2017; Pygas and others 2020; Borland and others 2021) and also demonstrate that the ecological significance of seafloor terrain can transcend habitat boundaries and structure nursery function in coastal seascapes.

Mangrove forests are nursery habitats for a diversity of species, but often grow high on intertidal zones where they are only available for short periods of each tidal cycle, and fish must retreat to subtidal structure when tides recede (Igulu and others 2014; Baker and others 2015). Our results show, for the first time, that the composition of nursery species in mangrove forests was modified by variation in plan curvature (5 species), roughness (2 species) and depth (1 species). Nursery species abundance, richness and the abundance of common silverbiddy were negatively correlated

with high average depths. Shallow mangrove forests contain high densities of juveniles from many species because predation risk is typically lower here than in deeper water, and these areas provide safe locations for juveniles to feed and disperse regardless of tidal state, or the availability of submerged vegetation (Ellis and Bell 2004; Rypel and others 2007; Rotherham and others 2011; Munsch and others 2016). The abundance of two nursery species, grass emperor and common silverbiddy, was correlated with terrain roughness (that is, backscatter). Grass emperor occupy mangroves with soft sediment terrain (that is, low roughness) because these substrates harbour a high abundance of their invertebrate prey (for example, crustaceans and molluscs) (Salini and others 1994; Brewer and others 1995). By contrast, common silverbiddy move between mangroves and subtidal habitats tidally, and we suggest that hard subtidal terrain features (for example, reefs with high backscatter) provide supplementary nursery habitats for this species when mangrove forests are exposed at low tide (Fowler and Booth 2013; Morton and Gladstone 2014). Nursery species abundance, richness and the abundance of four species (that is, striped scat, goldlined rabbitfish, mores perch and pacific seabream) were positively correlated with the presence of concave terrain features. Curvature in the seafloor can provide a degree of protection from hydrodynamic forces and predation pressure, and concave terrain features (for example, holes and undercuts) might provide nursery species with refugia that help to minimise energy expenditure and risk and maximise growth, when mangroves are not available (Johnston and Sheaves 2007; Pavlov and others 2008; Pirtle and others 2017). By contrast, the abundance of grass emperor was positively correlated with the presence of convex terrain features in the seascape. Juvenile grass emperor migrate tidally between seagrass meadows and mangrove forests to feed and shelter, and their association with convex terrain features (for example, bars and mounds) possibly reflects the accumulation of sediment in, and around, subtidal seagrass meadows (Wilson 1998; Kimball and others 2018; Quang Le and others 2020). Variation in the terrain of estuaries is, therefore, inherently linked to the nursery function of intertidal mangroves because topographically complex terrain features provide important subtidal refuge habitats that are critical components of coastal seascape nurseries (Nagelkerken and others 2015).

Seagrass meadows are nursery habitats that support the juveniles of many species in high abundance, but many nursery species that use

seagrass also undertake regular tidal and/or diurnal feeding migrations into adjacent soft sediments habitats (McDevitt-Irwin and others 2016; Whitfield 2017). Our findings demonstrate that the composition of nursery species in seagrass meadows was affected by variation in depth (1 species) and roughness (2 species). Nursery species abundance and the abundance of tarwhine were positively correlated with depth. Deep terrain features, such as tidal channels, are used as migration pathways and dispersal conduits by juveniles and larvae, which frequently settle in adjacent seagrass meadows that offer protection from hydrodynamic forces and a diversity of feeding opportunities (Heithaus 2004; Gullström and others 2008; Ford and others 2010; Kough and others 2017). Nursery species richness and the abundance of two species, sand whiting and luderick, were negatively correlated with roughness. Seagrass meadows that are interspersed with soft sediments (that is, low roughness) are often hotspots for juvenile fish diversity because these areas provide complementary foraging grounds for generalist zoobenthivores (for example, sand whiting) and omnivores (for example, luderick) (Raubenheimer and others 2005; Hadwen and others 2007). The larvae of some seagrass nursery species (for example, sand whiting) also settle over shallow soft sediments (for example, intertidal flats and tidal pools) before later migrating to seagrass, because these areas support few predators and abundant food (for example, nematodes) (Burchmore and others 1988; Krück and others 2009). The three-dimensional characteristics of surrounding estuarine seascapes is, therefore, likely connected to the ecological significance of seagrass nurseries because complex terrain features provide complementary habitats and support similar habitat functions (for example, foraging sites, predator refuges and larval settlement locations) to many seagrass meadows (Hynes and others 2014).

The ecological values of coastal nursery habitats depend on their position in the wider seascape, and the spatial distribution of fish assemblages has been linked to the two-dimensional proximity, area and connectivity (that is, seascape context) of complementary nursery habitats like mangrove forests, seagrass meadows and coral reefs (Harborne and others 2016; Berkstrom and others 2020). We show that the significance of nursery habitats can also be modified by the three-dimensional characteristics of the seafloor and demonstrate that a variety of terrain features combine to shape the distribution of fish assemblages in mangrove and seagrass ecosystems. These results support the findings of

other research, which has suggested that subtidal terrain features, such as shallow sand banks, steep rocky ledges and outcrops, and curved banks and gullies, provide nursery habitats for a diversity of species and often mirror habitat functions (for example, foraging grounds, predator refuges and spawning locations) that are provided by intertidal nurseries (Rochette and others 2010; Farmer and others 2017; Pirtle and others 2017). The synergistic roles of connected intertidal and subtidal habitats in underpinning nursery functions for a diversity of species is now widely accepted (see reviews by Nagelkerken 2009; Sheaves 2009; Olds and others 2016; Pittman 2018). Recognition of the significance of inter-habitat linkages culminated in the development of the “seascape nursery” concept (sensu Nagelkerken and others 2015), which advances the nursery habitat paradigm considerably, but still conceptualises nurseries as two-dimensional mosaics of interlinked benthic habitats. Given the ecological consequences of seafloor terrain variation for nursery habitat function (see Borland and others 2021), we suggest that the seascape nursery concept could be expanded to incorporate variation in the three-dimensional structure of the seafloor, with potential wider implications for the spatial conservation of nursery habitats and the management of fisheries for nursery species.

CONCLUSION

We report strong effects of three-dimensional terrain features on the ecological function of nursery habitats in coastal seascapes and demonstrate that bathymetric variability has distinct effects on species, depending on life stages and their utilisation of mangrove and seagrass nurseries as juvenile habitat. Our findings show that the use of nursery habitats by a diversity of fish species is affected by a suite of terrain attributes in the surrounding seascape. The results of this study demonstrate that the ecological consequences of terrain variation transcend the boundaries of ecosystems and can differ between mangrove and seagrass habitats. Given the significance of seafloor variation for nursery function, we recommend that nursery habitats and seascapes should be evaluated in three dimensions to better incorporate heterogeneity in the complexity, morphology and relief of undersea terrain. The key challenge now is for research to examine how three-dimensional terrain and two-dimensional seascape context combine to influence nursery function, such as the growth and survival of juveniles, and the consistency of these effects across a diversity of seascapes and habitat patches.

We suggest that integrating seafloor terrain into the seascape nursery concept should help to improve our understanding of nursery habitat function and might have wider implications for habitat prioritisation decisions in coastal conservation and restoration.

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DATA AVAILABILITY

Data available from the USC Research Bank (<http://doi.org/10.25907/00138>).

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