Borland, Hayden P., Gilby, Ben L., Henderson, Christopher J., Leon, Javier X., Schlacher, Thomas A., Connolly, Rod M., Pittman, Simon J., Sheaves, Marcus, and Olds, Andrew D. (2021) ***The influence of seafloor terrain on fish and fisheries: a global synthesis.*** **Fish and Fisheries, 22 (4) pp. 707-734.**

The influence of seafloor terrain on fish and fisheries: a global synthesis

Hayden P. Borland[1]*, Ben L. Gilby[1], Christopher J. Henderson[1], Javier X. Leon[1], Thomas A. Schlacher[1], Rod M. Connolly[2], Simon J. Pittman[3], Marcus Sheaves[4], Andrew D. Olds[1]

[1] School of Science and Engineering, University of the Sunshine Coast, Maroochydore, Australia

[2] Australian Rivers Institute – Coasts & Estuaries, School of Environment and Science, Griffith University, Gold Coast, Australia

[3] School of Biological and Marine Sciences, Marine Institute, University of Plymouth, Plymouth, United Kingdom

[4] College of Science and Engineering and Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Townsville, Australia

*Corresponding author: hayden.borland@research.usc.edu.au

Running title: Effects of terrain on fish assemblages

Abstract

The structure of seafloor terrain affects the distribution and diversity of animals in all seascapes. Effects of terrain on fish assemblages have been reported from most ecosystems, but it is unclear whether bathymetric effects vary among seascapes or change in response to seafloor modification by humans. We reviewed the global literature linking seafloor terrain to fish species and assemblages (96 studies) and determined that relief (e.g. depth), complexity (e.g. roughness), feature classes (e.g. substrate types) and morphology (e.g. curvature), have widespread effects on fish assemblages. Research on the ecological consequences of terrain have focused on coral reefs, rocky reefs, continental shelves and the deep sea ($n \geq 20$ studies), but are rarely tested in estuaries ($n = 7$). Fish associate with a variety of terrain attributes, and assemblages change with variation in the depth and aspect of bathymetric features in reef and shelf seascapes, and in the deep sea. Fish from different seascapes also respond to distinct metrics, with fluctuations in slope of slope (coral reefs), rugosity (rocky reefs) and slope (continental shelves, deep sea) each linked to changes in assemblage composition. Terrain simplification from coastal urbanisation (e.g. dredging) and resource extraction (e.g. trawling) can reduce fish diversity and abundance, but assemblages can also recover inside effective marine reserves. The consequences of these terrain changes for fish and fisheries are, however, rarely measured in most seascapes. The key challenge now is to examine how terrain modification and conservation combine to alter fish distributions and fisheries productivity across diverse coastal seascapes.

Keywords: bathymetry, fish, morphology, seafloor complexity, seascape ecology, vertical relief

Contents

1.0 INTRODUCTION

The spatial configuration of habitats, and the topographic complexity of seafloor terrain, combine to structure the distribution, abundance and diversity of fish populations and assemblages across seascapes (Bouchet et al., 2015; Brown et al., 2011; Pygas et al., 2020). These spatial attributes are important because fish use multiple habitat types to feed and reproduce, and often aggregate in areas where seascape connectivity (i.e. spatial linkages between different habitat types) and terrain complexity are elevated (Green et al., 2015; Nagelkerken et al., 2015; Olds et al., 2018b). Structurally complex fish habitats such as biogenic ecosystems (e.g. corals, oysters) and prominent geological structures (e.g. pinnacles, seamounts), are well recognised aggregators of both biodiversity and fisheries productivity, and have become focal points for spatial conservation planning and fisheries management (Bouchet et al., 2015; Pygas et al., 2020; Seitz et al., 2014). The two-dimensional configuration and three-dimensional complexity of these bathymetric features are now routinely mapped with a diverse range of technologies to create digital elevation models (DEMs) of the seafloor, which combined with the geospatial processing power of modern computers, provides rich opportunities for research to investigate the ecological effects of seafloor terrain variation on fish assemblages and fisheries productivity (Costa et al., 2018b; Pittman & Brown, 2011; Stamoulis et al., 2018).

The importance of seafloor terrain (e.g. relief, ruggedness, roughness) for fish is widely recognized (Moore et al., 2010; Pittman et al., 2009; Wedding et al., 2008), but not all metrics used to index terrain might be applicable (e.g. rugosity, Duvall et al., 2019; Pygas et al., 2020). The ecological effects of terrain, as well as, the importance of different terrain metrics, is likely to differ among seascapes (Bouchet et al., 2017; Rees et al., 2014; Wedding et al., 2019). Yet, there is no comprehensive synthesis that describes whether, and how, changes in seafloor terrain illicit distinct responses from fish assemblages in different seascapes. The terrain of most seascapes have been significantly modified by humans (e.g. via seafloor dredging, beach nourishing, trawling, urbanisation) and climate change (e.g.

through the mortality and degradation of reef-building corals), but the possible ecological effects of this terrain modification on fish assemblages and fisheries productivity are poorly understood (Collie et al., 2017; Madricardo et al., 2019; Perry & Alvarez-Filip, 2019; Stamoulis et al., 2018; Torres-Pulliza et al., 2020).

Here, we reviewed the published literature that links variation in seafloor terrain to the distribution, abundance and diversity of fish assemblages. We searched the Elsevier Scopus and ISI Web of Knowledge databases using the keywords “fish” and “marine”, “coast”, “seascape” or “ocean”, and at least one of the following terms: “bathymetr*”, “terrain”, “topograph*”, “digital elevation”, “three-dimension*, “lidar” or “sonar” (see Supporting Information for more detail on Methods). The primary goals of this review were to determine global patterns in the: (1) geographical distribution and focus of research linking fish assemblages to changes in seafloor terrain; (2) ecological effects of seafloor terrain on fish assemblages; (3) consequences of terrain variation among different seascapes; (4) impacts of human activities that modify seafloor terrain and fish assemblages; and (5) ability for prominent terrain features to serve as targets for seascape conservation and fisheries management.

2.0 SEASCAPE ECOLOGY OF FISH IN TWO AND THREE DIMENSIONS

Two-dimensional maps of benthic habitats exist for many ecosystems, and these are interrogated using models (e.g. patch-matrix and patch-mosaic) (see review by Wedding et al., 2011) to predict how the composition (e.g. area, richness and diversity of habitat types) and configuration (e.g. proximity between different habitat types) of ecosystems, shape the distribution of fish assemblages (Henderson et al., 2020a; Swadling et al., 2019; van Lier et al., 2018). This approach has been used in many seascapes and typically shows that fish are most diverse and abundant in ecosystems that provide a variety of high-relief habitat features (e.g. coral reefs, seagrass meadows, mangrove forests), particularly when these occur close to other habitat that also contain complex structures (Nagelkerken et al., 2015;

Olds et al., 2016; Pittman, 2018). These models over-simplify the complexity of seascapes by assuming that the ecological values of ecosystems are consistent in two-dimensional space (McGarigal et al., 2009; Pittman, 2018; Pittman & Olds, 2015). The significance of habitat for fish assemblages, and other organisms, is however, also likely to vary with changes in bathymetry across seascapes (Olds et al., 2018b; Stamoulis et al., 2018). Gradient models that incorporate variation in the three-dimensional complexity of seascapes (e.g. terrain) are, therefore, likely to out-perform patch-matrix and patch-mosaic models in predicting spatial patterns in fish diversity and abundance (Sekund & Pittman, 2017; Wedding et al., 2019).

Spatial variation in terrain (e.g. seafloor complexity and relief) can modify the distribution of ecosystems and topographically complex features, across seascapes (Goes et al., 2019; Ismail et al., 2018; Wicaksono et al., 2019). These three-dimensional terrain features alter the hydrodynamic properties of seascapes through their effects on currents, tides and waves (Genin, 2004; Harris et al., 2018; Rogers et al., 2018b), and provide fish with important refuges from predation, feeding areas and spawning zones (Bouchet et al., 2017; Farmer et al., 2017; Pirtle et al., 2017). Terrain features have been derived, and widely mapped, on coral and rocky reefs, over continental shelves and in some areas of the deep sea, using passive (e.g. satellite imagery) and active (e.g. Light Detection and Ranging: LiDAR; Sound Navigation and Ranging: SONAR) sensors (Costa et al., 2018a; Goodell et al., 2018; Sievers et al., 2016; Wedding et al., 2019), and through emerging techniques such as Structure-from-Motion (SfM) photogrammetry that derives digital terrain models from overlapping images (Bayley et al., 2019; González-Rivero et al., 2017; Leon et al., 2015; Storlazzi et al., 2016). They are typically measured using a variety of terrain metrics, which index variation in the depth, vertical relief, morphology and complexity of the seafloor (Cameron et al., 2014; Oyafuso et al., 2017; Pirtle et al., 2017) and are summarised (e.g. mean, max, min, range, standard deviation) at a variety of spatial scales (e.g. metres to kilometres) (Knudby et al., 2011; Rees et al., 2018; Sekund & Pittman, 2017). Terrain metrics quantify properties of benthic ecosystems that underpin their role in providing habitat for fish, and variation in fish diversity and abundance have been linked to spatial variation in terrain metrics (e.g. rugosity, slope, slope of slope) on coral and rocky reefs, continental shelves and the deep sea (Coleman et al., 2016; Moore et al., 2016; Parra et al., 2017; Wedding et al., 2019). Well known examples that illustrate the significance of terrain features as fish habitat include: high rugosity on coral reefs (Pittman et al., 2007; Wedding et al., 2008), sheltered caves on rocky reefs (Monk et al., 2010; Pirtle et al., 2017), low-sloping soft sediments on continental shelves (Moore et al., 2016; Smoliński & Radtke, 2017), and high relief pinnacles in the deep sea (Leitner et al., 2017; Oyafuso et al., 2017).

3.0 GLOBAL DISTRIBUTION OF RESEARCH EFFORT LINKING SEAFLOOR TERRAIN WITH FISH

We found 96 research articles in the peer-reviewed literature that investigated the effects of seafloor terrain on fish assemblages. This research was comprised of studies from coral reef (n = 27), rocky reef (n = 22), deep sea (depth range: 200 – 5000 m; n = 20), continental shelf (n = 20) and estuarine (n = 7) seascapes (Table S1). Research effort is geographically widespread, encompassing studies from the United States (n = 37), Australia (n = 20), France (n = 7), Antarctica (n = 4) and Brazil (n = 4) (Figure 1).

4.0 FOCUS OF RESEARCH LINKING SEAFLOOR TERRAIN WITH FISH

There was substantial variation in the approaches applied to quantify seafloor terrain structures, with 23 different terrain metrics being used across the 96 studies (mean per paper = 3, range: 1 - 10). Terrain metrics are derived using numerous Geographical Information Systems (GIS) (e.g. ArcGIS, QGIS, SAGA GIS) and toolboxes (e.g. Benthic Terrain Modeler, ArcGeomorphometry), which use discrete geoprocessing tools and mathematical equations to index different seafloor features (Rigol-Sanchez et al., 2015; Walbridge et al., 2018). However, many describe similar types of terrain variation, and are therefore, characterized by high co-linearity with other similar terrain metrics (e.g. rugosity, slope, slope of slope) (Leitner et al., 2017; Monk et al., 2010; Sekund & Pittman, 2017). To better understand patterns of metric applications, we grouped terrain metrics into four categories based on similarities in the terrain features being indexed: (1) seafloor relief; (2) seafloor complexity; (3) seafloor feature class; and (4) seafloor morphology (Table 1; Figure 1 & 2).

4.1 Seafloor relief

Seafloor relief is a measure of the depth and height of terrain features below sea level (Moore et al., 2010; Rees et al., 2014; Sievers et al., 2016). This component of terrain is widely recognized as a primary determinant in shaping both the distribution of fish populations, and the composition of fish assemblages (Coleman et al., 2018; Pereira et al., 2018; Stamoulis et al., 2018). This is because variation in seafloor depth and relief is strongly linked to changes in many abiotic features (e.g. temperature, salinity, light) that regulate photosynthesis, alter patterns in diel vertical migration and bentho-pelagic coupling, and modify the structure of food-webs (Barbini et al., 2018; Jankowski et al., 2015; Young et al., 2018) (Table 2). Prominent high-relief features of the seafloor (e.g. pinnacles, seamounts) also serve as focal points for fish spawning aggregations, and resting points during long distance migrations (Clark et al., 2010; Farmer et al., 2017; Kobara & Heyman, 2008; Rowden et al., 2010). Terrain metrics that index variation in seafloor depth and relief include: (1) average depth: the mean seafloor depth within a focal seascape (e.g. Pittman et al., 2009); (2) contour index: the percent change in depth, or vertical relief, within a focal seascape (e.g. Bouchet et al., 2017); and (3) vertical relief: the range of seafloor depths within a focal seascape (e.g. Moore et al., 2010) (Table 1; Figure 2).

4.2 Seafloor complexity

Seafloor complexity is a measure of the topographic roughness of terrain features (Kuffner et al., 2007; Pittman & Brown, 2011; Stamoulis et al., 2018). Variation in the complexity of the seafloor has been linked to changes in the abundance and diversity of fishes across most seascapes (Bayley et al., 2019; Ferrari et al., 2018b; Oyafuso et al., 2017). Rough, rugged, and high rugosity features of the seafloor support a range of fish populations in high abundance because these areas are characterized by high niche diversity, and provide foraging areas, refuges from predation, and spawning sites for species from the full suite of functional groups (Ferrari et al., 2018b; Pygas et al., 2020; Wedding et al., 2008) (Table 2). Historically, seafloor complexity was measured *in-situ* (e.g. chain and tape rugosity; Risk, 1972), and this is a useful predictor of fish abundance and diversity, but this technique is both time consuming and is typically limited to small areas of a single habitat (i.e. coral reefs) (Harborne et al., 2012; Kuffner et al., 2007; Wedding et al., 2008). Seafloor complexity can now be indexed with terrain metrics derived from bathymetric maps, which describe the complexity of the seafloor by comparing depth variation across a broad range of spatial scales (Dunn & Halpin, 2009; Pittman et al., 2007; Torres-Pulliza et al., 2020; Wilson et al., 2007). Terrain metrics that quantify variation in seafloor complexity include: (1) depth standard deviation: the standard deviation of the depth of a feature below sea level (e.g. Pittman et al., 2007); (2) fractal dimensions: a ratio measure of seafloor roughness, typically measured as values between 2 and 3 (e.g. Pittman et al., 2009); (3) rugosity: the ratio of bathymetric and planar surface areas (Kuffner et al., 2007); (4) slope: the maximum change in elevation measured in degrees (e.g. Wedding & Friedlander, 2008); (4) slope of slope: the maximum rate of slope change measured in degrees of degrees (e.g. Pittman et al., 2009); and (5) benthic terrain ruggedness index (TRI) or vector ruggedness index (VRM): the ruggedness of the seafloor measured by accounting for changes in both slope and aspect, with values typically falling between 0 (low ruggedness) and 1 (high ruggedness) (e.g. Young et al., 2010) (Table 1; Figure 2).

4.3 Seafloor feature class

Seafloor feature class is a measure of the unique terrain features, or habitats, within a seascape (Kenny et al., 2003; Lundblad et al., 2006). Seascapes are comprised of diverse ecosystems and seafloor features, which provide multiple habitat functions for marine fauna, including refuge from predators, foraging areas, spawning sites and dispersal corridors (Henderson et al., 2019; Sheaves et al., 2015; Whitfield, 2017) (Table 2). The ecological values of discrete terrain features, or seafloor feature classes, can differ markedly between features with distinct physical characteristics, and this modifies the composition of fish assemblages across seascapes (Cameron et al., 2014; Giddens et al., 2019; Purkis et al., 2008). Terrain metrics that represent this discrete variation in bathymetry, include: (1) backscatter: variation in the hardness, or softness, of the seafloor based on acoustic reflectance and scattering from multi-beam sonar (e.g. Monk et al., 2010); (2) bathymetric position index (BPI): categorises variation in seafloor elevation, with larger values indicating elevational highs (e.g. pinnacles, seamounts) and smaller values indicating elevational lows (e.g. valleys, trenches) (e.g. Iampietro et al., 2005); (3) depth-invariant index: variation among different habitats and substrates (e.g. reefs, seagrass, sand, mud, rock) based on the spectral bands of satellite imagery (e.g. Knudby et al., 2010); and (4) substratum classification: categorizes bathymetric maps into terrain features that differ in ecological or biophysical attributes, such as reefs and soft sediment (e.g. Hill et al., 2014; Moore et al., 2016), reefs and lagoons (e.g. Knudby et al., 2011; Purkis et al., 2008), and peaks, slopes and valleys (e.g. Young et al., 2010) (Table 1; Figure 2).

4.4 Seafloor morphology

Seafloor morphology is a measure of the shape of terrain features, which encompasses variation in both their orientation (i.e. aspect) and level of roundness (i.e. curvature) (Abdul Wahab et al., 2018; Pittman et al., 2009; Stamoulis et al., 2018). These metrics are derived from the physical and earth sciences (i.e. geology, hydrology, geomorphology) and were first developed to describe water flow, quantify erosion and deposition rates and measure solar radiation (Lecours et al., 2016; Leempoel et al., 2015; Moore, 1991; Pike, 2000). The aspect and curvature of terrain features can affect the distribution, diversity and abundance of marine fauna through their effects on local hydrodynamic conditions and light penetration (Bouchet et al., 2015; Pirtle et al., 2017; Stamoulis et al., 2018) (Table 2). These attributes combine to modify the distribution of: refuges to exposure (e.g. from currents, tides and waves), local productivity and food-web structure (e.g. through effects on plankton and algae), and both food and habitat availability for fish (Cameron et al., 2014; Moore et al., 2010; Pittman & Brown, 2011). The aspect of a terrain feature is typically measured as it's direction of orientation, with values ranging between 1 and -1 used to represent both "northness" (i.e. 1 = north; -1 = south) and "eastness" (i.e. 1 = east; -1 = west) (Table 1). A variety of other seafloor morphology metrics describe the characteristics of a curved surface, including: (1) curvature (i.e. absolute, maximum, mean, plan, profile or tangential curvature): the morphological shape of a feature, with negative values indicating convex curvature and positive values indicating concave curvature (e.g. Biber et al., 2014; Monk et al., 2010; Moore et al., 2009; Quattrini et al., 2012; Yates et al., 2019); (2) plane morphometry: the proportion of features without convexity or concavity (e.g. Cameron et al., 2014); (3) ridge morphometry: the proportion of convex features to cells with no curvature (e.g. Cameron et al., 2014); and (4) kurtosis: the sharpness of a curved feature (e.g. Bayley et al., 2019) (Table 1; Figure 2).

5.0 LINKS BETWEEN SEAFLOOR TERRAIN AND FISH DISTRIBUTION, ABUNDANCE AND DIVERSITY

Variation in seafloor terrain has been linked to changes in the distribution of fish populations, and fluctuations in the abundance and diversity of fish, from coral reef, rocky reef, deep sea, continental shelf and estuarine seascapes (Figure 3). Across all seascapes examined in this review, more studies report positive (n = 111) than negative (n = 55) effects, and more studies report significant (n = 166, combined positive and negative effects) then neutral effects (n = 146) of terrain, on fish diversity and abundance (Figure 3; see Supporting

Information for methods used to define variable responses). Variability in the direction and strength of association between terrain structure and fish response may relate to the way terrain was quantified (i.e. the choice of metrics), differences in the habitat structure of focal seascapes (i.e. coral reef, rocky reef, deep sea, continental shelf, estuary) and scale effects. Overall, there have been more positive and negative, than neutral, associations between fish diversity and abundance, and metrics that index seafloor relief, seafloor complexity and seafloor feature class (Figure 3). By contrast, there have been more neutral, than negative or positive, associations between fish diversity and abundance, and metrics that index seafloor morphology (Figure 3). These findings suggest that variation in fish abundance and diversity might be positively linked to the relief and complexity of terrain features, rather than the morphology of the seafloor (Moore et al., 2016; Oyafuso et al., 2017). There were, however, substantial differences in the ecological effects of seafloor terrain among seascapes.

There is a significant bias in the distribution of research on seafloor terrain among seascapes, with most studies focusing on the ecological effects of terrain variation on coral reefs (n = 27), rocky reefs (n = 22), the deep sea (n = 20) and continental shelves (n = 20), and comparatively fewer studies linking terrain features to fish assemblages in estuaries (n = 7) (Figure 3, Table S1). Positive effects of terrain on fish were more common in studies from rocky reefs and the deep sea, whereas negative effects were more common in studies from continental shelves and estuaries. By contrast, the effects of terrain on fish were highly variable in studies from coral reefs, which report more neutral, then either positive or negative, effects (Figure 3). These results indicate that the response of fish assemblages to seafloor terrain might vary among seascapes and suggest that different metrics may be needed to index terrain effects on fish in distinct ecosystems. A large number of studies (n = 146) report neutral effects of seafloor terrain on fish diversity and abundance, and these results might be hindered by the adoption of terrain metrics that are not particularly suited to the seascape of interest (e.g. slope on coral reefs, mean curvature on rocky reefs and rugosity on continental shelves) (Coleman et al., 2016; Schultz et al., 2014; Wedding & Friedlander, 2008). The prevalence of neutral effects might also reflect species-specific terrain associations that limit the detectability of significant effects of terrain on community metrics (e.g. fish abundance, diversity, biomass), or the application of statistical analyses that either fail to incorporate the correct linearity of fish-terrain relationships (e.g. using linear regressions to model non-linear relationships), or do not include variable interactions (Knudby et al., 2011; Oyafuso et al., 2017; Pittman et al., 2007).

6.0 CONSISTENCY IN TERRAIN EFFECTS AMONG MARINE SEASCAPES

6.1 Coral reef

Twenty-seven studies using a total of 17 different terrain metrics investigated the influence of seafloor terrain on coral reef fishes, including metrics to quantify seafloor relief (n = 16), complexity (n = 23), feature class (n = 10) and morphology (n = 9) (Table S1, Figure 4).

Seafloor relief

The ecological effects of seafloor relief on coral reef fishes were highly variable, with studies reporting positive (53%), negative (16%) and neutral (31%) effects (Figure 4). Two terrain metrics have been used to index effects of seafloor relief on coral reef fish: average depth (n = 14) and vertical relief (n = 5), with average depth being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor relief have been reported from research on both vertical relief (60%) and average depth (50%), negative effects from research on average depth (21%), and neutral effects from research on both vertical relief (40%) and average depth (29%) (Figure S1; see Tables 3 & S5 for additional details).

Seafloor complexity

The ecological effects of seafloor complexity on coral reef fishes were either positive (50%) or neutral (48%) (Figure 4). Five terrain metrics have been used to index effects of seafloor complexity on coral reef fish, including: rugosity (n = 15), slope (n = 8), slope of slope (n = 8), depth standard deviation (n = 6) and fractal dimensions (n = 1), with slope of slope being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor complexity have been reported from research on slope of slope (75%), rugosity (53%), slope (38%) and depth standard deviation (33%), negative effects from research on slope (12%), and neutral effects from research on fractal dimension (100%), depth standard deviation (67%), slope (50%), rugosity (47%) and slope of slope (25%) (Figure S1; see Tables 3 & S5 for additional details).

Seafloor feature class

The ecological effects of seafloor feature class on coral reef fishes were either positive (45%) or neutral (55%) (Figure 4). Four terrain metrics have been used to index effects of seafloor feature class on coral reef fishes: substratum classification (n = 4), backscatter (n = 3), BPI (n = 2) and depth-invariant index (n = 2), with substratum classification being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor feature class have been reported from research on substratum classification (100%) and backscatter (33%), and neutral effects from research on depth-invariant index (100%) and backscatter (67%) (Figure S1; see Tables 3 & S5 for additional details).

Seafloor morphology

The ecological effects of seafloor morphology on coral reef fishes were highly variable, with studies reporting positive (16%), negative (5%) and neutral (79%) effects (Figure 4). Six terrain metrics were used to index the effects of seafloor morphology on coral reef fish: plan curvature (n = 6), aspect (n = 4), mean curvature (n = 3), profile curvature (n = 3), absolute curvature (n = 2) and kurtosis (n = 1), with aspect being the best performing metric (Figures 5 & 6, Table S4). Most studies reported neutral effects of seafloor morphology on coral reef fishes, from research on absolute curvature (100%), mean curvature (100%), profile curvature (100%), kurtosis (100%), plan curvature (66%) and aspect (50%) (Figure

S1). Positive effects of seafloor morphology were, however, reported from research on aspect (50%) and plan curvature (17%), and negative effects were also reported from research on plan curvature (17%) (Figure S1; see Tables 3 & S5 for additional details).

6.2 Rocky reef

Twenty-two studies using 18 different terrain metrics investigated the ecological effects of seafloor terrain on rocky reef fishes, including metrics to quantify seafloor relief (n = 21), seafloor complexity (n = 21), seafloor feature class (n = 17) and seafloor morphology (n = 12) (Table S1, Figure 4).

Seafloor relief

The ecological effects of seafloor relief on rocky reef fishes were highly variable, with studies reporting positive (24%), negative (40%) and neutral (36%) effects (Figure 4). Two terrain metrics have been used to index the effects of seafloor relief on rocky reef fish: average depth (n = 18) and vertical relief (n = 7), with average depth being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor relief have been reported from research on both vertical relief (29%) and average depth (22%), negative effects from research on average depth (56%), and neutral effects from research on both vertical relief (71%) and average depth (22%) (Figure S2; see Tables 4 & S5 for additional details).

Seafloor complexity

The ecological effects of seafloor complexity on rocky reef fishes were also highly variable, with studies reporting positive (42%), negative (8%) and neutral (50%) results (Figure 4). Six terrain metrics have been used to index effects of seafloor complexity on rocky reef fish: slope (n = 13), rugosity (n = 11), depth standard deviation (n = 5), TRI (n = 3), slope of slope (n = 2) and fractal dimension (n = 2), with rugosity being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor complexity were reported from research on slope of slope (100%), rugosity (64%), fractal dimension (50%), slope (31%) and depth standard deviation (20%), negative effects from research on slope (23%), and neutral effects from research on TRI (100%), depth standard deviation (80%), fractal dimensions (50%), slope (46%) and rugosity (36%) (Figure S2; see Tables 4 & S5 for additional details).

Seafloor feature class

The ecological effects of seafloor feature class on rocky reef fishes were mostly positive (60%), but some studies also reported negative (15%) and neutral (25%) effects (Figure 4). Three terrain metrics have been used to index effects of seafloor feature class on rocky reef fishes: BPI (n = 13), backscatter (n = 5) and substratum classification (n = 2), with backscatter being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor feature class were reported from research on substratum classification (100%), backscatter (60%) and BPI (54%), negative effects from research on backscatter (20%) and BPI (15%), and neutral effects from research on BPI (31%) and backscatter (20%) (Figure S2; see Tables 4 & S5 for additional details).

Seafloor morphology

The ecological effects of seafloor morphology on rocky reef fishes were highly variable, with studies reporting positive (21%), negative (18%) and neutral (61%) effects (Figure 4). Seven terrain metrics were used to test for the effects of seafloor morphology on rocky reef fish: aspect (n = 11), mean curvature (n = 5), plan curvature (n = 4), profile curvature (n = 4), maximum curvature (n = 2), plane morphometry (n = 1) and ridge morphometry (n = 1), with aspect being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor morphology have been reported from research on maximum curvature (50%), aspect (36%) and profile curvature (25%), negative effects from research on maximum curvature (50%) and aspect (36%), and neutral effects from research on mean curvature (100%), plan curvature (100%), plane morphometry (100%), ridge morphometry (100%), profile curvature (75%) and aspect (28%) (Figure S2; see Tables 4 & S5 for additional details).

6.3 Deep sea

Twenty studies used 16 different terrain metrics to investigate the ecological effects of seafloor terrain on deep sea fishes, including metrics to quantify seafloor relief (n = 13), seafloor complexity (n = 15), seafloor feature class (n = 7) and seafloor morphology (n = 7) (Table S1, Figure 4).

Seafloor relief

The ecological effects of seafloor relief on deep sea fishes were mostly positive (60%), but there were also some reports of negative (20%) and neutral (20%) effects (Figure S1). Three terrain metrics were used to index the effects of seafloor relief on deep sea fish: average depth (n = 12), vertical relief (n = 2) and contour index (n = 1), with average depth being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor relief were reported from research on average depth (75%), negative effects from research on average depth (25%), and neutral effects from research on contour index (100%) and vertical relief (100%) (Figure S3; see Tables 5 & S5 for additional details).

Seafloor complexity

The effects of seafloor complexity on deep sea fishes were highly variable, with studies reporting either positive (38%) or neutral (62%) effects (Figure 4). Five terrain metrics were used to index effects of seafloor complexity on deep sea fish: slope (n = 10), rugosity (n = 4), TRI (n = 4), fractal dimensions (n = 2) and slope of slope (n = 1), with slope being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor complexity were reported from research on slope (50%), rugosity (50%) and TRI (25%), and neutral effects from research on fractal dimension (100%), slope of slope (100%), TRI (75%), rugosity (50%) and slope (50%) (Figure S3; see Tables 5 & S5 for additional details).

Seafloor feature class

The ecological effects of seafloor feature class on deep sea fishes were mostly positive (75%), but some studies also reported neutral effects (25%) (Figure 4). Three terrain metrics were used to index effects of seafloor feature class on deep sea fish: BPI (n = 5), backscatter (n = 2) and substratum classification (n = 1), BPI being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor feature class were reported from research on backscatter (100%), substratum classification (100%) and BPI (60%), and neutral effects were reported from research on BPI (40%) (Figure S3; see Tables 5 & S5 for additional details).

Seafloor morphology

The ecological effects of seafloor morphology were highly variable, with studies reporting positive (33%), negative (7%) and neutral (60%) effects on deep sea fishes (Figure 4). Five terrain metrics were used to index effects of seafloor morphology on deep sea fish: aspect (n = 7), mean curvature (n = 3), plan curvature (n = 2), profile curvature (n = 2) and tangential curvature (n = 1), with aspect being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor morphology have been reported from research on plan curvature (50%), profile curvature (50%), mean curvature (33%) and aspect (29%), negative effects from research on aspect (14%), and neutral effects from research on tangential curvature (100%), mean curvature (67%), aspect (57%), plan curvature (50%) and profile curvature (50%) (Figure S3; see Tables 5 & S5 for additional details).

6.4 Continental shelf

Twenty studies used 12 terrain metrics to investigate the effects of terrain on continental shelf fishes, including metrics to quantify seafloor relief (n = 16), seafloor complexity (n = 9), seafloor feature class (n = 7) and seafloor morphology (n = 4) (Table S1, Figure 4).

Seafloor relief

The ecological effects of seafloor relief on fish from continental shelves were highly variable, with studies reporting positive (11%), negative (61%) and neutral (28%) effects (Figure 4). Two terrain metrics have been used to index effects of seafloor relief on continental shelf fish: average depth (n = 16) and vertical relief (n = 2), average depth being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor relief were reported from research on vertical relief (50%) and average depth (6%), negative effects were reported from research on average depth (69%), and neutral effects from research on both vertical relief (50%) and average depth (25%) (Figure S4; see Tables 6 & S5 for additional details).

Seafloor complexity

The ecological effects of seafloor complexity on fish from continental shelves were highly variable, with studies reporting positive (17%), negative (33%) and neutral (50%) effects (Figure 4). Three terrain metrics were used to index the effects of seafloor relief on continental shelf fish: slope (n = 8), rugosity (n = 2) and TRI (n = 2), with slope being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor complexity were reported from research on TRI (50%) and slope (12%), negative effects from research on TRI (50%) and slope (38%), and neutral effects from research on rugosity (100%) and slope (50%) (Figure S4; see Tables 6 & S5 for additional details).

Seafloor feature class

The ecological effects of seafloor feature class on fish from continental shelves were either positive (29%), or negative (71%) (Figure 4). Two terrain metrics were used to index effects of seafloor feature class on continental shelf fish: backscatter (n = 6) and BPI (n = 1), with backscatter being the best performing metric (Figures 5 & 6, Table S4). Positive effects of seafloor feature class were reported from research on BPI (100%) and backscatter (17%), and negative effects from research on backscatter (83%) (Figure S4; see Tables 6 & S5 for additional details).

Seafloor morphology

The ecological effects of seafloor morphology on fish from continental shelves are equivocal (Figure 4). Five terrain metrics have been used to index the effects of seafloor morphology on continental shelf fish: aspect (n = 2), mean curvature (n = 2), plan curvature (n = 2), profile curvature (n = 2) and maximum curvature (n = 1), but to date all studies have reported inconsistent, and neutral, effects (Figures 5, 6 & S4).

6.5 Estuary

Seven studies used two terrain metrics to investigate the effects of seafloor terrain on estuarine fishes, including metrics to quantify seafloor relief (n = 7) and seafloor complexity (n = 1) (Table S1, Figure 4). The potential ecological effects of seafloor feature class and morphology have not been tested in estuarine seascapes (Figures 5, 6 & S5).

Seafloor relief

The ecological effects of seafloor relief on estuarine fishes were highly variable, with studies reporting positive (14%), negative (72%) and neutral (14%) effects (Figure 4). To date, only one terrain metric (average depth) has been used to index effects of seafloor relief on estuarine fish, and significant effects of variation in average depth have been reported in 86% of studies (Figures 5, 6 & S5; see Tables 7 & S5 for additional details).

Seafloor complexity

The ecological effects of seafloor complexity on estuarine fishes have only been examined in one study, which reported neutral effects of variation in slope (Miller et al., 2015) (Figures 5, 6 & S5).

7.0 IMPORTANCE OF SCALE IN STUDIES EXAMINING ECOLOGICAL EFFECTS OF TERRAIN VARIATION

The scale at which bathymetric features are measured can affect the ecological relevance of terrain metrics (Moudrý et al., 2019; Walbridge et al., 2018). Research articles included in this review have assessed the ecological effects of terrain on fish assemblages using metrics that were quantified across a variety of spatial scales (i.e. 0.5m – 1000m radii) (e.g. Coleman et al., 2016; Sievers et al., 2016). This is also known to affect the detectability of relationships between fish assemblages and terrain features, because fish habitat associations, movements and home ranges are scale dependent (Coleman et al., 2016; Knudby et al., 2011; Kuffner et al., 2007; Pittman & McAlpine, 2003). For example, fish use a variety of habitats throughout their life cycle, and home ranges can differ fundamentally between species, and indeed individuals, with variation in site fidelity and body size (Kuffner et al., 2007; Pittman & Brown, 2011; Pittman et al., 2009).

When insufficient information is available on the home ranges and movement patterns of fish species or assemblages, a multi-scale approach for quantifying terrain metrics is most suitable. This is because species respond to terrain variation differently, using distinct features at different scales, and these terrain associations can also change with life-stage progression (e.g. Monk et al., 2011; Pittman & Brown, 2011; Rees et al., 2018). The spatial scale over which terrain metrics are quantified, might also change among ecosystems, due to variation in both the complexity and relief of terrain features between consolidated (e.g. reefs) and unconsolidated (e.g. estuaries) seascapes. The ecological effects of terrain features are often reported from snapshots in time and over relatively small spatial scales (i.e. 100s of metres) in ecosystems containing complex structures (e.g. coral and rocky reefs) (e.g. Pittman & Brown, 2011; Rees et al., 2018). Responses of fish to terrain might, however, operate at large spatial scales (i.e. 1000s of metres) in unconsolidated ecosystems where terrain complexity is lower (e.g. continental shelves, estuaries) (e.g. Farmer et al., 2017; Lathrop et al., 2006). There is, however, no data that can be used to test whether the effects of terrain operate at distinct spatial scales in different seascapes. Nevertheless, identifying the scale that fish respond to seafloor terrain is critical for effective spatial conservation planning and fisheries management in coastal seascapes (Kuffner et al., 2007; Pittman & Brown, 2011; Wedding et al., 2019).

8.0 HUMANS MODIFY SEAFLOOR TERRAIN WITH CONSEQUENCES FOR FISH AND FISHERIES

Coastal seascapes are focal points for urban development, recreation, and fishing, and have been profoundly transformed to accommodate the demands of expanding human populations (Heery et al., 2017; Mayer-Pinto et al., 2018). In urban seascapes, natural ecosystems, such as mangroves, saltmarshes and seagrasses, are often degraded, become fragmented, or have been replaced, by hard artificial structures, including concrete walls, rock revetments, bridges, jetties and pontoons (Bishop et al., 2017; Bulleri & Chapman, 2010; Dafforn et al., 2015). The seafloor of many urban estuaries and coastal seas has also been modified by dredging to improve shipping, extraction of sand to replenish sandy beaches, the deposition of dredged sediments outside shipping channels, and the construction of groynes, breakwaters and other engineered structures (Freeman et al., 2019; Heery et al., 2017; Macura et al., 2019; Sheaves et al., 2014). These anthropogenic habitat changes significantly impact coastal fish populations, particularly when natural shorelines are replaced by engineered structures and when dredging results in the simplification of estuarine seafloors (Brook et al., 2018; Olds et al., 2018a; Rochette et al., 2010; Wenger et al., 2017). The impacts of terrain modification on fish are, however, rarely tested with empirical data.

Features of the seafloor that are characterized by high vertical relief, terrain complexity and morphological variability (e.g. seamounts, submarine canyons, shoals, pinnacles, ledges and caves) typically support a diversity of fishes in high abundance (Iampietro et al., 2005; Oyafuso et al., 2017; Pirtle et al., 2017; Rees et al., 2018). The significance of these 'hotspots' for fish assemblages is widely appreciated, and they are frequently targeted by commercial (e.g. offshore trawlers that harvest over seamounts), recreational (e.g. line fishers that target coastal ledges) and artisanal (e.g. woven trap fishers that focus on offshore pinnacles) fishers because they are aggregation sites, which concentrate desired fish species in great numbers (Borland et al., 2017; Forcada et al., 2010; Nilsson & Ziegler, 2007; Stamoulis et al., 2018; Williams et al., 2020). Seafloor terrain features that are characterized by high relief and complexity also support productive fisheries, and typically yield larger catches (per unit effort) of target species than areas of comparatively homogenous bathymetry (Bouchet et al., 2017; Fonseca et al., 2017; March et al., 2014; Salarpouri et al., 2018). Heavy fishing pressure can reduce the abundance and size of fish populations, modify the diversity of fish assemblages, and lead to trophic cascades that change the condition and functioning of entire ecosystems (Estes et al., 2011; Jackson et al., 2001; Pauly et al., 1998). Some fishing techniques (e.g. trawling, dredging, anchoring) impact directly upon the structure of the seafloor and fundamentally alter terrain features, which can result in the loss of habitat functions and lead to further declines in fisheries productivity (Bayley et al., 2019; Friedlander et al., 1999; Gascuel et al., 2016; Kaiser et al., 2002; Puig et al., 2012; Thrush & Dayton, 2002). These biophysical impacts from fishing are, however, usually examined independently from the potential ecological consequences of terrain modification. Nevertheless, there is some evidence to show that terrain simplification from destructive fishing practices is associated with declines in fish diversity and abundance in some seascapes (e.g. Bayley et al., 2019), but this is rarely linked to trends in fisheries catches.

Human actions modify the three-dimensional structure of the seafloor via a multitude of stressors, including urbanisation, dredging and fishing, and this often has negative consequences for fish assemblages, but some forms of seafloor modification (e.g. the construction of artificial structures, restoration initiatives) can result in increased seafloor complexity that has positive effects on fish abundance and diversity (Charbonnel et al., 2002; Gilby et al., 2018; Morris et al., 2018). The implementation of restoration initiatives (e.g. oyster reefs), artificial reefs and marine infrastructure (e.g. rock walls, pipelines, oil platforms, renewable energy structures) can provide high-relief habitat for a diversity of fish species, and these structures are often hotspots for fish diversity, especially when they are located within soft-sediment seascapes with low habitat diversity (e.g. estuaries, continental shelves) (Folpp et al., 2020; Gilby et al., 2019; Love et al., 2019; Raoux et al., 2017). There are many three-dimensional considerations that are incorporated into the design of restoration units and artificial structures (e.g. eco-engineering) (Gilby et al., 2018; Hylkema et al., 2020; Strain et al., 2018), but the effects of these seafloor modifications on fish assemblages are seldom linked to alterations to terrain complexity or morphology, and it is not known whether seafloor terrain surrounding artificial or restored fish habitats alters their ecological value for fish assemblages in coastal seascapes.

The ecological consequences of terrain modification can be measured, and monitored to inform adaptive management, using a variety of terrain metrics, which index variation in the depth, vertical relief, morphology and complexity of the seafloor (Goodell et al., 2018; Sievers et al., 2016; Wedding et al., 2019). Seafloor terrain features have been derived, and widely mapped, for many marine ecosystems and seascapes (see Section 5), but are rarely used to index the ecological effects of terrain alterations, on fish assemblages. The application of terrain metrics for describing, and measuring, the ecological impacts of anthropogenic seafloor modification is a promising avenue for future research, which should help to streamline decisions in marine spatial planning (Pittman & Brown, 2011; Stamoulis et al., 2018; Wedding et al., 2019).

9.0 TERRAIN FEATURES PROVIDE FOCAL POINTS FOR SEASCAPE CONSERVATION AND RESTORATION

In combination with ecological drivers, the two-dimensional configuration and three-dimensional complexity of seascapes strongly influences the distribution of fish populations and assemblages (Pittman & Olds, 2015; Wedding et al., 2019). Given the ecological significance of these features for fish, their spatial distribution in coastal seascapes is also likely to influence how fish populations and assemblages respond to coastal management, such as marine conservation and restoration initiatives (Pittman & Brown, 2011; Rees et al., 2018; Wedding et al., 2019).

Marine reserves, sanctuaries and restoration sites have been implemented worldwide in an attempt to promote biodiversity, enhance ecological health and resilience, and support the delivery of ecosystem services, by limiting the impacts of extractive and transformative anthropogenic stressors (e.g. fishing, urbanization, eutrophication) (Gaines et al., 2010; Halpern, 2003; Rey Benayas et al., 2009). Successful no-take marine reserves, and habitat restoration projects, can increase the abundance, diversity and biomass of fish, and support the productivity of linked fisheries, and are particularly effective when they are sited in locations that optimize two-dimensional spatial connectivity with a diversity of other fish habitats (Gilby et al., 2018; Magris et al., 2018; Olds et al., 2016). This is because many species move across seascapes, among habitats and high-relief habitat features, and these migrations link ecosystems, both within and between reserves and restoration areas. It is likely that these movements also depend on the bathymetric characteristics of the seafloor, and that they are positively connected to high terrain relief and complexity (Bouchet et al., 2015; Pygas et al., 2020). Some species might aggregate around these features, whilst others move regularly between them, and both effects could serve to promote the performance of local conservation and restoration projects that are designed and cited to preserve these terrain characteristics (Pittman & Brown, 2011; Wedding et al., 2019).

To date, three studies have investigated how variation in the three-dimensional structure of the seafloor might influence the potential responses of fish assemblages to environmental management actions, and all focused on the performance of marine reserves. The results of this research show that high terrain complexity (quantified by both depth standard deviation and rugosity) can enhance reserve effects on fish diversity and abundance in two coral and rocky reef seascapes in the Pacific (Bayley et al., 2019; Rees et al., 2018), but not on a coral reef in the Western Caribbean (Huntington et al., 2010). These findings are encouraging, but considerably more research is needed to describe how changes in seafloor terrain affect conservation and restoration performance, and to explore opportunities for integrating bathymetric data, particularly for high-relief terrain features that concentrate diversity, into spatial prioritization decisions (Ferrari et al., 2018a; Fonseca et al., 2017). Furthermore, bathymetric data has utility as a spatial proxy for the prioritisation of management actions, and predicting the spatial distribution of vulnerable species, in locations where biological data is poor (Ferrari et al., 2018a; Fonseca et al., 2017).

The effects of climate change pose a major challenge to the design, monitoring and performance of environmental management initiatives in marine seascapes (Magris et al., 2014; Roberts et al., 2017). Changes to the global climate are altering the abiotic conditions that characterize most marine ecosystems (e.g. temperature, pH, sea level), degrading the ecological condition and resilience of habitat forming species (e.g. corals, kelps and seagrasses) and terrain features (e.g. as a consequence of coral degradation), and causing range extensions and relocations for many species, which must move, either geographically or topographically (i.e. towards the poles or to greater depths), to escape extreme environmental perturbation, and follow the distribution of their ecological niches (Constable et al., 2014; Lauchlan & Nagelkerken, 2020; Nye et al., 2009). For example, climate change has already had deleterious impacts in coral reef seascapes, resulting in significant losses of live coral cover, the degradation of reef terrain complexity, and the poleward migration of numerous species (Alvarez-Filip et al., 2009; Hughes et al., 2003; Leggat et al., 2019; Munday et al., 2008; Rogers et al., 2018a). Prominent terrain features, which are located in water that is either deeper or at higher latitudes than current distributions might, therefore, provide supplementary habitats, or stepping stones, for migrating species, and could become hotspots that support high fish diversity and productive fisheries in the future (Brown

& Thatje, 2015; Vestfals et al., 2016). It is also possible that some terrain features (e.g. rocky headlands, deep channels, continental slopes, reefs and shoals) might serve as barriers that limit opportunities for range shifts and, consequently, increase the vulnerability of some species to climate change (Hollowed et al., 2013; Munday et al., 2008). To conserve fish species, protect fish habitats, and manage fisheries under a changing climate, it will be imperative to understand how fish populations and assemblages interact with seafloor terrain, and to identify which types of terrain features provide critical fish habitats that might facilitate, or obstruct, changes in the distribution of fish diversity, abundance and biomass in response to climate change (Goodell et al., 2018; Lenoir et al., 2011; Moore et al., 2009). Spatial scenarios that model the degradation of coral reef complexity on habitat suitability for fish species demonstrate the utility of high-resolution bathymetric maps in forecasting impacts from accelerated climate change, which can help inform the design of future management actions (Newman et al., 2015; Pittman et al., 2011).

10.0 FUTURE DIRECTIONS AND RESEARCH PRIORITIES

The role of seafloor terrain in shaping fish populations and assemblages is well documented (n = ≥ 20) for hard-bottom habitats with high seafloor complexity (e.g. rocky reefs, coral reefs), or soft-sediment habitats that have been the focus of intensive terrain mapping programs (e.g. deep sea, continental shelves) (Ferrari et al., 2018b; Pittman & Brown, 2011; Wedding et al., 2019). By contrast, much less is known about the effects of seafloor terrain on fish assemblages in shallow soft-sediment seascapes; we found only seven papers for estuaries and there has been no work on nearshore waters, such as the surf zones of sandy beaches, that are difficult to map with conventional techniques due to the harsh hydrodynamic activity (Borland et al., 2017; Bradley et al., 2017; Henderson et al., 2019; Mosman et al., 2020). Thus, focusing on data-deficient seascapes in the coastal zone, particularly estuaries and surf zones, is timely (research priority 1, Table 8).

Fish respond to terrain features at a variety of spatial scales, and this varies between species, and with changes in life stages and movement capabilities, which necessitates the adoption of a multi-scale approach in fish – terrain research (Pittman & Brown, 2011; Rees et al., 2018; Sievers et al., 2016). The scale over which terrain features influence fish assemblages might also vary with changes in the structure and complexity of the seafloor, for example fish might respond to terrain differently in coral reef and estuarine environments, but there is no data that can be used to measure whether the ecological effects of terrain operate at distinct spatial scales in different seascapes (research priority 2, Table 8).

Fish move through seascapes to feed, breed and disperse, and these migrations are partly determined by the spatial configuration of habitats (i.e. seascape context), which shape the distribution, abundance and diversity of fish assemblages in most seascapes (Olson et al., 2019; Ortodossi et al., 2019; Perry et al., 2018). Seafloor terrain can also modify the movement of fish species between different habitats, and these properties likely interact with seascape context to determine the spatial distribution of fish populations (Moore et al., 2011; Sekund & Pittman, 2017; Wedding et al., 2019). We do not know, however, whether variation in the three-dimensional properties of the seafloor influence the effects of two-dimensional seascape context, and connectivity, on fish assemblages (research priority 3, Table 8).

Seafloor terrain features are commonly utilized as foraging areas, resting sites, and spawning locations by numerous fish species. Fish move among these as they grow and mature, and as their resource requirements change, and may use particular terrain features as stepping stones (e.g. high-relief pinnacles) or dispersal corridors (e.g. deep channels) (Engelhard et al., 2017; Green et al., 2015; Olds et al., 2016). The movement of many fish species has been linked to prominent high-relief features in some seascapes (e.g. deep channels in estuaries, seamounts in the deep sea, rocky shoals in continental shelves) (Holland & Dean Grubbs, 2008; Hondorp et al., 2017; Siceloff & Howell, 2013), but these movements are rarely linked to terrain (but see Fabrizio et al., 2013; Huff et al., 2011), and it is not clear whether the location and characteristics of terrain features shape the movement of fish across seascapes (research priority 4, Table 8).

Some terrain features (i.e. unconsolidated sand bars and channels, rocky shoals and banks) are thought to be important nursery sites for some fish species (Pirtle et al., 2017; Rochette et al., 2010; Trimoreau et al., 2013). Effective nursery habitats enhance the abundance, growth and survival of juvenile fish, and contribute a greater biomass of these individuals to adult populations, which reside elsewhere in the wider seascape (Beck et al., 2001; Whitfield & Pattrick, 2015). There is, however, no data that can be used to determine the ecological values of prominent terrain features as nursery habitats for fish (research priority 5, Table 8).

Fish perform a diversity of ecological functions (e.g. predation, herbivory, scavenging, nutrient cycling) that are critical for maintaining the ecological health, condition and resilience of ecosystems to disturbance (Catano et al., 2015; Henderson et al., 2020b; Martin et al., 2018; Ruttenberg et al., 2019). Variation in seafloor terrain can modify the trophic composition of fish assemblages in most seascapes, and alter the spatial distribution of many fish trophic guilds (e.g. piscivores, herbivores, corallivores) (Ferrari et al., 2018b; Pittman et al., 2009; Purkis et al., 2008). It is not clear, however, whether these structural effects of terrain complexity on fish assemblages have functional consequences that shape the spatial distribution of key ecological processes (e.g. predation, herbivory) (research priority 6, Table 8).

High relief, and complex, terrain features (e.g. pinnacles, ledges, caves) often support a diversity of apex predators because they provide important resting points on long-distance migrations, aggregation sites for spawning, and abundant feeding opportunities (Farmer et al., 2017; Kuffner et al., 2010; Morato et al., 2010; Pirtle et al., 2017). It is likely that these higher-order predators also exert strong top-down effects in local ecosystems, via both direct predation and elevated predation risk effects, which alter the distribution, abundance and behavior of their prey, and cascade through food-webs to shape the composition of benthic assemblages (Atwood et al., 2015; Baum & Worm, 2009; Estes et al., 2011). We do not know, however, whether the abundance and diversity of apex predators is linked to variation in the type, or characteristics, of undersea terrain features, or whether changes in seafloor relief and complexity modify the spatial distribution of predation events, and the intensity of trophic cascades (research priority 7, Table 8).

In urban seascapes the seafloor is frequently heavily modified and fragmented by anthropogenic activity (e.g. shoreline hardening, dredging, trawling, fishing, the construction of groynes and breakwaters), which reduces the quality, and changes the structure, of terrain features (Freeman et al., 2019; Macura et al., 2019; Sheaves et al., 2014). It is plausible that the modification and fragmentation of seafloor terrain features can have ecological consequences for the spatial distribution and composition of fish assemblages (e.g. Bayley et al., 2019; Kaiser et al., 2002; Rochette et al., 2010), but this hypothesis has rarely been tested with empirical data (research priority 8, Table 8).

There is limited data that can be used to describe the ecological effects of seafloor terrain on fish conservation, or the restoration of fish habitats. Only three studies have investigated the conservation benefits of terrain for fish, and results are inconclusive, indicating positive effects of complex terrain features on rocky reef reserves (Rees et al., 2018), and either positive (Bayley et al., 2019), or neutral (Huntington et al., 2010), effects of terrain complexity in reserves on coral reefs. Variation in the structure and complexity of the seafloor is also likely to influence the effectiveness of habitat restoration for fish (Gilby et al., 2018), but this hypothesis has not been examined. More empirical data is, therefore, required to identify if seafloor terrain has conservation and restoration benefits for fish in coastal seascapes (research priority 9, Table 8).

Coastal seascapes are under threat from the increasing effects of climate change (Harley et al., 2006; Magris et al., 2014; Roberts et al., 2017), and recent research provides evidence that many species are already relocating to deeper habitats, or towards the poles, to track the abiotic conditions that characterize their ecological niches (Brown & Thatje, 2015; Lauchlan & Nagelkerken, 2020; Vestfals et al., 2016). It is also likely that as species alter their spatial distributions, some terrain features may provide supplementary habitats, and facilitate migration, whilst others might obstruct the expansion of species home ranges (Hollowed et al., 2013; Lenoir et al., 2011). The potential for prominent terrain features to serve as stepping-stones and sinks for climate driven range extensions will impact our capacity to effectively manage marine ecosystems, and data is therefore needed to identify terrain features that might serve as focal hotspots for conservation and restoration (research priority 10, Table 8).

11.0 CONCLUSIONS

Variation in seafloor terrain is associated with significant, and widespread, ecological effects on fish populations and assemblages. Spatial patterns in fish diversity and abundance are linked to bathymetry on coral and rocky reefs, in the deep sea, over continental shelfs and in estuaries, and changes in the distribution of fish assemblages are most strongly correlated with variation in the average depth, slope, rugosity and aspect of terrain features. The ecological significance of these terrain properties for fish does, however, differ among seascapes, as does the spatial scale of their influence on fish populations and assemblages, and this likely reflects variation in seafloor complexity. Despite the clear importance of terrain features for fish, research is needed to better describe how changes in seafloor relief, complexity, class and morphology combine to shape the distribution, composition and functioning of fish assemblages in most seascapes. There is a reasonable to good coverage of studies on the effects of terrain variation on fish in coral and rocky reefs, but soft-sediment seascapes are either data-poor (e.g. estuaries) or completely neglected (e.g. surf zones). Humans have substantially modified the bathymetry of many seascapes, via cumulative impacts resulting from urbanization, dredging and fishing. Yet, it is largely unknown whether and how, multiple anthropogenic stressors on seafloor terrain interact to affect the way fish species use coastal seascapes. The potential significance of bathymetric variation for conservation and restoration performance is also rarely tested with empirical data, despite the fact that these management actions typically restrict, or restore, actions that modify terrain complexity. A clearer understanding of how seafloor terrain shapes fish assemblages, and data to describe whether these relationships change with seafloor modification, conservation and restoration is essential for optimizing marine spatial planning and improving fisheries management.

Acknowledgements

This work was funded by the Queensland Department of Agriculture and Fisheries, Healthy Land and Water and the Sea World Research and Rescue Foundation. The authors would like to thank Ashley Rummell and Nicholas Ortodossi for helpful discussions and comments on the manuscript.

Data availability statement

Data that support the findings of this study are available from the USC Research Bank (https://doi.org/10.25907/00032).

References

Abdul Wahab, M. A., Radford, B., Cappo, M., Colquhoun, J., Stowar, M., Depczynski, M., . . . Heyward, A. (2018). Biodiversity and spatial patterns of benthic habitat and associated demersal fish communities at two tropical submerged reef ecosystems. *Coral Reefs, 37*(2), 327-343. doi:10.1007/s00338-017-1655-9

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings. Biological sciences, 276*(1669), 3019-3025. doi:10.1098/rspb.2009.0339

Atwood, T. B., Connolly, R. M., Ritchie, E. G., Lovelock, C. E., Heithaus, M. R., Hays, G. C., . . . Macreadie, P. I. (2015). Predators help protect carbon stocks in blue carbon ecosystems. *Nature climate change, 5*(12), 1038-1045. doi:10.1038/Nclimate2763

Auster, P. J., Joy, K., & Valentine, P. C. (2001). Fish species and community distributions as proxies for seafloor habitat fistributions: the Stellwagen Bank National Marine Sanctuary example (Northwest Atlantic, Gulf of Maine). *Environmental Biology of Fishes, 60*(4), 331-346. doi:10.1023/A:1011022320818

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. *Reviews in Fish Biology and Fisheries, 28*(3), 625-636. doi:10.1007/s11160-018-9522-5

Barcala, E., Bellido, J. M., Bellodi, A., Carbonara, P., Carlucci, R., Casciaro, L., . . . Pennino, M. G. (2020). Spatio-temporal variability in the distribution pattern of anglerfish species in the Mediterranean Sea. *Scientia Marina, 83*(S1). doi:10.3989/scimar.04966.11A

Bassett, M., Lindholm, J., Garza, C., Kvitek, R., & Wilson-Vandenberg, D. (2018). Lingcod (Ophiodon elongatus) habitat associations in California: implications for conservation and management. *Environmental Biology of Fishes, 101*(1), 203-213. doi:10.1007/s10641-017-0692-0

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology, 78*(4), 699-714. doi:10.1111/j.1365-2656.2009.01531.x

Bayley, D. T. I., Mogg, A. O. M., Purvis, A., & Koldewey, H. J. (2019). Evaluating the efficacy of small-scale marine protected areas for preserving reef health: A case study applying emerging monitoring technology. *Aquatic Conservation: Marine and Freshwater Ecosystems, 29*(12), 2026-2044. doi:10.1002/aqc.3215

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., . . . Weinstein, M. R. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience, 51*(8), 633-641. doi:10.1641/0006-3568(2001)051[0633:ticamo]2.0.co;2

Becker, A., Whitfield, A. K., Cowley, P. D., & Cole, V. J. (2017). Does water depth influence size composition of estuary-associated fish? Distributions revealed using mobile acoustic-camera transects along the channel of a small shallow estuary. *Marine and Freshwater Research, 68*(11), 2163-2169. doi:10.1071/MF16230

Bejarano, S., Mumby, P. J., & Sotheran, I. (2011). Predicting structural complexity of reefs and fish abundance using acoustic remote sensing (RoxAnn). *Marine Biology, 158*(3), 489-504. doi:10.1007/s00227-010-1575-5

Bellido, J. M., Brown, A. M., Valavanis, V. D., Giráldez, A., Pierce, G. J., Iglesias, M., & Palialexis, A. (2008). Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologia, 612*(1), 171-184. doi:10.1007/s10750-008-9481-2

Biber, M. F., Duineveld, G. C. A., Lavaleye, M. S. S., Davies, A. J., Bergman, M. J. N., & van den Beld, I. M. J. (2014). Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. *Deep-Sea Research Part II: Topical Studies in Oceanography, 99*, 134-145. doi:10.1016/j.dsr2.2013.05.022

Bishop, M. J., Mayer-Pinto, M., Airoldi, L., Firth, L. B., Morris, R. L., Loke, L. H. L., . . . Dafforn, K. A. (2017). Effects of ocean sprawl on ecological connectivity: impacts and solutions. *Journal of Experimental Marine Biology and Ecology, 492*, 7-30. doi:10.1016/j.jembe.2017.01.021

Borland, H. P., Schlacher, T. A., Gilby, B. L., Connolly, R. M., Yabsley, N. A., & Olds, A. D. (2017). Habitat type and beach exposure shape fish assemblages in the surf zones of ocean beaches. *Marine Ecology Progress Series, 570*, 203-211. doi:10.3354/meps1211

Bouchet, P. J., Meeuwig, J. J., Huang, Z., Letessier, T. B., Nichol, S. L., Caley, M. J., & Watson, R. A. (2017). Continental-scale hotspots of pelagic fish abundance inferred from commercial catch records. *Global Ecology and Biogeography, 26*(10), 1098-1111. doi:10.1111/geb.12619

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. *Biological Reviews, 90*(3), 699-728. doi:10.1111/brv.12130

Bradley, M., Baker, R., & Sheaves, M. (2017). Hidden components in tropical seascapes: Deep-estuary habitats support unique fish assemblages. *Estuaries and Coasts, 40*(4), 1195-1206. doi:10.1007/s12237-016-0192-z

Brook, T. W., Gilby, B. L., Olds, A. D., Connolly, R. M., Henderson, C. J., & Schlacher, T. A. (2018). The effects of shoreline armouring on estuarine fish are contingent upon the broader urbanisation context. *Marine Ecology Progress Series, 605*, 195-206. doi:10.3354/meps12756

Brown, A., & Thatje, S. (2015). The effects of changing climate on faunal depth distributions determine winners and losers. *Global Change Biology, 21*(1), 173-180. doi:10.1111/gcb.12680

Brown, C. J., Smith, S. J., Lawton, P., & Anderson, J. T. (2011). Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuarine, Coastal and Shelf Science, 92*(3), 502-520. doi:10.1016/j.ecss.2011.02.007

Bulleri, F., & Chapman, M. G. (2010). The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology, 47*(1), 26-35. doi:10.1111/j.1365-2664.2009.01751.x

Cameron, M. J., Lucieer, V., Barrett, N. S., Johnson, C. R., & Edgar, G. J. (2014). Understanding community-habitat associations of temperate reef fishes using fine-resolution bathymetric measures of physical structure. *Marine Ecology Progress Series, 506*, 213-229. doi:10.3354/meps10788

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. *Journal of Animal Ecology, 85*(1), 146-156. doi:10.1111/1365-2656.12440

Chang, Y.-J., Sun, C.-L., Chen, Y., Yeh, S.-Z., & Dinardo, G. (2012). Habitat suitability analysis and identification of potential fishing grounds for swordfish, Xiphias gladius, in the South Atlantic Ocean. *International Journal of Remote Sensing, 33*(23), 7523-7541. doi:10.1080/01431161.2012.685980

Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J. G., & Jensen, A. (2002). Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). *ICES Journal of Marine Science, 59*(SUPPL.), S208-S213. doi:10.1006/jmsc.2002.1263

Clark, M. R., Rowden, A. A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K. I., . . . Hall-Spencer, J. M. (2010). The ecology of seamounts: structure, function, and human impacts. *Annual Review of Marine Science, 2*, 253-278. doi:10.1146/annurev-marine-120308-081109

Coleman, M. A., Ingleton, T., Millar, R. B., Davies, P. L., Jordan, A., & Kelaher, B. P. (2016). Remotely sensed habitat variables are poor surrogates for functional traits of rocky reef fish assemblages. *Environmental Conservation, 43*(4), 368-375. doi:10.1017/S0376892916000205

Coleman, R. R., Copus, J. M., Coffey, D. M., Whitton, R. K., & Bowen, B. W. (2018). Shifting reef fish assemblages along a depth gradient in Pohnpei, Micronesia. *PeerJ, 2018*(4). doi:10.7717/peerj.4650

Collie, J., Hiddink, J. G., van Kooten, T., Rijnsdorp, A. D., Kaiser, M. J., Jennings, S., & Hilborn, R. (2017). Indirect effects of bottom fishing on the productivity of marine fish. *Fish and Fisheries, 18*(4), 619-637. doi:10.1111/faf.12193

Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., . . . Ziegler, P. (2014). Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global Change Biology, 20*(10), 3004-3025. doi:10.1111/gcb.12623

Costa, B., Taylor, J. C., Kracker, L., Battista, T., & Pittman, S. (2014). Mapping reef fish and the seascape: Using acoustics and spatial modeling to guide coastal management. *PLoS One, 9*(1). doi:10.1371/journal.pone.0085555

Costa, B., Walker, B. K., & Dijkstra, J. A. (2018a). Mapping and quantifying seascape patterns. In S. J. Pittman (Ed.), *Seascape Ecology*. Malaysia: WILEY Blackwell.

Costa, B., Walker, B. K., & Dijkstra, J. A. (2018b). Mapping and quantifying seascape patterns. In S. J. Pittman (Ed.), *Seascape Ecology* (pp. 27-56): WILEY Blackwell.

Cote, D., Scruton, D. A., Niezgoda, G. H., & McKinley, R. S. (1998). A coded acoustic telemetry system for high precision monitoring of fish location and movement: application to the study of nearshore nursery habitat of juvenile Atlantic cod (Gadus Morhua). *Marine Technology Society Journal, 32*(1), 54.

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. *Frontiers in Ecology and the Environment, 13*(2), 82-90. doi:10.1890/140050

Dunn, D. C., & Halpin, P. N. (2009). Rugosity-based regional modeling of hard-bottom habitat. *Marine Ecology Progress Series, 377*, 1-11. doi:10.3354/meps07839

Duvall, M. S., Hench, J. L., & Rosman, J. H. (2019). Collapsing complexity: Quantifying multiscale properties of reef topography. *Journal of Geophysical Research: Oceans, 124*(7), 5021-5038. doi:10.1029/2018JC014859

Engelhard, S. L., Huijbers, C. M., Stewart-Koster, B., Olds, A. D., Schlacher, T. A., & Connolly, R. M. (2017). Prioritising seascape connectivity in conservation using network analysis. *Journal of Applied Ecology, 54*(4), 1130-1141. doi:10.1111/1365-2664.12824

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., . . . Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science, 333*(6040), 301-306. doi:10.1126/science.1205106

Fabrizio, M. C., Manderson, J. P., & Pessutti, J. P. (2013). Habitat associations and dispersal of black sea bass from a mid-Atlantic Bight reef. *Marine Ecology Progress Series, 482*, 241-253. doi:10.3354/meps10302

Farmer, N. A., Heyman, W. D., Karnauskas, M., Kobara, S., Smart, T. I., Ballenger, J. C., . . . Sedberry, G. R. (2017). Timing and locations of reef fish spawning off the southeastern United States. *PLoS One, 12*(3). doi:10.1371/journal.pone.0172968

Ferrari, R., Malcolm, H., Neilson, J., Lucieer, V., Jordan, A., Ingleton, T., . . . Hill, N. (2018a). Integrating distribution models and habitat classification maps into marine protected area planning. *Estuarine, Coastal and Shelf Science, 212*, 40-50. doi:10.1016/j.ecss.2018.06.015

Ferrari, R., Malcolm, H. A., Byrne, M., Friedman, A., Williams, S. B., Schultz, A., . . . Figueira, W. F. (2018b). Habitat structural complexity metrics improve predictions of fish abundance and distribution. *Ecography, 41*(7), 1077-1091. doi:10.1111/ecog.02580

Folpp, H. R., Schilling, H. T., Clark, G. F., Lowry, M. B., Maslen, B., Gregson, M., & Suthers, I. M. (2020). Artificial reefs increase fish abundance in habitat-limited estuaries. *Journal of Applied Ecology, 57*(9), 1752-1761. doi:10.1111/1365-2664.13666

Fonseca, V. P., Pennino, M. G., de Nóbrega, M. F., Oliveira, J. E. L., & de Figueiredo Mendes, L. (2017). Identifying fish diversity hot-spots in data-poor situations. *Marine Environmental Research, 129*, 365-373. doi:10.1016/j.marenvres.2017.06.017

Forcada, A., Valle, C., Sánchez-Lizaso, J. L., Bayle-Sempere, J. T., & Corsi, F. (2010). Structure and spatio-temporal dynamics of artisanal fisheries around a Mediterranean marine protected area. *ICES Journal of Marine Science, 67*(2), 191-203. doi:10.1093/icesjms/fsp234

Freeman, L. A., Corbett, D. R., Fitzgerald, A. M., Lemley, D. A., Quigg, A., & Steppe, C. N. (2019). Impacts of urbanization and development on estuarine ecosystems and water quality. *Estuaries and Coasts, 42*(7), 1821-1838. doi:10.1007/s12237-019-00597-z

Friedlander, A. M., Boehlert, G. W., Field, M. E., Mason, J. E., Gardner, J. V., & Dartnell, P. (1999). Sidescan-sonar mapping of benthic trawl marks on the shelf and slope off Eureka, California. *Fishery Bulletin, 97*(4), 786-801.

Gaines, S. D., White, C., Carr, M. H., & Palumbi, S. R. (2010). Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences of the United States of America, 107*(43), 18286-18293. doi:10.1073/pnas.0906473107

Galaiduk, R., Radford, B. T., Wilson, S. K., & Harvey, E. S. (2017). Comparing two remote video survey methods for spatial predictions of the distribution and environmental niche suitability of demersal fishes. *Scientific Reports, 7*(1), 17633. doi:10.1038/s41598-017-17946-2

Gascuel, D., Coll, M., Fox, C., Guénette, S., Guitton, J., Kenny, A., . . . Shephard, S. (2016). Fishing impact and environmental status in European seas: A diagnosis from stock assessments and ecosystem indicators. *Fish and Fisheries, 17*(1), 31-55. doi:10.1111/faf.12090

Genin, A. (2004). Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems, 50*(1), 3-20. doi:10.1016/j.jmarsys.2003.10.008

Giannoulaki, M., Pyrounaki, M. M., Liorzou, B., Leonori, I., Valavanis, V. D., Tsagarakis, K., . . . Machias, A. (2011). Habitat suitability modelling for sardine juveniles (Sardina pilchardus) in the Mediterranean Sea. *Fisheries Oceanography, 20*(5), 367-382. doi:10.1111/j.1365-2419.2011.00590.x

Giddens, J., Goodell, W., Friedlander, A., Salinas-de-León, P., Shepard, C., Henning, B., . . . Turchik, A. (2019). Patterns in bathyal demersal biodiversity and community composition around archipelagos in the Tropical Eastern Pacific. *Frontiers in Marine Science, 6*(JUL). doi:10.3389/fmars.2019.00388

Gilby, B. L., Olds, A. D., Henderson, C. J., Ortodossi, N. L., Connolly, R. M., & Schlacher, T. A. (2019). Seascape context modifies how fish respond to restored oyster reef structures. *ICES Journal of Marine Science, 76*(4), 1131-1139. doi:10.1093/icesjms/fsz019

Gilby, B. L., Olds, A. D., Peterson, C. H., Connolly, R. M., Voss, C. M., Bishop, M. J., . . . Schlacher, T. A. (2018). Maximizing the benefits of oyster reef restoration for finfish and their fisheries. *Fish and Fisheries, 19*(5), 931-947. doi:10.1111/faf.12301

Goes, E. R., Brown, C. J., & Araújo, T. C. (2019). Geomorphological classification of the benthic structures on a tropical continental shelf. *Frontiers in Marine Science, 6*(FEB). doi:10.3389/fmars.2019.00047

Gomez, C., Williams, A. J., Nicol, S. J., Mellin, C., Loeun, K. L., & Bradshaw, C. J. (2015). Species distribution models of tropical deep-sea snappers. *PLoS One, 10*(6), e0127395. doi:10.1371/journal.pone.0127395

González-Rivero, M., Harborne, A. R., Herrera-Reveles, A., Bozec, Y. M., Rogers, A., Friedman, A., . . . Hoegh-Guldberg, O. (2017). Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Scientific Reports, 7*(1), 13965. doi:10.1038/s41598-017-14272-5

Goodell, W., Stamoulis, K. A., & Friedlander, A. M. (2018). Coupling remote sensing with in situ surveys to determine reef fish habitat associations for the design of marine protected areas. *Marine Ecology Progress Series, 588*, 121-134. doi:10.3354/meps12388

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., . . . White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews, 90*(4), 1215-1247. doi:10.1111/brv.12155

Halpern, B. S. (2003). The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications, 13*(1), 117-137.

Harborne, A. R., Mumby, P. J., & Ferrari, R. (2012). The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environmental Biology of Fishes, 94*(2), 431-442. doi:10.1007/s10641-011-9956-2

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., . . . Williams, S. L. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters, 9*(2), 228-241. doi:10.1111/j.1461-0248.2005.00871.x

Harris, D. L., Rovere, A., Casella, E., Power, H., Canavesio, R., Collin, A., . . . Parravicini, V. (2018). Coral reef structural complexity provides important coastal protection from waves under rising sea levels. *Science Advances, 4*(2), eaao4350. doi:10.1126/sciadv.aao4350

Heery, E. C., Bishop, M. J., Critchley, L. P., Bugnot, A. B., Airoldi, L., Mayer-Pinto, M., . . . Dafforn, K. A. (2017). Identifying the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine Biology and Ecology, 492*, 31-48. doi:10.1016/j.jembe.2017.01.020

Henderson, C. J., Gilby, B., Schlacher, T. A., Connolly, R. M., Sheaves, M., Maxwell, P. S., . . . Olds, A. D. (2020a). Landscape transformation alters functional diversity in coastal seascapes. *Ecography, 43*(1), 138-148. doi:10.1111/ecog.04504

Henderson, C. J., Gilby, B. L., Schlacher, T. A., Connolly, R. M., Sheaves, M., Flint, N., . . . Olds, A. D. (2019). Contrasting effects of mangroves and armoured shorelines on fish assemblages in tropical estuarine seascapes. *ICES Journal of Marine Science, 76*(4), 1052-1061. doi:10.1093/icesjms/fsz007

Henderson, C. J., Gilby, B. L., Schlacher, T. A., Connolly, R. M., Sheaves, M., Maxwell, P. S., . . . Olds, A. D. (2020b). Low redundancy and complementarity shape ecosystem functioning in a low-diversity ecosystem. *Journal of Animal Ecology, 89*(3), 784-794. doi:10.1111/1365-2656.13148

Hill, N. A., Barrett, N., Lawrence, E., Hulls, J., Dambacher, J. M., Nichol, S., . . . Hayes, K. R. (2014). Quantifying fish assemblages in large, offshore marine protected areas: An Australian case study. *PLoS One, 9*(10), e110831. doi:10.1371/journal.pone.0110831

Hill, N. A., Foster, S. D., Duhamel, G., Welsford, D., Koubbi, P., & Johnson, C. R. (2017). Model-based mapping of assemblages for ecology and conservation management: A case study of demersal fish on the Kerguelen Plateau. *Diversity and Distributions, 23*(10), 1216-1230. doi:10.1111/ddi.12613

Holland, K. N., & Dean Grubbs, R. (2008). Fish Visitors to Seamounts: Tunas and Bill Fish at Seamounts. In *Seamounts: Ecology, Fisheries & Conservation* (pp. 189-201).

Hollowed, A. B., Planque, B., & Loeng, H. (2013). Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean. *Fisheries Oceanography, 22*(5), 355-370. doi:10.1111/fog.12027

Hondorp, D. W., Bennion, D. H., Roseman, E. F., Holbrook, C. M., Boase, J. C., Chiotti, J. A., . . . Krueger, C. C. (2017). Use of navigation channels by Lake Sturgeon: Does channelization increase vulnerability of fish to ship strikes? *PLoS One, 12*(7). doi:10.1371/journal.pone.0179791

Huff, D. D., Lindley, S. T., Rankin, P. S., & Mora, E. A. (2011). Green sturgeon physical habitat use in the Coastal Pacific Ocean. *PLoS One, 6*(9), e25156. doi:10.1371/journal.pone.0025156

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., . . . Roughgarden, J. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science, 301*(5635), 929-933. doi:10.1126/science.1085046

Huntington, B. E., Karnauskas, M., Babcock, E. A., & Lirman, D. (2010). Untangling natural seascape variation from marine reserve effects using a landscape approach. *PLoS One, 5*(8), e12327. doi:10.1371/journal.pone.0012327

Hylkema, A., Debrot, A. O., Osinga, R., Bron, P. S., Heesink, D. B., Izioka, A. K., . . . Murk, A. J. (2020). Fish assemblages of three common artificial reef designs during early colonization. *Ecological Engineering, 157*. doi:10.1016/j.ecoleng.2020.105994

Iampietro, P. J., Kvitek, R. G., & Morris, E. (2005). Recent advances in automated genus-specific marine habitat mapping enabled by high-resolution multibeam bathymetry. *Marine Technology Society Journal, 39*(3), 83-93. doi:10.4031/002533205787442495

Iampietro, P. J., Young, M. A., & Kvitek, R. G. (2008). Multivariate prediction of rockfish habitat suitability in Cordell Bank National Marine sanctuary and Del Monte Shalebeds, California, USA. *Marine Geodesy, 31*(4), 359-371. doi:10.1080/01490410802466900

Ismail, K., Huvenne, V., & Robert, K. (2018). Quantifying spatial heterogeneity in submarine canyons. *Progress in Oceanography, 169*, 181-198. doi:10.1016/j.pocean.2018.03.006

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., . . . Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science, 293*(5530), 629-637. doi:10.1126/science.1059199

Jankowski, M. W., Graham, N. A. J., & Jones, G. P. (2015). Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: Implications for the depth-refuge hypothesis. *Marine Ecology Progress Series, 540*, 203-215. doi:10.3354/meps11523

Kaiser, M. J., Collie, J. S., Hall, S. J., Jennings, S., & Poiner, I. R. (2002). Modification of marine habitats by trawling activities: Prognosis and solutions. *Fish and Fisheries, 3*(2), 114-136. doi:10.1046/j.1467-2979.2002.00079.x

Kenny, A. J., Cato, I., Desprez, M., Fader, G., Schüttenhelm, R. T. E., & Side, J. (2003). An overview of seabed-mapping technologies in the context of marine habitat classification. *ICES Journal of Marine Science, 60*(2), 411-418. doi:10.1016/S1054-3139(03)00006-7

Knudby, A., LeDrew, E., & Brenning, A. (2010). Predictive mapping of reef fish species richness, diversity and biomass in Zanzibar using IKONOS imagery and machine-learning techniques. *Remote Sensing of Environment, 114*(6), 1230-1241. doi:10.1016/j.rse.2010.01.007

Knudby, A., Roelfsema, C., Lyons, M., Phinn, S., & Jupiter, S. (2011). Mapping fish community variables by integrating field and satellite data, object-based image analysis and modeling in a traditional Fijian fisheries management area. *Remote Sensing, 3*(3), 460-483. doi:10.3390/rs3030460

Kobara, S., & Heyman, W. D. (2008). Geomorphometric patterns of Nassau grouper (Epinephelus striatus) spawning aggregation sites in the Cayman Islands. *Marine Geodesy, 31*(4), 231-245. doi:10.1080/01490410802466397

Kuffner, I. B., Brock, J. C., Grober-Dunsmore, R., Bonito, V. E., Hickey, T. D., & Wright, C. W. (2007). Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. *Environmental Biology of Fishes, 78*(1), 71-82. doi:10.1007/s10641-006-9078-4

Kuffner, I. B., Grober-dunsmore, R., Brock, J. C., & Hickey, T. D. (2010). Biological community structure on patch reefs in Biscayne National Park, FL, USA. *Environmental Monitoring and Assessment, 164*(1-4), 513-531. doi:10.1007/s10661-009-0910-0

Lathrop, R. G., Cole, M., Senyk, N., & Butman, B. (2006). Seafloor habitat mapping of the New York Bight incorporating sidescan sonar data. *Estuarine, Coastal and Shelf Science, 68*(1), 221-230. doi:10.1016/j.ecss.2006.01.019

Lauchlan, S. S., & Nagelkerken, I. (2020). Species range shifts along multistressor mosaics in estuarine environments under future climate. *Fish and Fisheries, 21*(1), 32-46. doi:10.1111/faf.12412

Le Pape, O., Chauveta, F., Mahévas, S., Lazure, P., Guérault, D., & Désaunay, Y. (2003). Quantitative description of habitat suitability for the juvenile common sole (Solea solea, L.) in the Bay of Biscay (France) and the contribution of different habitats to the adult population. *Journal of Sea Research, 50*(2-3), 139-149. doi:10.1016/S1385-1101(03)00059-5

Lecours, V., Dolan, M. F. J., Micallef, A., & Lucieer, V. L. (2016). A review of marine geomorphometry, the quantitative study of the seafloor. *Hydrology and Earth System Sciences, 20*(8), 3207-3244. doi:10.5194/hess-20-3207-2016

Leempoel, K., Parisod, C., Geiser, C., Daprà, L., Vittoz, P., & Joost, S. (2015). Very high-resolution digital elevation models: Are multi-scale derived variables ecologically relevant? *Methods in Ecology and Evolution, 6*(12), 1373-1383. doi:10.1111/2041-210X.12427

Leggat, W. P., Camp, E. F., Suggett, D. J., Heron, S. F., Fordyce, A. J., Gardner, S., . . . Ainsworth, T. D. (2019). Rapid coral decay is associated with marine heatwave mortality events on reefs. *Current Biology, 29*(16), 2723-2730. doi:10.1016/j.cub.2019.06.077

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 Research Part I: Oceanographic Research Papers, 125*, 65-80. doi:10.1016/j.dsr.2017.04.017

Lenoir, S., Beaugrand, G., & Lecuyer, É. (2011). Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Global Change Biology, 17*(1), 115-129. doi:10.1111/j.1365-2486.2010.02229.x

Leon, J. X., Roelfsema, C. M., Saunders, M. I., & Phinn, S. R. (2015). Measuring coral reef terrain roughness using 'Structure-from-Motion' close-range photogrammetry. *Geomorphology, 242*, 21-28. doi:10.1016/j.geomorph.2015.01.030

Loots, C., Koubbi, P., & Duhamel, G. (2007). Habitat modelling of Electrona antarctica (Myctophidae, Pisces) in Kerguelen by generalized additive models and geographic information systems. *Polar Biology, 30*(8), 951-959. doi:10.1007/s00300-007-0253-7

Love, M. S., Claisse, J. T., & Roeper, A. (2019). An analysis of the fish assemblages around 23 oil and gas platforms off California with comparisons with natural habitats. *Bulletin of Marine Science, 95*(4), 477-514. doi:10.5343/bms.2018.0061

Lundblad, E. R., Wright, D. J., Miller, J., Larkin, E. M., Rinehart, R., Naar, D. F., . . . Battista, T. (2006). A benthic terrain classification scheme for American Samoa. *Marine Geodesy, 29*(2), 89-111. doi:10.1080/01490410600738021

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. *Environmental Evidence, 8*(1). doi:10.1186/s13750-019-0157-3

Madricardo, F., Foglini, F., Campiani, E., Grande, V., Catenacci, E., Petrizzo, A., . . . Trincardi, F. (2019). Assessing the human footprint on the sea-floor of coastal systems: the case of the Venice Lagoon, Italy. *Scientific Reports, 9*(1), 6615. doi:10.1038/s41598-019-43027-7

Magris, R. A., Andrello, M., Pressey, R. L., Mouillot, D., Dalongeville, A., Jacobi, M. N., & Manel, S. (2018). Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. *Conservation Letters, 11*(4). doi:10.1111/conl.12439

Magris, R. A., Pressey, R. L., Weeks, R., & Ban, N. C. (2014). Integrating connectivity and climate change into marine conservation planning. *Biological Conservation, 170*, 207-221. doi:10.1016/j.biocon.2013.12.032

Maravelias, C. D. (1999). Habitat selection and clustering of a pelagic fish: Effects of topography and bathymetry on species dynamics. *Canadian Journal of Fisheries and Aquatic Sciences, 56*(3), 437-450.

March, D., Alós, J., & Palmer, M. (2014). Geospatial assessment of fishing quality considering environmental and angler-related factors. *Fisheries Research, 154*, 63-72. doi:10.1016/j.fishres.2014.01.020

Martin, T. S. H., Olds, A. D., Olalde, A. B. H., Berkström, C., Gilby, B. L., Schlacher, T. A., . . . Connolly, R. M. (2018). Habitat proximity exerts opposing effects on key ecological functions. *Landscape Ecology, 33*(8), 1273-1286. doi:10.1007/s10980-018-0680-6

Mayer-Pinto, M., Cole, V. J., Johnston, E. L., Bugnot, A., Hurst, H., Airoldi, L., . . . Dafforn, K. A. (2018). Functional and structural responses to marine urbanisation. *Environmental Research Letters, 13*(1). doi:10.1088/1748-9326/aa98a5

McGarigal, K., Tagil, S., & Cushman, S. A. (2009). Surface metrics: an alternative to patch metrics for the quantification of landscape structure. *Landscape Ecology, 24*(3), 433-450. doi:10.1007/s10980-009-9327-y

Meynecke, J.-O., Poole, G. C., Werry, J., & Lee, S. Y. (2008). Use of PIT tag and underwater video recording in assessing estuarine fish movement in a high intertidal mangrove and salt marsh creek. *Estuarine, Coastal and Shelf Science, 79*(1), 168-178. doi:10.1016/j.ecss.2008.03.019

Miller, K. B., Huettmann, F., & Norcross, B. L. (2015). Efficient spatial models for predicting the occurrence of subarctic estuarine-associated fishes: implications for management. *Fisheries Management and Ecology, 22*(6), 501-517. doi:10.1111/fme.12148

Misa, W. F. X. E. (2013). Establishing species–habitat associations for 4 eteline snappers with the use of a baited stereo-video camera system. *Fishery Bulletin, 111*(4), 293-308. doi:10.7755/FB.111.4.1

Monk, J., Ierodiaconou, D., Bellgrove, A., Harvey, E., & Laurenson, L. (2011). Remotely sensed hydroacoustics and observation data for predicting fish habitat suitability. *Continental Shelf Research, 31*(2), S17-S27. doi:10.1016/j.csr.2010.02.012

Monk, J., Ierodiaconou, D., Versace, V. L., Bellgrove, A., Harvey, E., Rattray, A., . . . Quinn, G. P. (2010). Habitat suitability for marine fishes using presence-only modelling and multibeam sonar. *Marine Ecology Progress Series, 420*, 157-174. doi:10.3354/meps08858

Moore, C., Drazen, J. C., Radford, B. T., Kelley, C., & Newman, S. J. (2016). Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. *Marine Policy, 69*, 32-41. doi:10.1016/j.marpol.2016.03.021

Moore, C. H., Harvey, E. S., & Van Niel, K. (2010). The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. *Marine Biology, 157*(12), 2717-2729. doi:10.1007/s00227-010-1531-4

Moore, C. H., Harvey, E. S., & Van Niel, K. P. (2009). Spatial prediction of demersal fish distributions: enhancing our understanding of species–environment relationships. *ICES Journal of Marine Science, 66*(9), 2068-2075. doi:10.1093/icesjms/fsp205

Moore, C. H., Van Niel, K., & Harvey, E. S. (2011). The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. *Ecography, 34*(3), 425-435. doi:10.1111/j.1600-0587.2010.06436.x

Moore, I. D. (1991). Digital terrain modelling: A review of hydrological, geomorphological, and biological applications. *Hydrological processes, 5*(1), 3-30.

Morato, T., Hoyle, S. D., Allain, V., & Nicol, S. J. (2010). Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences, 107*(21), 9707. doi:10.1073/pnas.0910290107

Morris, R. L., Porter, A. G., Figueira, W. F., Coleman, R. A., Fobert, E. K., & Ferrari, R. (2018). Fish-smart seawalls: a decision tool for adaptive management of marine infrastructure. *Frontiers in Ecology and the Environment, 16*(5), 278-287. doi:10.1002/fee.1809

Mosman, J. D., Henderson, C. J., Olds, A. D., Gilby, B. L., & Schlacher, T. A. (2020). Seascape connectivity exerts differing effects for fish assemblages in distinct habitats of the surf zones of ocean beaches. *ICES Journal of Marine Science*. doi:10.1093/icesjms/fsaa018

Moudrý, V., Lecours, V., Malavasi, M., Misiuk, B., Gábor, L., Gdulová, K., . . . Wild, J. (2019). Potential pitfalls in rescaling digital terrain model-derived attributes for ecological studies. *Ecological Informatics, 54*, 100987. doi:10.1016/j.ecoinf.2019.100987

Munday, P. L., Jones, G. P., Pratchett, M. S., & Williams, A. J. (2008). Climate change and the future for coral reef fishes. *Fish and Fisheries, 9*(3), 261-285. doi:10.1111/j.1467-2979.2008.00281.x

Nagelkerken, I., Sheaves, M., Baker, R., & Connolly, R. M. (2015). The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries, 16*(2), 362-371. doi:10.1111/faf.12057

Newman, S. P., Meesters, E. H., Dryden, C. S., Williams, S. M., Sanchez, C., Mumby, P. J., & Polunin, N. V. C. (2015). Reef flattening effects on total richness and species responses in the Caribbean. *Journal of Animal Ecology, 84*(6), 1678-1689. doi:10.1111/1365-2656.12429

Nicolas, D., Le Loc'h, F., Désaunay, Y., Hamon, D., Blanchet, A., & Le Pape, O. (2007). Relationships between benthic macrofauna and habitat suitability for juvenile common sole (Solea solea, L.) in the Vilaine estuary (Bay of Biscay, France) nursery ground. *Estuarine, Coastal and Shelf Science, 73*(3-4), 639-650. doi:10.1016/j.ecss.2007.03.006

Nilsson, P., & Ziegler, F. (2007). Spatial distribution of fishing effort in relation to seafloor habitats in the Kattegat, a GIS analysis. *Aquatic Conservation: Marine and Freshwater Ecosystems, 17*(4), 421-440. doi:10.1002/aqc.792

Nye, J. A., Link, J. S., Hare, J. A., & Overholtz, W. J. (2009). Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series, 393*, 111-129. doi:10.3354/meps08220

Olds, A. D., Connolly, R. M., Pitt, K. A., Pittman, S. J., Maxwell, P. S., Huijbers, C. M., . . . Schlacher, T. A. (2016). Quantifying the conservation value of seascape connectivity: a global synthesis. *Global Ecology and Biogeography, 25*(1), 3-15. doi:10.1111/geb.12388

Olds, A. D., Frohloff, B. A., Gilby, B. L., Connolly, R. M., Yabsley, N. A., Maxwell, P. S., . . . Schlacher, T. A. (2018a). Urbanisation supplements ecosystem functioning in disturbed estuaries. *Ecography, 41*(12), 2104-2113. doi:10.1111/ecog.03551

Olds, A. D., Nagelkerken, I., Huijbers, C. M., Gilby, B. L., Pittman, S. J., & Schlacher, T. A. (2018b). Connectivity in coastal seascapes. In S. J. Pittman (Ed.), *Seascape Ecology* (pp. 259-292): WILEY Blackwell.

Olson, A. M., Hessing-Lewis, M., Haggarty, D., & Juanes, F. (2019). Nearshore seascape connectivity enhances seagrass meadow nursery function. *Ecological Applications, 29*(5). doi:10.1002/eap.1897

Ortodossi, N. L., Gilby, B. L., Schlacher, T. A., Connolly, R. M., Yabsley, N. A., Henderson, C. J., & Olds, A. D. (2019). Effects of seascape connectivity on reserve performance along exposed coastlines. *Conserv Biol, 33*(3), 580-589. doi:10.1111/cobi.13237

Oyafuso, Z. S., Drazen, J. C., Moore, C. H., & Franklin, E. C. (2017). Habitat-based species distribution modelling of the Hawaiian deepwater snapper-grouper complex. *Fisheries Research, 195*, 19-27. doi:10.1016/j.fishres.2017.06.011

Parra, H. E., Pham, C. K., Menezes, G. M., Rosa, A., Tempera, F., & Morato, T. (2017). Predictive modeling of deep-sea fish distribution in the Azores. *Deep Sea Research Part II: Topical Studies in Oceanography, 145*, 49-60. doi:10.1016/j.dsr2.2016.01.004

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres Jr, F. (1998). Fishing down marine food webs. *Science, 279*(5352), 860-863. doi:10.1126/science.279.5352.860

Pereira, P. H. C., Macedo, C. H., Nunes, J. D. A. C. C., Marangoni, L. F. D. B., & Bianchini, A. (2018). Effects of depth on reef fish communities: Insights of a “deep refuge hypothesis” from Southwestern Atlantic reefs. *PLoS One, 13*(9), e0203072. doi:10.1371/journal.pone.0203072

Péron, C., Welsford, D. C., Ziegler, P., Lamb, T. D., Gasco, N., Chazeau, C., . . . Duhamel, G. (2016). Modelling spatial distribution of Patagonian toothfish through life-stages and sex and its implications for the fishery on the Kerguelen Plateau. *Progress in Oceanography, 141*, 81-95. doi:10.1016/j.pocean.2015.12.003

Perry, C. T., & Alvarez-Filip, L. (2019). Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology, 33*(6), 976-988. doi:10.1111/1365-2435.13247

Perry, D., Staveley, T. A. B., & Gullström, M. (2018). Habitat connectivity of fish in temperate shallow-water seascapes. *Frontiers in Marine Science, 4*(JAN). doi:10.3389/fmars.2017.00440

Pike, R. J. (2000). Geomorphometry - diversity in quantitative surface analysis. *Progress in Physical Geography: Earth and Environment, 24*(1), 1-20. doi:10.1177/030913330002400101

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 Research Part II: Topical Studies in Oceanography, 165*, 303-321. doi:10.1016/j.dsr2.2017.12.005

Pittman, S. J. (2018). Introducing seascape ecology. In S. J. Pittman (Ed.), *Seascape Ecology*. Malaysia: WILEY Blackwell.

Pittman, S. J., & Brown, K. A. (2011). Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS One, 6*(5), e20583. doi:10.1371/journal.pone.0020583

Pittman, S. J., Christensen, J. D., Caldow, C., Menza, C., & Monaco, M. E. (2007). Predictive mapping of fish species richness across shallow-water seascapes in the Caribbean. *Ecological Modelling, 204*(1), 9-21. doi:10.1016/j.ecolmodel.2006.12.017

Pittman, S. J., Costa, B., Jeffrey, C. F., & Caldow, C. (2011). Importance of seascape complexity for resilient fish habitat and sustainable fisheries *Proceedings of the Gulf and Caribbean Fisheries Institute, 63*, 420-426.

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. *Journal of Coastal Research, 25*(6), 27-38. doi:10.2112/si53-004.1

Pittman, S. J., & McAlpine, C. A. (2003). Movements of marine fish and decapod crustaceans: Process, theory and application. In *Advances in Marine Biology* (Vol. 44, pp. 205-294). London, England: Elsevier Ltd.

Pittman, S. J., & Olds, A. D. (2015). Seascape ecology of fishes on coral reefs. In *Ecology of Fishes on Coral Reefs* (pp. 274-282). Cambridge, United Kingdom: Cambridge University Press.

Price, D. M., Robert, K., Callaway, A., Lo Iacono, C., Hall, R. A., & Huvenne, V. A. I. (2019). Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. *Coral Reefs, 38*(5), 1007-1021. doi:10.1007/s00338-019-01827-3

Puig, P., Canals, M., Company, J. B., Martín, J., Amblas, D., Lastras, G., . . . Calafat, A. M. (2012). Ploughing the deep sea floor. *Nature, 489*(7415), 286-289. doi:10.1038/nature11410

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*(1), 167-178. doi: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. *Estuarine, Coastal and Shelf Science, 235*, 106468. doi:10.1016/j.ecss.2019.106468

Quattrini, A. M., Ross, S. W., Carlson, M. C. T., & Nizinski, M. S. (2012). Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA. *Marine Biology, 159*(5), 1079-1094. doi:10.1007/s00227-012-1888-7

Raoux, A., Tecchio, S., Pezy, J. P., Lassalle, G., Degraer, S., Wilhelmsson, D., . . . Niquil, N. (2017). Benthic and fish aggregation inside an offshore wind farm: Which effects on the trophic web functioning? *Ecological Indicators, 72*, 33-46. doi:10.1016/j.ecolind.2016.07.037

Rees, M. J., Jordan, A., Price, O. F., Coleman, M. A., & Davis, A. R. (2014). Abiotic surrogates for temperate rocky reef biodiversity: Implications for marine protected areas. *Diversity and Distributions, 20*(3), 284-296. doi:10.1111/ddi.12134

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. *Biological Conservation, 224*, 100-110. doi:10.1016/j.biocon.2018.04.040

Rey Benayas, J. M., Newton, A. C., Diaz, A., & Bullock, J. M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: A meta-analysis. *Science, 325*(5944), 1121-1124. doi:10.1126/science.1172460

Rigol-Sanchez, J. P., Stuart, N., & Pulido-Bosch, A. (2015). ArcGeomorphometry: A toolbox for geomorphometric characterisation of DEMs in the ArcGIS environment. *Computers & Geosciences, 85*, 155-163. doi:10.1016/j.cageo.2015.09.020

Risk, M. J. (1972). Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin, 153*.

Roberts, C. M., O'Leary, B. C., McCauley, D. J., Cury, P. M., Duarte, C. M., Lubchenco, J., . . . Castilla, J. C. (2017). Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences of the United States of America, 114*(24), 6167-6175. doi:10.1073/pnas.1701262114

Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., & Le Pape, O. (2010). Effect of nursery habitat degradation on flatfish population: Application to Solea solea in the Eastern Channel (Western Europe). *Journal of Sea Research, 64*(1-2), 34-44. doi:10.1016/j.seares.2009.08.003

Rogers, A., Blanchard, J. L., & Mumby, P. J. (2018a). Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology, 55*(3), 1041-1049. doi:10.1111/1365-2664.13051

Rogers, J. S., Maticka, S. A., Chirayath, V., Woodson, C. B., Alonso, J. J., & Monismith, S. G. (2018b). Connecting flow over complex terrain to hydrodynamic roughness on a coral reef. *Journal of Physical Oceanography, 48*(7), 1567-1587. doi:10.1175/JPO-D-18-0013.1

Roos, N. C., Carvalho, A. R., Lopes, P. F. M., & Pennino, M. G. (2015). Modeling sensitive parrotfish (Labridae: Scarini) habitats along the Brazilian coast. *Marine Environmental Research, 110*, 92-100. doi:10.1016/j.marenvres.2015.08.005

Rowden, A. A., Dower, J. F., Schlacher, T. A., Consalvey, M., & Clark, M. R. (2010). Paradigms in seamount ecology: fact, fiction and future. *Marine Ecology, 31*(s1), 226-241. doi:10.1111/j.1439-0485.2010.00400.x

Ruttenberg, B. I., Adam, T. C., Duran, A., & Burkepile, D. E. (2019). Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. *Ecological Applications, 29*(4), e01893. doi:10.1002/eap.1893

Salarpouri, A., Kamrani, E., Kaymaram, F., & Najafabadi, R. M. (2018). Essential fish habitats (EFH) of small pelagic fishes in the north of the Persian Gulf and Oman Sea, Iran. *Iranian Journal of Fisheries Sciences, 17*(1), 74-94.

Schultz, A. L., Malcolm, H. A., Bucher, D. J., Linklater, M., & Smith, S. D. A. (2014). Depth and medium-scale spatial processes influence fish assemblage structure of unconsolidated habitats in a subtropical Marine Park. *PLoS One, 9*(5), e96798. doi:10.1371/journal.pone.0096798

Schultz, A. L., Malcolm, H. A., Linklater, M., Jordan, A. R., Ingleton, T., & Smith, S. D. A. (2015). Sediment variability affects fish community structure in unconsolidated habitats of a subtropical marine park. *Marine Ecology Progress Series, 532*, 213-226. doi:10.3354/meps11311

Seitz, R. D., Wennhage, H., Bergström, U., Lipcius, R. N., & Ysebaert, T. (2014). Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science, 71*(3), 648-665. doi:10.1093/icesjms/fst152

Sekund, L., & Pittman, S. (2017). Explaining island-wide geographical patterns of Caribbean fish diversity: A multi-scale seascape ecology approach. *Marine Ecology, 38*(3), e12434. doi:10.1111/maec.12434

Sheaves, M., Baker, R., Nagelkerken, I., & Connolly, R. M. (2015). True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. *Estuaries and Coasts, 38*(2), 401-414. doi:10.1007/s12237-014-9846-x

Sheaves, M., Brookes, J., Coles, R., Freckelton, M., Groves, P., Johnston, R., & Winberg, P. (2014). Repair and revitalisation of Australia׳s tropical estuaries and coastal wetlands: Opportunities and constraints for the reinstatement of lost function and productivity. *Marine Policy, 47*, 23-38. doi:10.1016/j.marpol.2014.01.024

Siceloff, L., & Howell, W. H. (2013). Fine-scale temporal and spatial distributions of Atlantic cod (Gadus morhua) on a western Gulf of Maine spawning ground. *Fisheries Research, 141*, 31-43. doi:10.1016/j.fishres.2012.04.001

Sievers, K. T., Barr, R. J., Maloney, J. M., Driscoll, N. W., & Anderson, T. W. (2016). Impact of habitat structure on fish populations in kelp forests at a seascape scale. *Marine Ecology Progress Series, 557*, 51-63. doi:10.3354/meps11885

Smith, J. G., & Lindholm, J. (2016). Vertical stratification in the distribution of demersal fishes along the walls of the La Jolla and Scripps submarine canyons, California, USA. *Continental Shelf Research, 125*, 61-70. doi:10.1016/j.csr.2016.07.001

Smoliński, S., & Radtke, K. (2017). Spatial prediction of demersal fish diversity in the Baltic Sea: Comparison of machine learning and regression-based techniques. *ICES Journal of Marine Science, 74*(1), 102-111. doi:10.1093/icesjms/fsw136

Stamoulis, K. A., Delevaux, J. M. S., Williams, I. D., Poti, M., Lecky, J., Costa, B., . . . Friedlander, A. M. (2018). Seascape models reveal places to focus coastal fisheries management. *Ecological Applications, 28*(4), 910-925. doi:10.1002/eap.1696

Stein, A. B., Friedland, K. D., & Sutherland, M. (2004). Atlantic sturgeon marine distribution and habitat use along the northeastern coast of the United States. *Transactions of the American Fisheries Society, 133*(3), 527-537. doi:10.1577/T02-151.1

Storlazzi, C. D., Dartnell, P., Hatcher, G. A., & Gibbs, A. E. (2016). End of the chain? Rugosity and fine-scale bathymetry from existing underwater digital imagery using structure-from-motion (SfM) technology. *Coral Reefs, 35*(3), 889-894. doi:10.1007/s00338-016-1462-8

Strain, E. M. A., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R. L., Bugnot, A. B., . . . Bishop, M. J. (2018). Eco-engineering urban infrastructure for marine and coastal biodiversity: Which interventions have the greatest ecological benefit? *Journal of Applied Ecology, 55*(1), 426-441. doi:10.1111/1365-2664.12961

Swadling, D. S., Knott, N. A., Rees, M. J., & Davis, A. R. (2019). Temperate zone coastal seascapes: seascape patterning and adjacent seagrass habitat shape the distribution of rocky reef fish assemblages. *Landscape Ecology, 34*(10), 2337-2352. doi:10.1007/s10980-019-00892-x

Thrush, S. F., & Dayton, P. K. (2002). Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Annual Review of Ecology and Systematics, 33*(1), 449-473. doi:10.1146/annurev.ecolsys.33.010802.150515

Ticzon, V. S., Foster, G., David, L. T., Mumby, P. J., Samaniego, B. R., & Madrid, V. R. (2015). Delineating optimal settlement areas of juvenile reef fish in Ngederrak Reef, Koror state, Republic of Palau. *Environmental Monitoring and Assessment, 187*(1), 4089. doi:10.1007/s10661-014-4089-7

Torres-Pulliza, D., Dornelas, M. A., Pizarro, O., Bewley, M., Blowes, S. A., Boutros, N., . . . Madin, J. S. (2020). A geometric basis for surface habitat complexity and biodiversity. *Nature Ecology & Evolution*. doi:10.1038/s41559-020-1281-8

Trimoreau, E., Archambault, B., Brind'Amour, A., Lepage, M., Guitton, J., & Le Pape, O. (2013). A quantitative estimate of the function of soft-bottom sheltered coastal areas as essential flatfish nursery habitat. *Estuarine, Coastal and Shelf Science, 133*, 193-205. doi:10.1016/j.ecss.2013.08.027

van Lier, J. R., Wilson, S. K., Depczynski, M., Wenger, L. N., & Fulton, C. J. (2018). Habitat connectivity and complexity underpin fish community structure across a seascape of tropical macroalgae meadows. *Landscape Ecology, 33*(8), 1287-1300. doi:10.1007/s10980-018-0682-4

Vestfals, C. D., Ciannelli, L., & Hoff, G. R. (2016). Changes in habitat utilization of slope-spawning flatfish across a bathymetric gradient. *ICES Journal of Marine Science, 73*(7), 1875-1889. doi:10.1093/icesjms/fsw112

Walbridge, S., Slocum, N., Pobuda, M., & Wright, J. D. (2018). Unified geomorphological analysis workflows with Benthic Terrain Modeler. *Geosciences, 8*(3). doi:10.3390/geosciences8030094

Walker, B. K., Jordan, L. K. B., & Spieler, R. E. (2009). Relationship of reef fish assemblages and topographic complexity on southeastern Florida coral reef habitats. *Journal of Coastal Research, 25*(6), 39-48. doi:10.2112/si53-005.1

Wedding, L., & Yoklavich, M. M. (2015). Habitat-based predictive mapping of rockfish density and biomass off the central California coast. *Marine Ecology Progress Series, 540*, 235-250. doi:10.3354/meps11442

Wedding, L. M., & Friedlander, A. (2008). Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Marine Geodesy, 31*(4), 246-266. doi:10.1080/01490410802466504

Wedding, L. M., Friedlander, A. M., McGranaghan, M., Yost, R. S., & Monaco, M. E. (2008). Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. *Remote Sensing of Environment, 112*(11), 4159-4165. doi:10.1016/j.rse.2008.01.025

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 Sensing in Ecology and Conservation, 5*(2), 150-159. doi:10.1002/rse2.115

Wedding, L. M., Lepczyk, C. A., Pittman, S. J., Friedlander, A. M., & Jorgensen, S. (2011). Quantifying seascape structure: Extending terrestrial spatial pattern metrics to the marine realm. *Marine Ecology Progress Series, 427*, 219-232. doi:10.3354/meps09119

Weijerman, M., Grüss, A., Dove, D., Asher, J., Williams, I. D., Kelley, C., & Drazen, J. T. C. (2019). Shining a light on the composition and distribution patterns of mesophotic and subphotic fish communities in Hawaii. *Marine Ecology Progress Series, 630*, 161-182. doi:10.3354/meps13135

Wenger, A. S., Harvey, E., Wilson, S., Rawson, C., Newman, S. J., Clarke, D., . . . Evans, R. D. (2017). A critical analysis of the direct effects of dredging on fish. *Fish and Fisheries, 18*(5), 967-985. doi:10.1111/faf.12218

Whitfield, A. K. (2017). The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries, 27*(1), 75-110. doi:10.1007/s11160-016-9454-x

Whitfield, A. K., & Pattrick, P. (2015). Habitat type and nursery function for coastal marine fish species, with emphasis on the Eastern Cape region, South Africa. *Estuarine, Coastal and Shelf Science, 160*, 49-59. doi:10.1016/j.ecss.2015.04.002

Wicaksono, P., Aryaguna, P. A., & Lazuardi, W. (2019). Benthic habitat mapping model and cross validation using machine-learning classification algorithms. *Remote Sensing, 11*(11). doi:10.3390/rs11111279

Wieczorek, M. M., Spallek, W. A., Niedzielski, T., Godbold, J. A., & Priede, I. G. (2014). Use of remotely-derived bathymetry for modelling biomass in marine environments. *Pure and Applied Geophysics, 171*(6), 1029-1045. doi:10.1007/s00024-013-0705-7

Williams, A., Althaus, F., Maguire, K., Green, M., Untiedt, C., Alderslade, P., . . . Schlacher, T. A. (2020). The fate of deep-sea coral reefs on seamounts in a fishery-seascape: what are the impacts, ehat remains, and what is protected? *Frontiers in Marine Science, 7*(798). doi:10.3389/fmars.2020.567002

Williams, J., Jordan, A., Harasti, D., Davies, P., & Ingleton, T. (2019). Taking a deeper look: Quantifying the differences in fish assemblages between shallow and mesophotic temperate rocky reefs. *PLoS One, 14*(3), e0206778. doi:10.1371/journal.pone.0206778

Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geodesy, 30*(1-2), 3-35. doi:10.1080/01490410701295962

Yates, K. L., Mellin, C., Caley, M. J., Radford, B. T., & Meeuwig, J. J. (2016). Models of marine fish biodiversity: Assessing predictors from three habitat classification schemes. *PLoS One, 11*(6), e0155634. doi:10.1371/journal.pone.0155634

Yates, P., Ziegler, P., Welsford, D., Wotherspoon, S., Burch, P., & Maschette, D. (2019). Distribution of Antarctic toothfish Dissostichus mawsoni along East Antarctica: Environmental drivers and management implications. *Fisheries Research, 219*. doi:10.1016/j.fishres.2019.105338

Yeager, L. A., Deith, M. C. M., McPherson, J. M., Williams, I. D., & Baum, J. K. (2017). Scale dependence of environmental controls on the functional diversity of coral reef fish communities. *Global Ecology and Biogeography, 26*(10), 1177-1189. doi:10.1111/geb.12628

Young, M., & Carr, M. H. (2015). Application of species distribution models to explain and predict the distribution, abundance and assemblage structure of nearshore temperate reef fishes. *Diversity and Distributions, 21*(12), 1428-1440. doi:10.1111/ddi.12378

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. *Marine Ecology Progress Series, 415*, 247-261. doi:10.3354/meps08760

Young, M. J., Feyrer, F. V., Colombano, D. D., Louise Conrad, J., & Sih, A. (2018). Fish-habitat relationships along the etuarine gradient of the Sacramento-San Joaquin Delta, California: Implications for habitat restoration. *Estuaries and Coasts*, 1-21. doi:10.1007/s12237-018-0417-4

Tables

Table 1 Metrics used to link changes in terrain to variation in the composition of fish assemblages. Terrain metrics are grouped into four categories (i.e. seafloor relief, seafloor complexity, seafloor feature class and seafloor morphology) based on similarities in the terrain features they index. Descriptions and example references are provided for each terrain metric.

Terrain metric	Description	Example
Seafloor relief		
Average depth	Average depth of a feature below sea level	Maravelias (1999)
Contour index	Percent change in the depth of a feature	Bouchet et al. (2017)
Vertical relief	Maximum range in the depth of a feature	Moore et al. (2010)
Seafloor complexity		
Depth (standard deviation)	Standard deviation of the depth of a feature below sea level	Pittman et al. (2007)
Fractal dimensions	A ratio measure of seafloor roughness	Pittman et al. (2009)
Rugosity	Index of seafloor complexity: surface area to planar area ratio	Kuffner et al. (2007)
Slope	Maximum change in elevation (degrees)	Wedding and Friedlander (2008)
Slope of slope	Maximum rate of slope change (degrees of degrees)	Pittman et al. (2009)
Terrain ruggedness index (TRI)	3D complexity of grid cells in surrounding neighbourhood	Young et al. (2010)
Seafloor feature class		
Backscatter	Classifies features from the hardness or softness of the seafloor	Maravelias (1999)
Bathymetric position index (BPI)	Classifies features from seafloor elevation	Iampietro et al. (2005)
Depth-invariant index	Classifies features from the reflectance of different spectral bands	Knudby et al. (2010)
Substratum classification	Classifies features from bathymetric maps	Purkis et al. (2008)
Seafloor morphology		
Absolute curvature	Maximum curvature of a feature (convex or concave)	Knudby et al. (2011)
Aspect	Compass direction of a feature	Iampietro et al. (2008)
Kurtosis	The sharpness of a curved surface	Bayley et al. (2019)
Maximum curvature	Maximum convexity of a feature	Monk et al. (2010)
Mean curvature	Combines the index of both profile and plan curvature (see below)	Moore et al. (2009)
Plan curvature	Horizontal curvature of a feature	Pittman et al. (2009)
Plane morphometry	Proportion of cells without concavity or convexity	Cameron et al. (2014)
Profile curvature	Vertical curvature of a feature	Quattrini et al. (2012)
Ridge morphometry	Proportion of convex cells at right angles to cells with no curvature	Cameron et al. (2014)
Tangential curvature	Curvature of a feature perpendicular to the slope gradient	Biber et al. (2014)

Table 2 Summary of common mechanisms proposed to account for observed relationships between fish and seafloor terrain.

Terrain metric category	Mechanism	Rationale	References
Seafloor relief	Predator refuge	Shallow and high-relief features provide refuge locations for small-bodied fishes by limiting the manoeuvrability of large-bodied predators	Bassett et al. (2018); Parra et al. (2017); Pirtle et al. (2017)
	Food and habitat availability	Seafloor relief alters light availability, and primary production, and modifies the availability of food resources and vegetative habitat	Galaiduk et al. (2017); Hill et al. (2014)
	Fisheries avoidance	Large-bodied fish inhabit deep, high-relief seascapes where fishing susceptibility is reduced	Stamoulis et al. (2018)
	Water quality	Abiotic water conditions (e.g. oxygen, temperature, pH, salinity) change with variation in seafloor relief	Parra et al. (2017); Smoliński and Radtke (2017); Weijerman et al. (2019)
Seafloor complexity	Predator refuge	Seafloors with high architectural complexity have more spaces for small species and juveniles to hide from predators	Pittman et al. (2007); Ticzon et al. (2015); Wedding et al. (2019)
	Predator detection	High terrain variability limits the ability for species to detect approaching predators	Catano et al. (2015); Ferrari et al. (2018b)
	Food availability	Seafloor complexity modifies the abundance and availability of prey species	Coleman et al. (2016); Rees et al. (2018); Weijerman et al. (2019)
	Foraging habitats	Seafloor complexity modifies the distribution of foraging grounds	Catano et al. (2015); Ferrari et al. (2018b)
Seafloor feature class	Food availability	Different terrain features support distinct prey species and provide unique foraging opportunities	Fabrizio et al. (2013); Leitner et al. (2017)
	Predator refuge	Variation in the structure of terrain features modifies their utility as predator refuges	Auster et al. (2001); Misa (2013); Ticzon et al. (2015)
	Reproduction sites	Suitable spawning locations are determined by the distinct physical characteristics of terrain features	Farmer et al. (2017); Maravelias (1999)
Seafloor morphology	Hydrodynamic conditions	Seafloor morphology modifies the intensity and direction of water currents and wave conditions	Cameron et al. (2014); Coleman et al. (2016); Pirtle et al. (2017)
	Food availability	Altered hydrodynamic activity modifies the availability of prey species	Coleman et al. (2016); Weijerman et al. (2019); Young et al. (2010)
	Nutrient inputs	Terrain morphology alters the prevalence, and intensity, of chemicals transported by run-off	Stamoulis et al. (2018)
	Fisheries avoidance	Species avoid hydrodynamically sheltered areas, that are target locations for fishers	Stamoulis et al. (2018)

Table 3 Summary of the effects of terrain on fish assemblages in coral reef seascapes (see Table S5 for more details).

Terrain metric category	Terrain metric	Fish metric	Effect	Reference
Seafloor relief	Average depth	Total abundance, diversity or biomass	Positive	Knudby et al. (2011); Stamoulis et al. (2018); Walker et al. (2009)
		Abundance, biomass or presence of 7 species	Positive	Pittman and Brown (2011); Pittman et al. (2009); Roos et al. (2015); Yates et al. (2016)
		Biomass of 1 family	Positive	Pittman et al. (2009)
		Biomass of 1 functional group	Positive	Pittman et al. (2009)
		Total abundance, diversity, density or biomass	Negative	Abdul Wahab et al. (2018); Costa et al. (2014); Wedding et al. (2019)
		Abundance or presence of 2 species	Negative	Goodell et al. (2018); Pittman and Brown (2011)
	Vertical relief	Total diversity	Positive	Walker et al. (2009)
Seafloor complexity	Depth (SD)	Total diversity or density	Positive	Costa et al. (2014); Pittman et al. (2007)
	Rugosity	Total abundance, diversity or biomass	Positive	Bayley et al. (2019); Knudby et al. (2010); Purkis et al. (2008); Walker et al. (2009); Wedding et al. (2008)
		Abundance, biomass or presence of 3 species	Positive	Pittman and Brown (2011); Pittman et al. (2009)
		Abundance or diversity of 3 functional groups	Positive	Catano et al. (2015); (Pittman et al., 2009); Purkis et al. (2008)
	Slope	Total abundance, biomass or length	Positive	Abdul Wahab et al. (2018); Stamoulis et al. (2018)
		Abundance or biomass of 1 species	Positive	Pittman et al. (2009)
		Abundance of 1 functional group	Positive	Pittman et al. (2009)
		Total diversity, functional diversity or functional redundancy	Negative	Yeager et al. (2017)
	Slope of slope	Total abundance, diversity, body length, density or biomass	Positive	Pittman et al. (2009); Roos et al. (2015); Stamoulis et al. (2018); Wedding et al. (2019)
		Abundance or biomass of 4 species	Positive	Pittman and Brown (2011); Pittman et al. (2009)
		Biomass of 2 families	Positive	Pittman et al. (2009)
		Abundance, biomass or diversity of 2 functional groups	Positive	Pittman et al. (2009)
Seafloor feature class	Backscatter	Density or biomass of 5 species	Positive	Bejarano et al. (2011)
	Substratum classification	Total abundance, diversity or biomass	Positive	Knudby et al. (2011); Purkis et al. (2008); Ticzon et al. (2015); Walker et al. (2009);
Seafloor morphology	Aspect	Total biomass or length	Positive	Stamoulis et al. (2018); Wedding et al. (2019)
	Plan curvature	Abundance or biomass of 3 species	Positive	Pittman and Brown (2011); Pittman et al. (2007)
		Biomass of 1 family	Positive	Pittman et al. (2007)
		Biomass of 1 functional group	Positive	Pittman et al. (2007)

Table 4 Summary of the effects of terrain on fish assemblages in rocky reef seascapes (see Table S5 for more details).

Terrain metric category	Terrain metric	Fish metric	Effect	Reference
Seafloor relief	Average depth	Abundance, presence or biomass of 20 species	Positive	Bassett et al. (2018); Cameron et al. (2014); Ferrari et al. (2018a); Monk et al. (2010); Moore et al. (2010); Wedding and Yoklavich (2015)
		Abundance of 1 functional group	Positive	Ferrari et al. (2018a)
		Total diversity	Negative	Cameron et al. (2014)
		Abundance or presence of 16 species	Negative	Cameron et al. (2014); Fabrizio et al. (2013); Huff et al. (2011); Iampietro et al. (2008); Monk et al. (2010); Moore et al. (2010); Pirtle et al. (2017); Sievers et al. (2016)
		Biomass of 1 family	Negative	Ferrari et al. (2018a)
		Abundance, biomass or presence of 6 functional groups	Negative	Ferrari et al. (2018a); Ferrari et al. (2018b); Weijerman et al. (2019)
	Vertical relief	Biomass, density or length of 3 species	Positive	Sievers et al. (2016)
		Abundance of 1 family	Positive	Williams et al. (2019)
		Density of 2 species	Negative	Sievers et al. (2016)
Seafloor complexity	Depth (SD)	Abundance of 1 species	Positive	Rees et al. (2018)
	Fractal dimensions	Abundance of 6 species	Positive	Ferrari et al. (2018a)
	Rugosity	Total abundance & diversity	Positive	Cameron et al. (2014); Coleman et al. (2016); Williams et al. (2019)
		Abundance or presence of 5 species	Positive	Monk et al. (2011); Monk et al. (2010); Williams et al. (2019)
		Abundance of 1 family	Positive	Williams et al. (2019)
		Abundance of 2 functional groups	Positive	Ferrari et al. (2018b)
	Slope	Abundance of 6 species	Positive	Cameron et al. (2014); Fabrizio et al. (2013); Williams et al. (2019)
		Abundance of 1 family	Positive	Williams et al. (2019)
		Biomass or presence of 2 functional groups	Positive	Weijerman et al. (2019)
		Total diversity	Negative	Cameron et al. (2014)
		Presence of 5 species	Negative	Pirtle et al. (2017)
		Abundance of 3 functional groups	Negative	Ferrari et al. (2018b)
	Slope of slope	Total diversity	Positive	Young and Carr (2015)
		Abundance, density or biomass of 9 species	Positive	Wedding and Yoklavich (2015); Young and Carr (2015)
Seafloor feature class	Backscatter	Abundance, density, presence or length of 10 species	Positive	Fabrizio et al. (2013); Monk et al. (2010); Sievers et al. (2016)

		Biomass & presence of 2 functional groups	Positive	Weijerman et al. (2019)
		Presence or length of 3 species	Negative	Monk et al. (2011); Sievers et al. (2016)
	BPI	Total diversity	Positive	Cameron et al. (2014)
		Biomass, density or presence of 15 species	Positive	Huff et al. (2011); Iampietro et al. (2005); Iampietro et al. (2008); Moore et al. (2010); Pirtle et al. (2017); Young and Carr (2015); Young et al. (2010)
		Presence of 2 species	Negative	Pirtle et al. (2017)
	Substratum classification	Presence of 1 species	Positive	Huff et al. (2011)
Seafloor morphology	Aspect	Total diversity	Positive	Cameron et al. (2014)
		Abundance or presence of 12 species	Positive	Cameron et al. (2014); Iampietro et al. (2008); Monk et al. (2010); (Pirtle et al., 2017)
		Total diversity	Negative	Coleman et al. (2016)
		Abundance or presence of 7 species	Negative	Huff et al. (2011); Moore et al. (2010); Pirtle et al. (2017)
		Presence or biomass of 3 functional groups	Negative	Weijerman et al. (2019)
	Maximum curvature	Presence of 1 species	Positive	Monk et al. (2011)
		Presence of 3 species	Negative	Monk et al. (2010)

Table 5 Summary of the effects of terrain on fish assemblages in deep sea seascapes (see Table S5 for more details).

Terrain metric category	Terrain metric	Fish metric	Effect	Reference
Seafloor relief	Average depth	Presence, biomass or length of 7 species	Positive	Biber et al. (2014); Chang et al. (2012); Hill et al. (2017); Loots et al. (2007); Oyafuso et al. (2017); Péron et al. (2016); Wieczorek et al. (2014); Yates et al. (2019)
		Presence of 3 genera	Positive	Gomez et al. (2015)
		Abundance, biomass or presence of 16 species	Negative	Barcala et al. (2020); Chang et al. (2012); Hill et al. (2017); Lenoir et al. (2011); Oyafuso et al. (2017); Parra et al. (2017)
Seafloor complexity	Fractal dimensions	Abundance of 1 species	Negative	Quattrini et al. (2012)
	Rugosity	Abundance or presence of 7 species	Positive	Biber et al. (2014); Oyafuso et al. (2017); Quattrini et al. (2012)
	Slope	Abundance or size of 11 species	Positive	Oyafuso et al. (2017); Parra et al. (2017); Quattrini et al. (2012)
		Presence or abundance of 2 species	Negative	Oyafuso et al. (2017); Quattrini et al. (2012)
	VRI	Total abundance	Positive	Price et al. (2019)
Seafloor feature class	Backscatter	Abundance or size of 6 species	Positive	Misa (2013); Oyafuso et al. (2017)
		Presence of 2 species	Negative	Oyafuso et al. (2017)
	BPI	Total abundance, diversity or length	Positive	Giddens et al. (2019); Leitner et al. (2017)
		Abundance of 8 species	Positive	Leitner et al. (2017)
	Substratum classification	Presence of 3 species	Positive	Parra et al. (2017)
		Presence of 3 species	Negative	Parra et al. (2017)
Seafloor morphology	Aspect	Abundance or presence of 13 species	Positive	Leitner et al. (2017); Parra et al. (2017); Quattrini et al. (2012)
		Abundance or presence of 6 species	Negative	Oyafuso et al. (2017); Parra et al. (2017); Quattrini et al. (2012)
	Mean curvature	Abundance or presence of 4 species	Positive	Oyafuso et al. (2017); Quattrini et al. (2012)
		Abundance of 1 species	Negative	Quattrini et al. (2012)
	Plan curvature	Abundance of 3 species	Positive	Quattrini et al. (2012)
	Profile curvature	Abundance of 2 species	Positive	Quattrini et al. (2012)

Table 6 Summary of the effects of terrain on fish assemblages in continental shelf seascapes (see Table S5 for more details).

Terrain metric category	Terrain metric	Fish metric	Effect	Reference
Seafloor relief	Average depth	Presence of 9 species	Positive	Galaiduk et al. (2017); Lathrop et al. (2006); Moore et al. (2016)
		Total abundance or diversity	Negative	Hill et al. (2014); Schultz et al. (2014); Smoliński and Radtke (2017)
		Abundance or presence of 9 species	Negative	Bellido et al. (2008); Cote et al. (1998); Galaiduk et al. (2017); Giannoulaki et al. (2011); Maravelias (1999); Moore et al. (2016); Salarpouri et al. (2018); Stein et al. (2004)
	Vertical relief	Presence of 2 species	Positive	Galaiduk et al. (2017)
		Presence of 2 species	Negative	Galaiduk et al. (2017)
Seafloor complexity	Slope	Presence of 3 species	Positive	Moore et al. (2016)
		Total abundance or diversity	Negative	Smith and Lindholm (2016); Smoliński and Radtke (2017)
		Presence of 2 species	Negative	Salarpouri et al. (2018)
	TRI	Total abundance or diversity	Negative	Smith and Lindholm (2016)
Seafloor feature class	Backscatter	Abundance of 3 species	Positive	Auster et al. (2001); Farmer et al. (2017); Schultz et al. (2015)
		Total diversity	Negative	Schultz et al. (2015)
		Abundance or presence of 12 species	Negative	Auster et al. (2001); Farmer et al. (2017); Lathrop et al. (2006); Maravelias (1999); Moore et al. (2016); Schultz et al. (2015)
	BPI	Presence of 2 species	Positive	Farmer et al. (2017)
		Presence of 1 species	Negative	Farmer et al. (2017)

Table 7 Summary of the effects of terrain on fish assemblages in estuarine seascapes (see Table S5 for more details).

Terrain metric category	Terrain metric	Fish metric	Effect	Reference
Seafloor relief	Average depth	Abundance, density, presence or length of 3 species	Negative	Becker et al. (2017); Le Pape et al. (2003); Nicolas et al. (2007); Rochette et al. (2010); Trimoreau et al. (2013)
		Length of 2 species	Positive	Meynecke et al. (2008)

Table 8 Priority questions for research on the effects of terrain on fish assemblages. References provide examples of methods that could be used to investigate each question.

Priority research questions
1. **Data-deficient ecosystems:** how does terrain variation shape fish assemblages in soft-sediment seascapes that are under-sampled (e.g. estuaries, coastal seas) (e.g. Becker et al., 2017).
2. **Spatial scale**: do the effects of seafloor terrain operate at distinct spatial scales in different seascapes (e.g. Pittman & Brown, 2011)?
3. **Seascape context:** does seafloor terrain modify the importance of spatial context between ecosystems (e.g. mangroves, seagrasses, coral reefs) for fish (e.g. Sekund & Pittman 2017)?
4. **Fish movement**: does terrain determine how fish move throughout seascapes and what seafloor features are pivotal in shaping fish movements (e.g. Huff et al., 2011)?
5. **Nursery habitats**: which terrain features are most important for creating favourable conditions for the recruitment, survival and growth of juvenile fish (e.g. Trimoreau et al., 2013)?
6. **Functional ecology**: does seafloor terrain change the context that species perform different ecological functions (e.g. scavenging, herbivory, predation) (e.g. Catano et al., 2015)?
7. **Predators**: are apex predators consistently associated with particular terrain features and does this correspond to changes in the trophic and assemblage composition of fish (e.g. Weijerman et al., 2019)?
8. **Urbanization**: how do multiple anthropogenic stressors (i.e. dredging, shoreline armouring) change the ecological value of terrain features for fish (e.g. Rochette et al., 2010)?
9. **Marine reserves**: how do fish respond to terrain within a conservation context, and can seafloor terrain enhance the performance of marine reserves for fish (e.g. Rees et al., 2018)?
10. **Climate change**: are there terrain features that could provide supplementary habitat, or obstructions, for species that alter their spatial distributions in response to climate change (e.g. Lenoir et al., 2011)?

Figure Legends

Figure 1 Global distribution of research linking changes in seafloor terrain to variation in the composition of fish assemblages (n = 96). Pie charts illustrate the categories of terrain metrics examined and are scaled to represent the number of studies from each country. Arrows indicate the geographic region of research for large countries where research effort has been intensive. Global bathymetry map courtesy of GEBCO (https://www.gebco.net/). mbsl = metres below sea level. Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

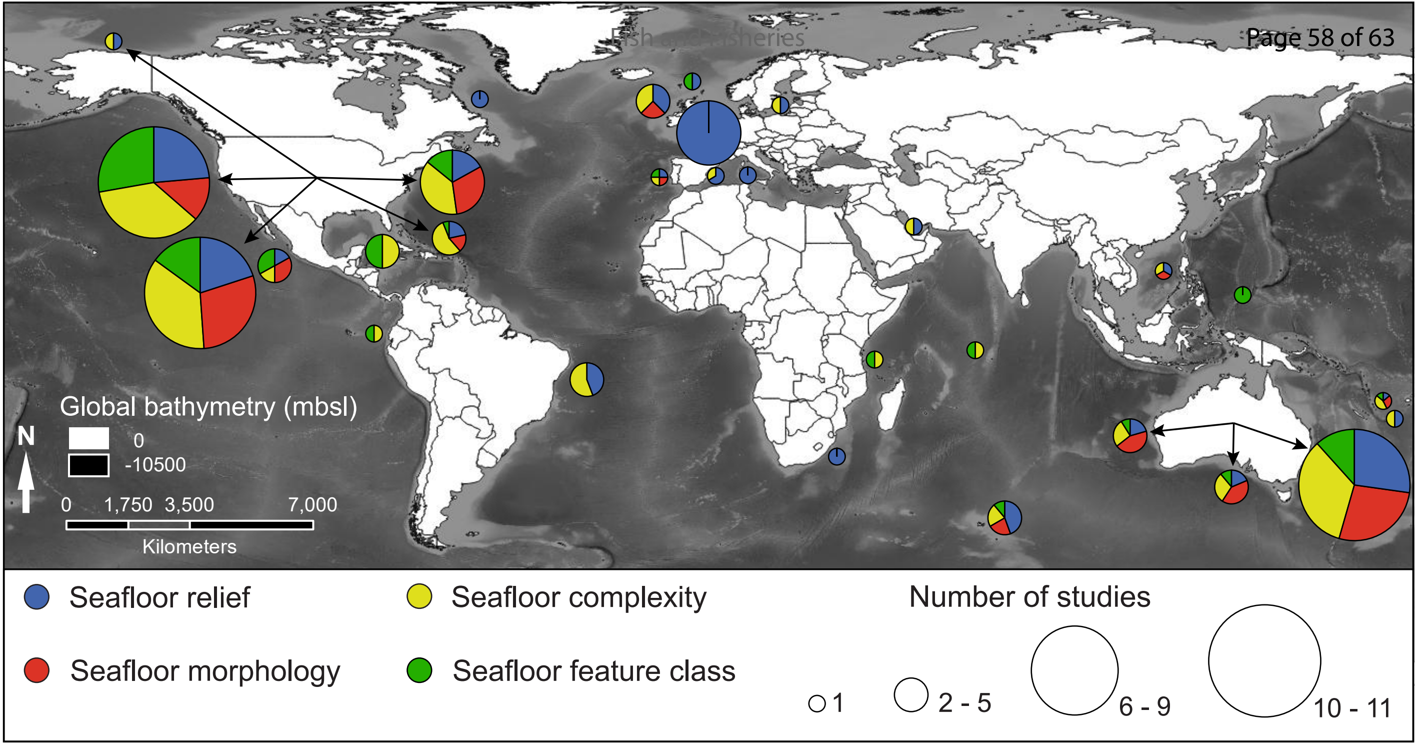
Figure 2 Terrain metrics were grouped into four categories based on similarities in the bathymetric features they index. Seafloor relief metrics (a) measure the depth and height of bathymetric features (e.g. average depth, vertical relief). Seafloor complexity metrics (b) describe the vertical roughness of the seabed (e.g. rugosity, slope, slope of slope). Seafloor feature class (c) metrics categorise features based on discrete bathymetric variation (e.g. rock, soft sediment). Seafloor morphology metrics (d) quantify the physical characteristics of bathymetric features (e.g. aspect, curvature) (Table 1). Symbols courtesy of the IAN Network (http://ian.umces.edu/symbols/). Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

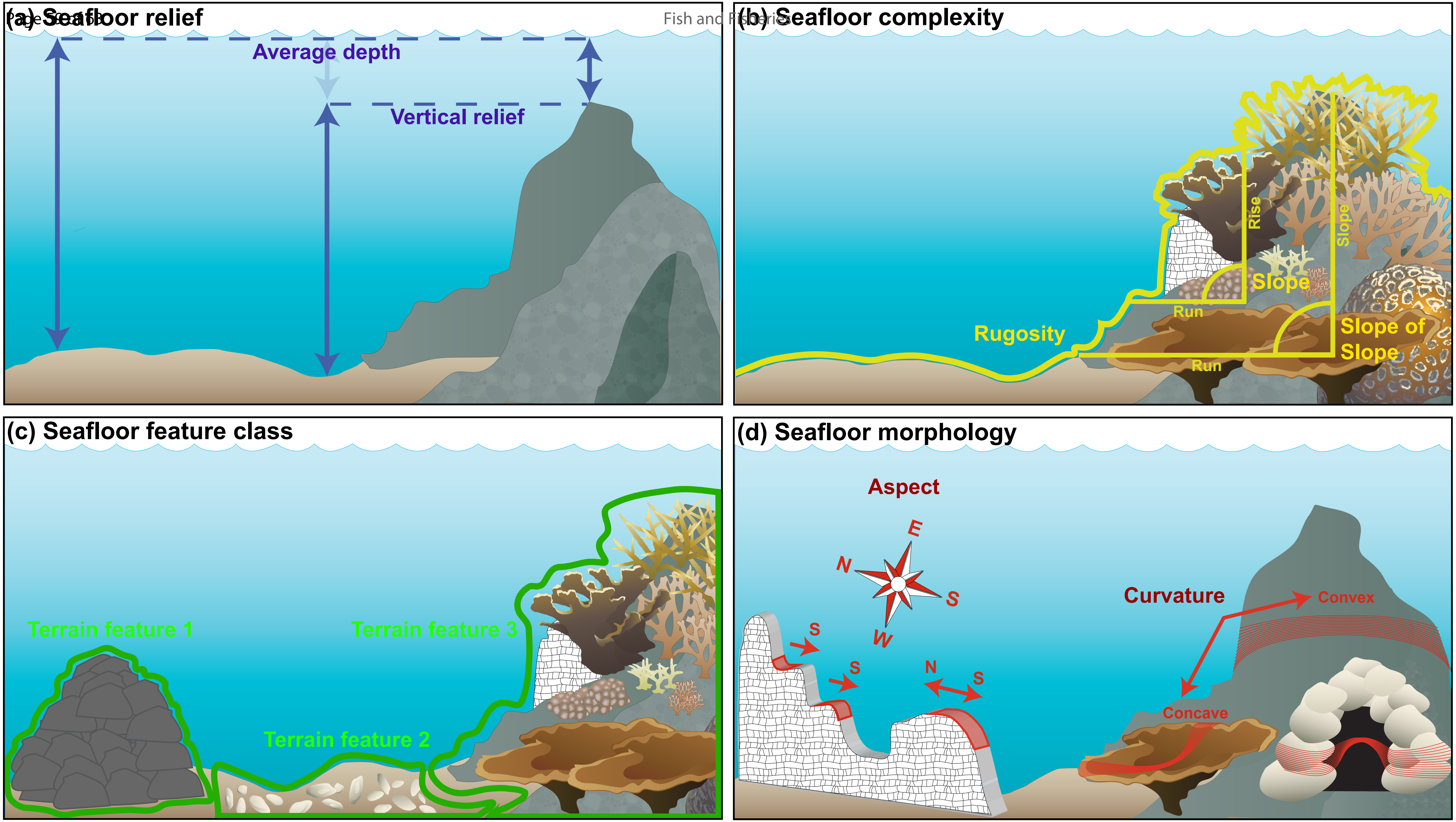
Figure 3 Non-metric multidimensional scaling (nMDS) ordinations and scaled segmented bubble plots illustrating differences in the number of studies that reported positive, negative and neutral effects of terrain metrics within each category, and seascape. P-values were derived from two-way permutational analysis of variance (PERMANOVA) testing for differences in the predictive performance of terrain metrics among seascapes and terrain metric categories (Table S2). Dotted lines around ordinations illustrate significant differences ($p < 0.05$) in the predictive performance of groups of terrain metrics (i.e. number of positive, negative and neutral effects) among seascapes and terrain metric categories, as defined by pair-wise tests following PERMANOVA (Table S3). Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

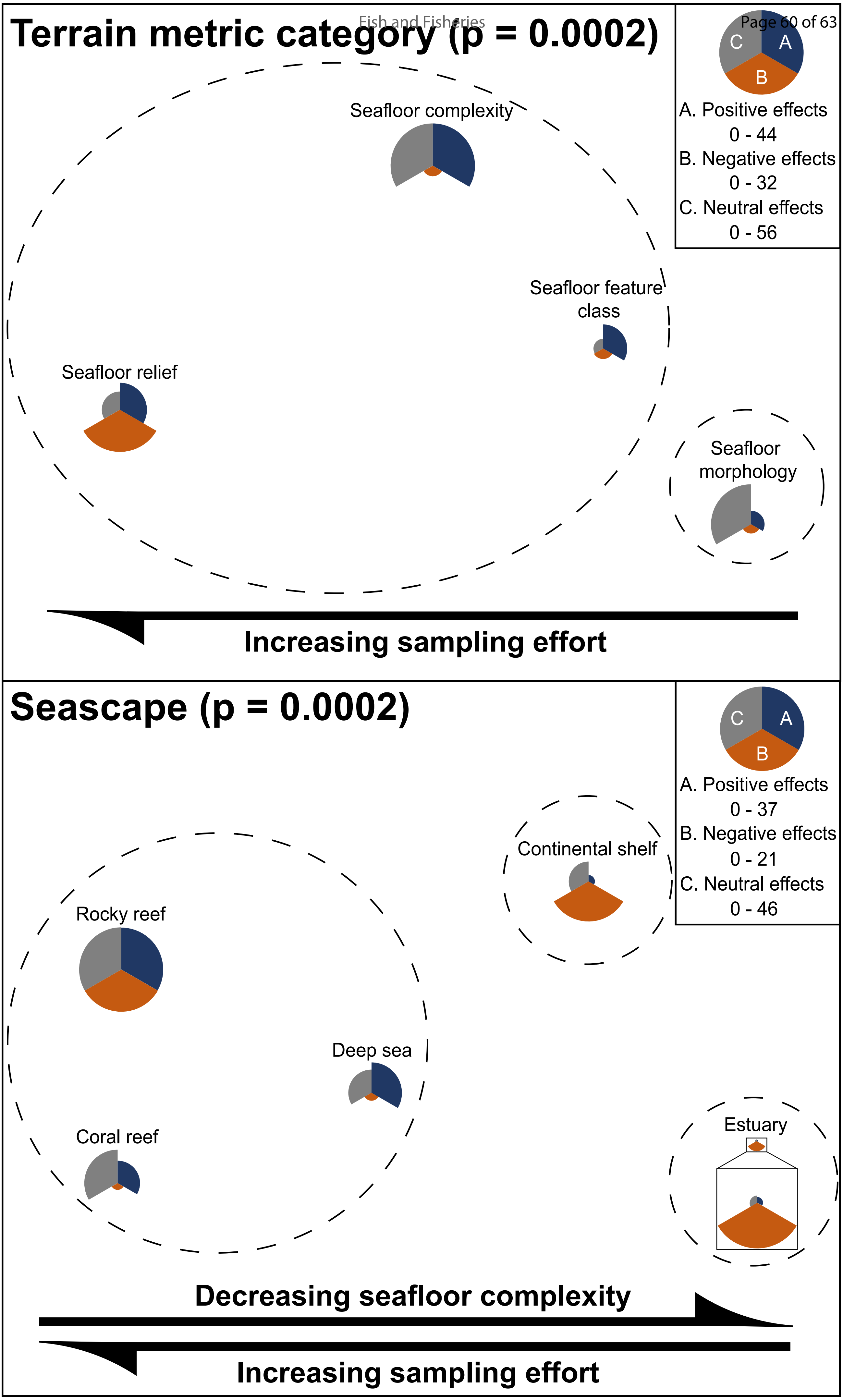
Figure 4 Summary of studies reporting positive, negative or neutral effects of seafloor terrain (indexed as variation in relief, morphology, complexity and feature class) on fish assemblages from coral reef, rocky reef, deep sea, continental shelf and estuarine seascapes. Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

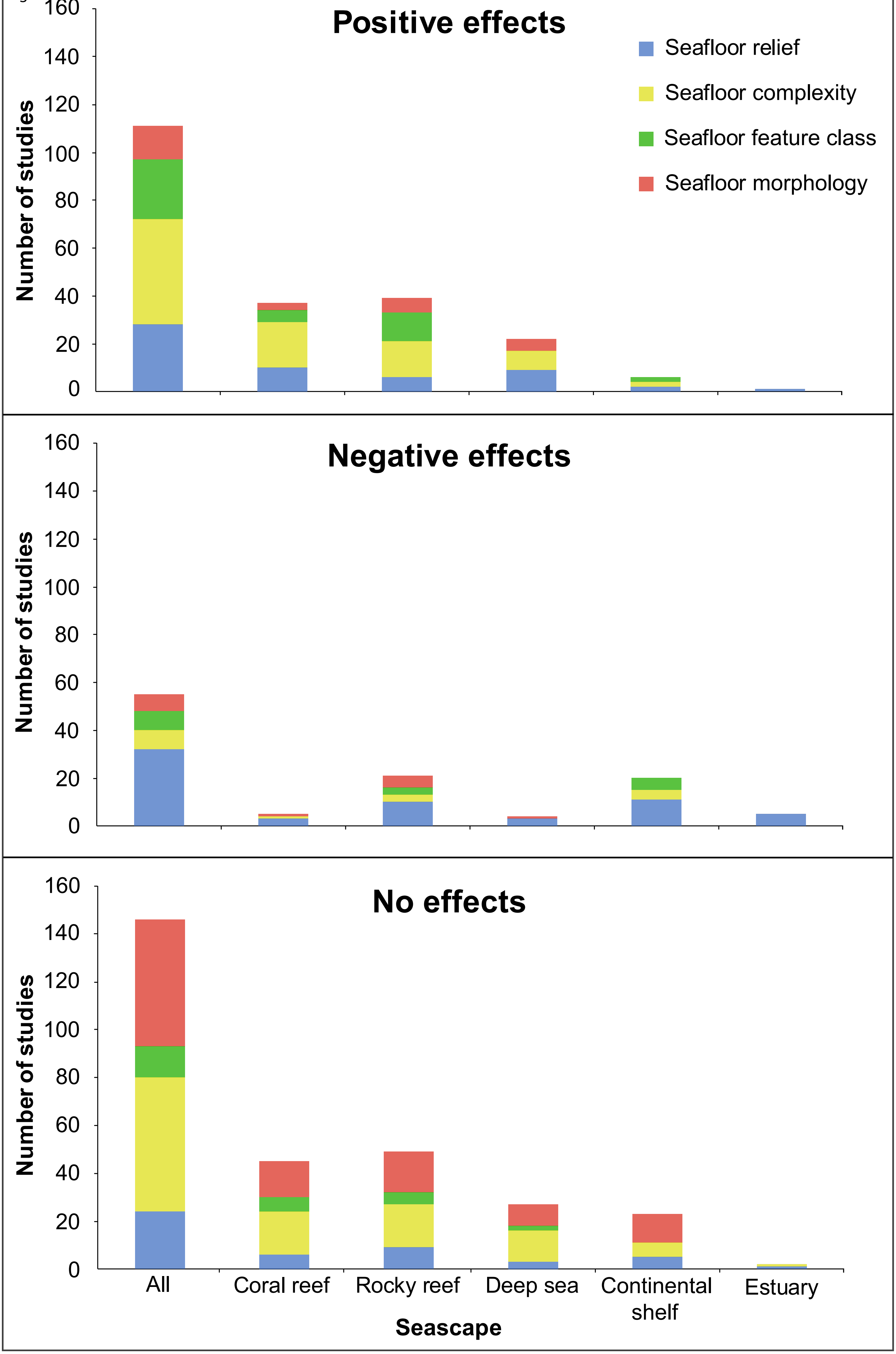
Figure 5 Consistency in the predictive performance of terrain metrics among seascapes (i.e. the proportion of studies reporting significant positive or negative effects from those that measured each metric). Coloured boxes designate terrain metric categories: blue (seafloor relief), yellow (seafloor complexity), green (seafloor feature class) and red (seafloor morphology). Black bars highlight the best performing terrain metric in each category for each seascape (e.g. average depth was the best seafloor relief metric in all seascapes, and rugosity was the best seafloor complexity metric in rocky reef seascapes). Terrain metrics that were used in two, or fewer, studies were omitted from performance calculations due to data limitations. SD = standard deviation. Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

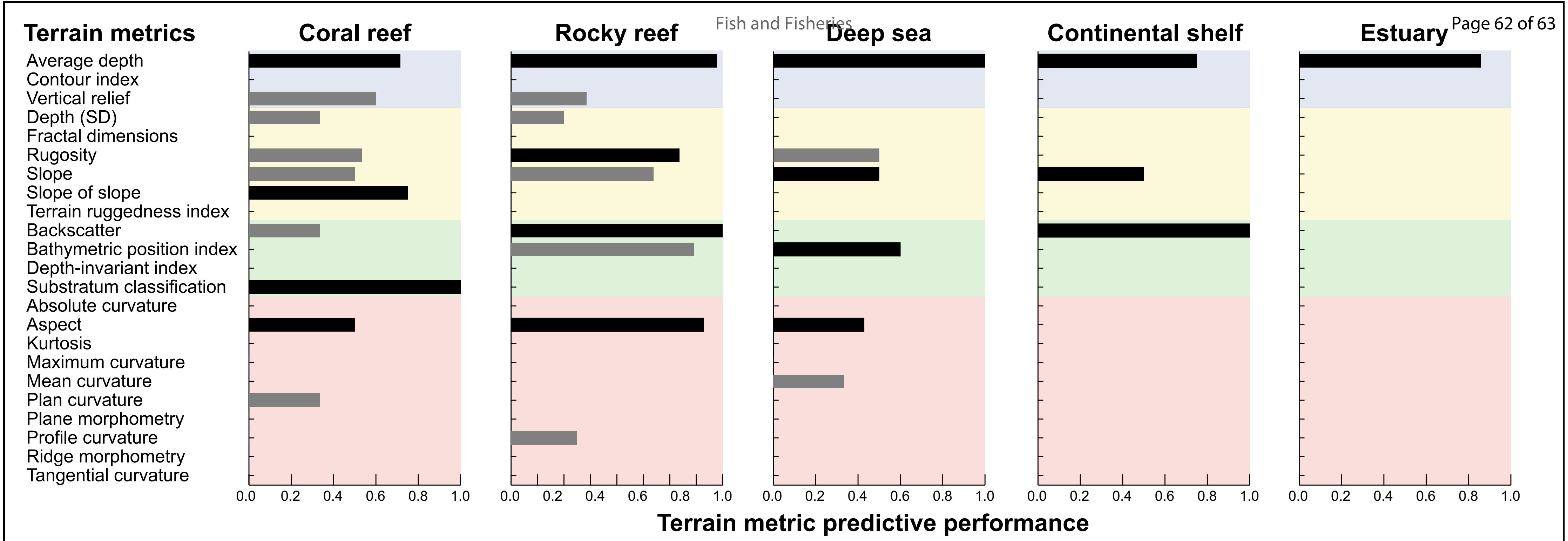
Figure 6 Summary of terrain metrics that were correlated with the strongest effects on fish assemblages in each seascape. Numbers represent the total research effort for each terrain metric, and pie charts illustrate the proportion of studies reporting positive (blue), negative (orange) or neutral (grey) effects (see Figures S1 – S5 for data on the performance of each terrain metric in each seascape). Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

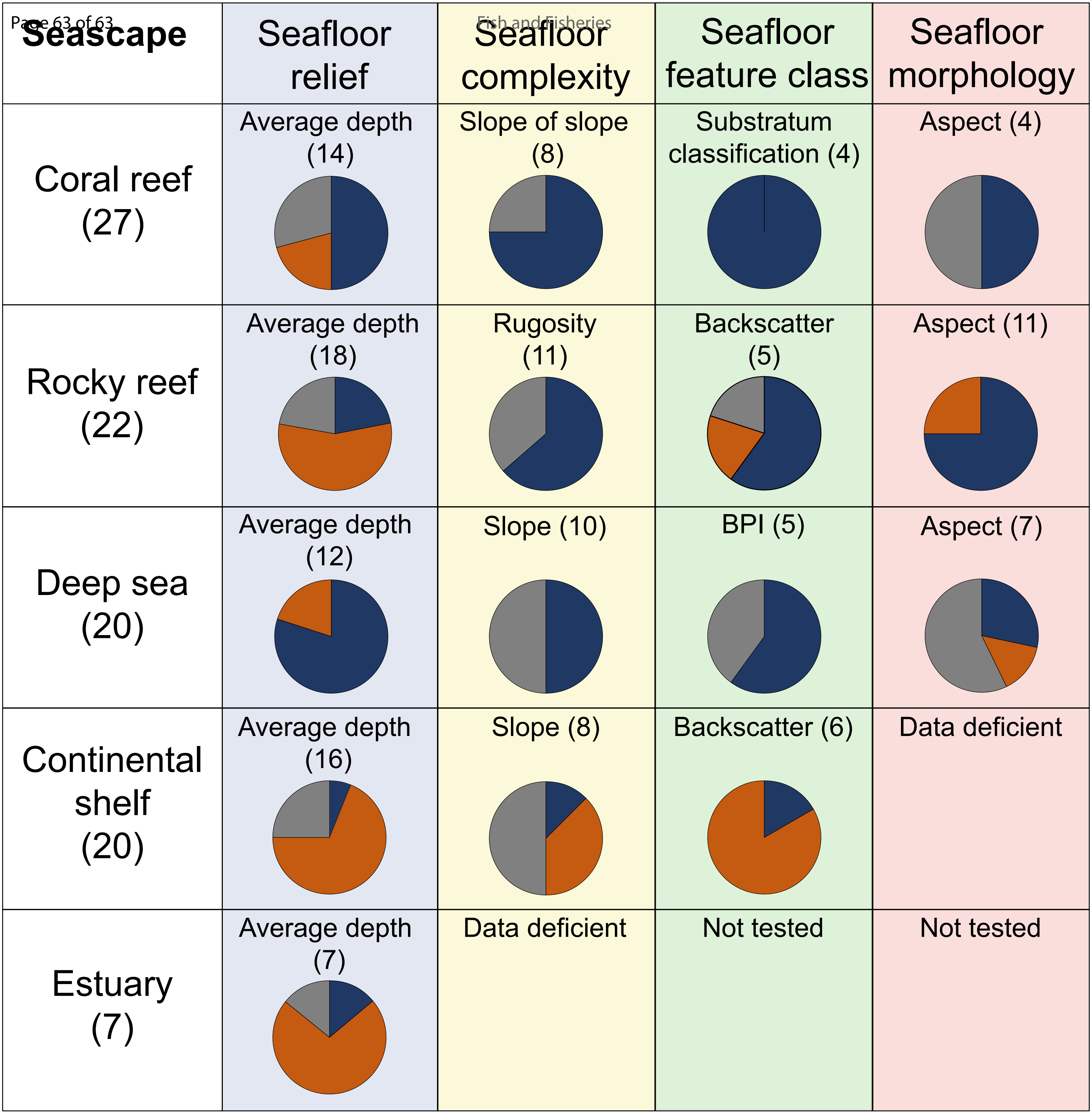

Global bathymetry (mbsl)
0
-10500
N
0 1,750 3,500 7,000
Kilometers
Seafloor relief
Seafloor morphology
Seafloor complexity
Seafloor feature class
Number of studies
1
2 - 5
6 - 9
10 - 11


(a) Seafloor relief
Average depth
Vertical relief
(b) Seafloor complexity
Rise
Slope
Slope
Run
Rugosity
Slope of Slope
Run
(c) Seafloor feature class
Terrain feature 1
Terrain feature 3
Terrain feature 2
(d) Seafloor morphology
Aspect
E
N
S
W
S
S
N
S
Curvature
Convex
Concave


Terrain metric category (p = 0.0002)
C
A
B
A. Positive effects
0 - 44
B. Negative effects
0 - 32
C. Neutral effects
0 - 56
Seafloor complexity
Seafloor feature class
Seafloor relief
Seafloor morphology
Increasing sampling effort
Seascape (p = 0.0002)
C
A
B
A. Positive effects
0 - 37
B. Negative effects
0 - 21
C. Neutral effects
0 - 46
Continental shelf
Rocky reef
Deep sea
Coral reef
Estuary
Decreasing seafloor complexity
Increasing sampling effort


Positive effects
Negative effects
No effects
Seafloor relief
Seafloor complexity
Seafloor feature class
Seafloor morphology
Number of studies
0
20
40
60
80
100
120
140
160
All
Coral reef
Rocky reef
Deep sea
Continental shelf
Estuary
Seascape


Terrain metrics
Coral reef
Rocky reef
Deep sea
Continental shelf
Estuary
Average depth
Contour index
Vertical relief
Depth (SD)
Fractal dimensions
Rugosity
Slope
Slope of slope
Terrain ruggedness index
Backscatter
Bathymetric position index
Depth-invariant index
Substratum classification
Absolute curvature
Aspect
Kurtosis
Maximum curvature
Mean curvature
Plan curvature
Plane morphometry
Profile curvature
Ridge morphometry
Tangential curvature
0.0 0.2 0.4 0.6 0.8 1.0
Terrain metric predictive performance


Seascape
Seafloor relief
Seafloor complexity
Seafloor feature class
Seafloor morphology
Coral reef (27)
Average depth (14)
Slope of slope (8)
Substratum classification (4)
Aspect (4)
Rocky reef (22)
Average depth (18)
Rugosity (11)
Backscatter (5)
Aspect (11)
Deep sea (20)
Average depth (12)
Slope (10)
BPI (5)
Aspect (7)
Continental shelf (20)
Average depth (16)
Slope (8)
Backscatter (6)
Data deficient
Estuary (7)
Average depth (7)
Data deficient
Not tested
Not tested