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## Review



# Topography-based modulation of environmental factors as a mechanism for intertidal microhabitat formation: A basis for marine ecological design

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## ABSTRACT

Topographic complexity is often considered to be closely associated with habitat complexity and niche diversity; however, complex topography *per se* does not imply habitat suitability. Rather, ecologically suitable habitats may emerge if topographic features interact with environmental factors and thereby alter their surrounding micro-environment to the benefit of local organisms (e.g., resource provisioning, stress mitigation). Topography may thus act as a key modulator of abiotic stressors and biotic pressures, particularly in environmentally challenging intertidal systems. Here, we review how topography can alter microhabitat conditions with respect to four resources required by intertidal organisms: a source of energy (light, suspended food particles, prey, detritus), water (hydration, buffering of light, temperature and hydrodynamics), shelter (temperature, wave exposure, predation), and habitat space (substratum area, propagule settlement, movement). We synthesize mechanisms and quantitative findings of how environmental factors can be altered through topography and suggest an organism-centered ‘form-follows-ecological-function’ approach to designing multifunctional marine infrastructure.

## 1. Introduction

Loss and replacement of coastal habitats is intensifying globally (Bugnot et al., 2021), and may amplify the environmentally challenging conditions that intertidal species are naturally exposed to. Buffering of, or escape from, abiotic stressors (e.g., temperature, hydrodynamics, desiccation) and biotic pressures (e.g., predation, competition) can be a necessity for survival in these highly dynamic environments. While some intertidal species have evolved strategies to compensate stress (i.e., stimuli that disturb the homeostatic state of an organism) through physiological or morphological plasticity (e.g., Harley et al., 2009; McAfee et al., 2018), organismal success can also rely on the inherent capacity of the substratum topography to alter its surrounding micro-environment. On rocky shores, topographic structural features (e.g., shaded overhangs, crevices, rockpools) can cause shifts in abiotic and biotic microhabitat conditions along environmental gradients, thus forming niches that are ecologically distinct from the wider environment (Daniel and Boyden, 1975; Jackson, 2010; Meager et al., 2011). As such,

topographic features can buffer environmental factors, thereby creating more stable micro-climatic conditions (Thompson et al., 1996; Jackson, 2010; but see O'Donnell and Denny, 2008). For an organism, this may cause microhabitat suitability to change at small spatial scales (Fig. 1). Shifts that yield ecological benefits for an organism (e.g., enhanced survival rates) may occur in environments where organismal distribution is limited by predation pressure or stress tolerance (e.g., temperature, wave exposure). As such, topographic features may alter refuge availability (Hixon and Menge, 1991), light exposure gradients, and hydrodynamics (Wing et al., 2007), thus shifting microhabitat conditions closer to the organism's optimum range.

While natural rocky habitats often contain an abundance of microhabitats (i.e., small-scale habitat patches <1 m that are topographically, abiotically and/or biotically distinct from neighbouring habitats), these niches are generally absent or simplified on the smooth, vertical concrete surfaces of modern coastal infrastructure (e.g., seawalls, rock armour) (Chapman and Blockley, 2009; Chapman and Underwood, 2011; Lawrence et al., 2021). Artificial substrata therefore often show reduced

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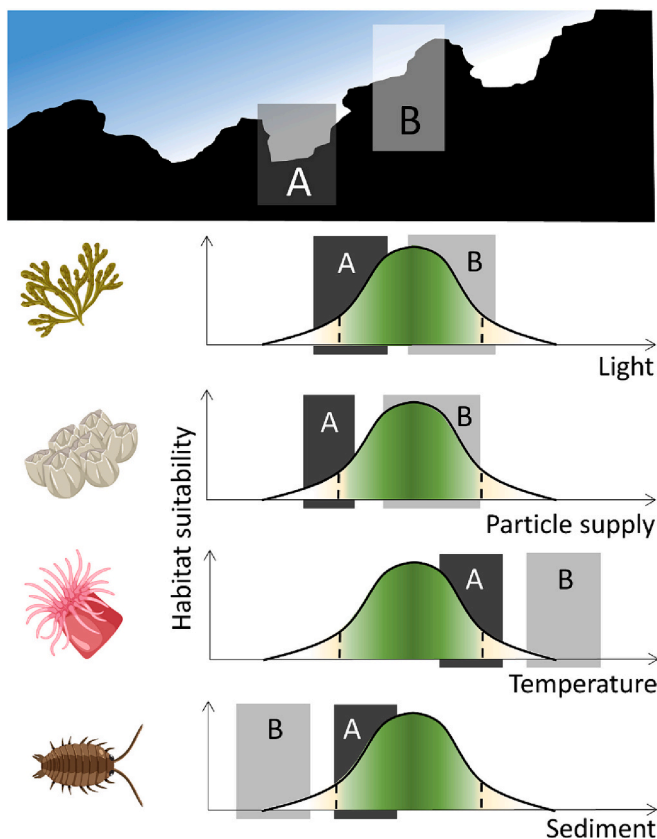
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**Fig. 1.** Illustration of how topographic features can shift microenvironmental conditions and alter (micro-)habitat suitability. Stress tolerance curves are depicted for four model taxa (fucoid macroalgae, barnacles, sea anemones, infaunal isopods) along four environmental gradients. Dotted lines delineate the optimum range (green). Curve tails represent the lower and upper stress tolerance range. Habitat suitability is represented as a unimodal curve for simplicity. (A) Sheltered niche (dark grey). (B) Exposed niche (light grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

microhabitat diversity and limited capacity to buffer abiotic and biotic stressors, ultimately supporting lower biodiversity and fewer ecosystem services (Strain et al., 2021). In recognition of this, marine eco-engineering methods strive to mimic the structural complexity and niche diversity of natural habitat substrata, thus providing functionally equivalent habitat conditions on artificial structures. Methods include the incorporation of rugosity, void spaces (crevices, grooves, pits), water- and sediment-retaining features as well as alterations in surface orientation (slope, overhangs) (Evans et al., 2016; Strain et al., 2021; Bishop et al., 2022). Additional topographic complexity can be created through the arrangement of different structural components in various sizes, densities, spatial configurations and relative abundances (Loke et al., 2014, 2015). Positive effects of structural complexity on biodiversity, community composition and species abundance have been widely demonstrated (Firth et al., 2016a; Loke and Todd, 2016; Bishop et al., 2022), with neutral or negative effects occasionally also reported (Firth et al., 2020; Strain et al., 2021; Bishop et al., 2022). The latter may highlight the importance of creating structural complexity tailored to the ecological needs of organisms.

There has been considerable difficulty in defining what constitutes ‘habitat complexity’ and the term has often been used synonymously with structural complexity (Loke and Chisholm, 2022). The use of structural complexity metrics (e.g., rugosity, fractal dimension) to characterise habitat complexity may, however, distort how organisms perceive and interact with their habitat, since organisms might not be

capable of perceiving structural complexity in the first place. Rather, organisms are more likely responding to the microenvironment (‘microclimate’) created by topography, not the topographic features *per se*. Structural complexity would thus only be ecologically impactful to an organism if the structure alters the microhabitat in ways that fulfil (or impede) organismal needs.

Here, we synthesize mechanisms and quantitative measurements of how substratum topography can modulate environmental factors, and can thus contribute to the formation of microhabitats distinct across multiple environmental gradients. Topographic features may alter both abiotic and biotic factors, and thereby mitigate stressors or provide organisms with resources (Fig. 2). We distinguish between four organismal needs, subdivided into ecological forms and functions: (1) a source of energy (light availability, suspended food particles, prey, detritus), (2) water (hydration, buffering of light, temperature and hydrodynamics), (3) shelter (temperature stress, wave exposure, predation), and (4) habitat space (substratum area, propagule settlement, movement). Thus, we consider habitat complexity from an organismal perspective of microhabitat suitability, and argue for a ‘form-follows-function’ approach to developing eco-engineering solutions. The mechanisms of topography-environment interactions summarized here are largely focused on topographic structures at micrometre to metre scale that can be incorporated into infrastructure design and construction. Microhabitat conditions created through abiotic material properties (e.g., rock type) or biotic substrata (e.g., calcifying organisms) are only included in so far as their ecological effects are structure-based (e.g., porosity of rock types, rugosity of calcifying organisms). Microhabitat conditions emerging independent of topography, for instance due to location-specific (e.g., turbidity), temporal (e.g., seasonality, emersion time), or purely biological impacts (e.g., within-niche competition), are beyond the scope of this review.

## 2. Source of energy

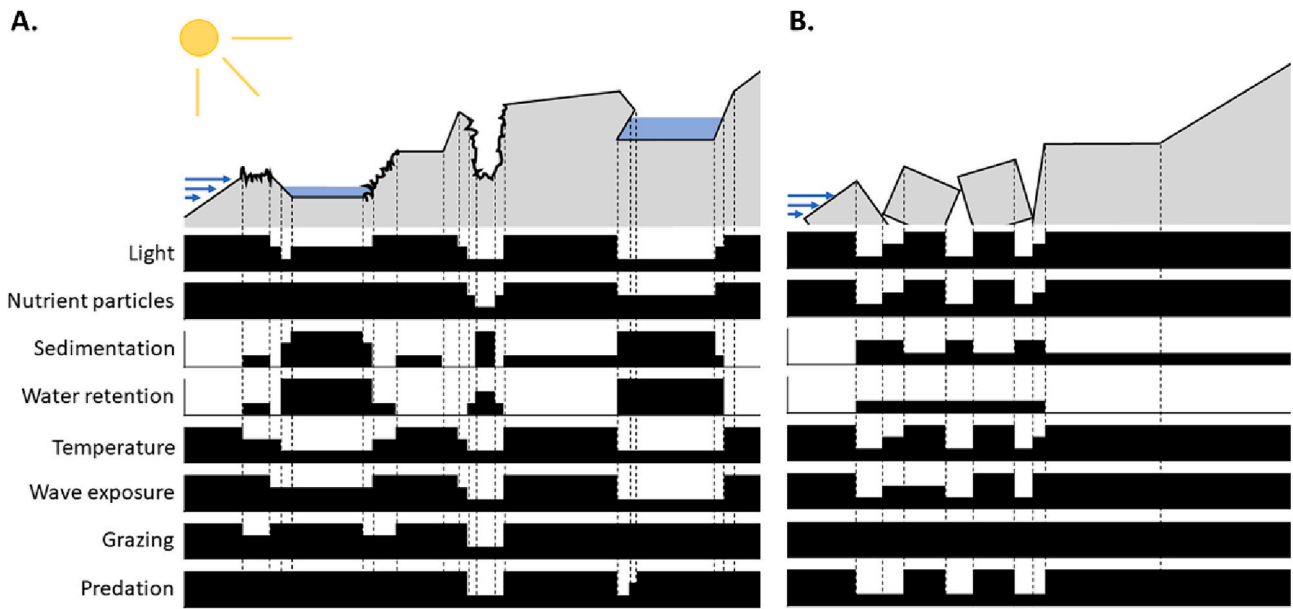
### 2.1. Light availability

Photosynthetically active radiation is the primary energy source for microalgal biofilms (e.g., Thompson et al., 2005) and macroalgae (e.g., Norton, 1991), with knock-on effects on larval settlement processes, food availability and biogenic habitat formation. Different light requirements, and sensitivity to photoinhibition and bleaching, however, may cause some algae to rely on shade provisioning, abiotically (e.g., crevices) or biotically (e.g., canopy cover) (Jenkins et al., 1999a). Varying light exposure can thereby locally enhance or limit algal settlement, thus providing habitat for epibiont and understory species (Wahl, 1989; Rubach et al., 2011) or conversely, shaded microhabitats for heterotrophs.

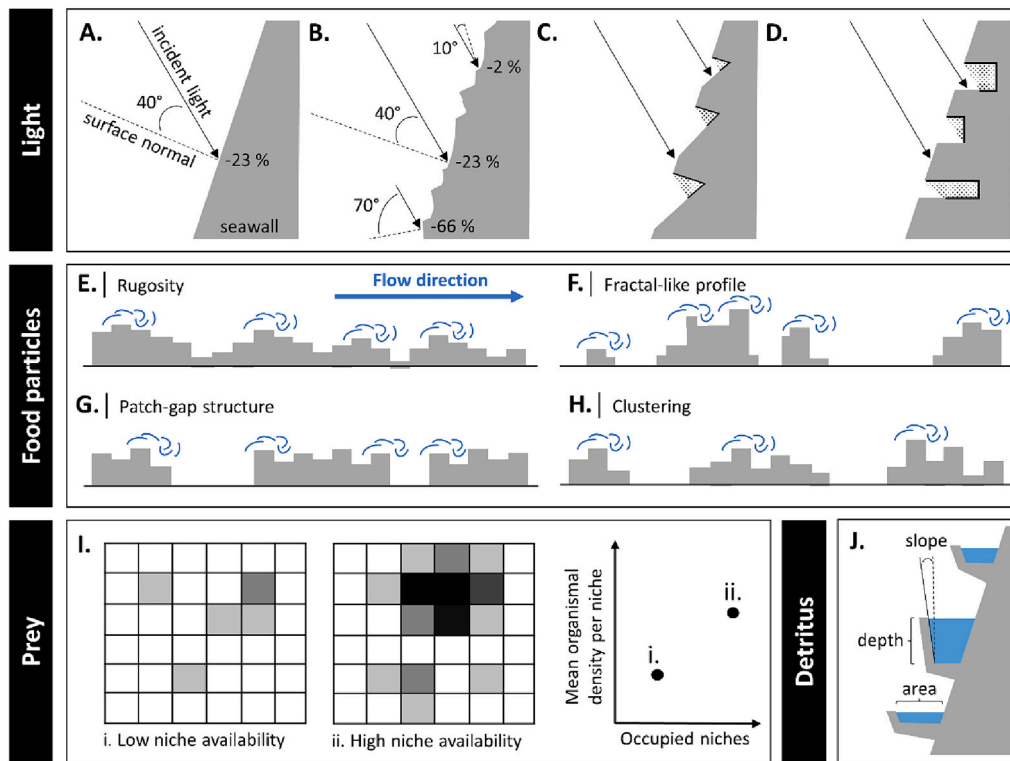
Light exposure can be altered topographically through alterations in surface orientation relative to the light source (Fig. 3A) (Zhao et al., 2019). Assuming constant light emission from a source (sun, at a given time), the light intensity that a surface is exposed to is highest if the surface is oriented perpendicular towards the light (e.g., Yadav and Chandel, 2013). Photon number per surface area decreases with increasing incidence angle, driven by the inverse relationship between the amount of incident light and the surface area over which the light is distributed (dependent on slope and topography). As such, the average solar irradiation per area on a surface tilted by 45° is 29 % lower than on the same surface oriented perpendicular to the sun, and likewise 50 % lower when tilted 60°. This relationship (formula: Daut et al., 2011) can be adjusted to additional parameters, such as daily and seasonal solar position (Yadav and Chandel, 2013).

$$\text{Solar irradiation}_{\text{Surface}} = \text{Solar irradiation}_{\text{Incident}} * \cos(\text{incidence angle})$$

Incorporation of rugosity into surfaces could create topographically distinct areas with different light exposures (Fig. 3B). Rugosity effects on light are linked to surface orientation, as rugosity creates areas with



**Fig. 2.** Illustration of the potential impacts of topographic variation on environmental factors acting on a (A) natural, and (B) artificial shore habitat at low tide. The intertidal is depicted as a mosaic of microhabitats, defined by topographic features and ecological functions. Black bars ('rows') represent environmental variables at four levels of magnitude (absent to predominant). Dotted vertical lines separate microenvironments ('columns').



**Fig. 3.** Effects of topography on different organismal sources of energy. Light exposure of a seawall surface dependent on (A) slope, (B) rugosity, (C) shaded overhangs, and (D) cavities of different dimensions. Percentages in (A, B) denote reductions in light intensity driven by incidence angle, relative to a perpendicular surface ( $0^\circ$ ). Turbulence generation and particle fluxes (blue) at elevated edges and ridges, created through (E) substratum rugosity, (F) fractal geometry, (G) patch-gap structure, and (H) cluster formation. (I) Planar view of a substratum area, with (i) low niche availability and associated low organismal density per niche, and (ii) high niche availability and associated high organismal density per niche. Grey intensity represents the density (abundance) of a theoretical organism per niche, which increases proportional to niche availability (adapted from [Borregaard and Rahbek, 2010](#)). Niches are defined as small-scale habitat patches (grid squares) suitable for organismal settlement and survival. (J) Detritus retention (e.g., wrack subsidies) by rock pools with different capture areas, depths and internal topographies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

different tilt ('sloping') within a surface. Thus, rugose topography alters light gradients according to the spatial scale and orientation of its 'surface patches'. Rugosity at fine scales would result in light variation at small spatial scales, while rugosity at coarser scales would create larger 'patches'.

Light exposure can furthermore be reduced through shading via overhangs (Fig. 3C) or cavities (Fig. 3D). Waltham and Sheaves (2018) deployed rock pool units tilted by 45°, thus creating shaded overhangs inside and outside the units. While light measurements were not reported, biodiversity assessment showed higher species cover on inner overhangs, including light- and desiccation-sensitive species such as crustose algae, oysters, sponges, snails and tubeworms (Waltham and Sheaves, 2018). Similarly, Strain et al. (2020) found that light intensities in crevices of grooved settlement tiles (5 cm deep, 1.5–5 cm wide) were reduced by ~50 % compared to ridges. The magnitude of shading within cavities is strongly dependent on structural characteristics, such as the cavity opening area, depth and internal topography, as well as the orientation of the cavity opening towards the sun (Roldán et al., 2004). Light availability in a cavity would be expected to be low if the cavity opening is small, the depth and internal surface area large, and the opening oriented away from the light.

## 2.2. Supply of suspended food particles

Suspended food particles (particulate organic material) are supplied to filter feeders (e.g., mussels, barnacles) through a combination of horizontal advection and vertical turbulent mixing (e.g., Fréchette et al., 1989). Boundary layer thickness and replenishment of near-bottom food particle fluxes can be enhanced through vertical mixing processes, resulting from interactions between local hydrodynamics and physical structures (Fréchette et al., 1989; Folkard and Gascoigne, 2009; Lim et al., 2020). In laboratory flume experiments, arrays of cylindrical or pyramidal protrusions have been shown to alter boundary layer flows and friction, with effects on turbulence generation, energy dissipation and flow reduction (Di Cicca et al., 2018; Salaudín et al., 2021). Likewise, the physical structure of mussel beds, polychaete tubes and barnacle hummocks can modify flow and particle supply rates (Carey, 1983; Bertness et al., 1998; Folkard and Gascoigne, 2009). Understanding the structure and arrangement of naturally occurring filter feeder assemblages may allow for the artificial *a priori* creation of hydrodynamically beneficial environments for these organisms, thereby facilitating their establishment.

Turbulent flow and near-bottom mixing are driven by the shape, size and density of roughness elements as well as their spatial arrangement. Effects of mussel bed rugosity on particle supply are thus primarily based on the protrusion of mussels above the patch (profile height variation) and the gaps between individuals (Fig. 3E) (Fréchette et al., 1989; Commito and Rusignuolo, 2000; Nielsen and Vismann, 2014). Highest profile complexity tends to be found at intermediate or high mussel densities ( $\geq 50$  %) with clustered, rather than regular, arrangements (Snover and Commito, 1998; Commito and Rusignuolo, 2000). Commito and Rusignuolo (2000) found the profile of *Mytilus* beds (50–85 % cover) to exhibit an intermediate fractal dimension of  $D = 1.12$ – $1.25$  (scale 1.4–200 mm), which creates roughness across spatial scales and may thus enhance edge effects on water flow. Consequently, fractal-based topography (Fig. 3F), underpinned by clustered arrangements, can drive turbulent mixing and increase particle transport to mussel beds (Commito and Rusignuolo, 2000; Lim et al., 2020).

Edge effects can also occur at patch boundaries, created by discontinuous spatial arrangements of mussel patches, interspersed with bare areas ('patch-gap structure' *sensu* Folkard and Gascoigne, 2009; Fig. 3G). Folkard and Gascoigne (2009) investigated hydrodynamics across two patch-gap scenarios, and found that small patches (40 cm) with small gaps (20 cm) increased turbulence across the full length of the mussel bed, with no clear hydrodynamic difference between patches and gaps. Above large mussel patches (80 cm) with large gaps (60 cm), however,

turbulence only increased above patches, but decreased in gaps, with less turbulent kinetic energy generated across the mussel bed overall. Folkard and Gascoigne (2009) further demonstrated that due to flow blockage at the upstream edge and 'overshooting' at the downstream edge, most turbulence was generated at patch edges, with associated benefits for mussel feeding and growth (Knights, 2012). Patch formation (clustering/hummocking, Fig. 3H) may also reduce dislodgement risk within the aggregate, enabling mussels to maintain filtration activity under high current velocities (Nielsen and Vismann, 2014). Collectively, protruding structural elements (e.g., with rugose or fractal geometry), arranged into intermediate-sized clusters separated by short gaps, may provide various functions for filter feeders, such as enhanced vertical turbulent mixing and particle supply, as well as dissipation of wave energy and resilience to dislodgement.

Mechanistically similar to mussels, the projecting tubes of reef-building polychaete worms can also affect hydrodynamic regimes (Bruschetti, 2019), for instance by altering boundary flow and eddy formation in the wake of tubes. Carey (1983) showed that arrays of polychaete tubes ( $\leq 5$  cm height, 0.5 cm width) locally reduce near-bottom current velocities by up to 80 %, while increasing turbulent flow. Consequently, polychaetes may increase their own particle capture efficiency, while also providing hard substratum habitat and shelter for other species as well as enhancing sediment deposition rates (Carey, 1983; Bruschetti, 2019). Mimicking these tube structures abiotically may functionally replicate their hydrodynamic effects.

## 2.3. Prey availability

Food availability for both herbivores and carnivores depends on prey diversity and abundance, as well as on the accessibility of these resources. Prey diversity is a function of niche diversity, and is thus closely linked to topographic elements that provide different resources to prey organisms (Hixon and Menge, 1991). Prey abundance, on the other hand, may depend on the presence and quantity of suitable niches, for instance as a result of settlement space availability (see section 5.1) and niche density within the habitat (Hixon and Beets, 1989). Abundance-distribution relationships are important drivers of prey availability, since habitats with a larger occupancy area are also more likely to support a higher density of prey organisms within locally occupied niches (Gaston et al., 2000; Borregaard and Rahbek, 2010). Thus, prey availability would be expected to increase disproportionately with available habitat area and the density of suitable niches (Fig. 3I). Lastly, topographic features can limit predator access to prey-occupied niches through the size differences common between predators and prey (Hixon and Beets, 1989; Strain et al., 2018a). Niches of spatial dimensions close to the prey size provide effective refugia against larger-bodied herbivores and carnivores alike (see section 4.3). Stable predator-prey relationships may thus be established through the creation of niches (e.g., cavities of different dimensions, Fig. 5K) at densities at which these topographic features exist in natural habitats, or alternatively, at ratios at which predator and prey populations naturally co-exist.

## 2.4. Detritus

Detritus, such as macroalgal and seagrass wrack subsidies, provides nutrients and shelter to various organisms (Heerhartz et al., 2014, 2016; Lepoint and Hyndes, 2022). However, availability of detrital plant material is typically reduced along armoured shorelines due to a narrowed intertidal zone and disrupted marine-terrestrial connectivity, leading to fewer wrack-associated invertebrates (Heerhartz et al., 2014, 2016). Strain et al. (2018b) investigated the entrapment and retention of wrack in artificial rockpools and found pools to contain 1.5–3.0 times more macroalgal biomass and cover than intertidal areas at the bottom of unmodified seawalls. Artificial rockpools also retained 1.1–3.8 times more wrack biomass per pool area than natural pools. Differences in

wrack retention were likely due to differences in pool dimensions, with artificial rockpools on average being deeper and larger (0.6 m depth, 20 m<sup>2</sup> area) than natural ones (0.2 m depth, 0.09 m<sup>2</sup> area) (Strain et al., 2018b). These findings indicate that rockpools can retain biomass and sediments alike (Firth et al., 2016a; Bone et al., 2022), and that modification of structural parameters such as pool depth and area can increase retention. As such, the surface area can be considered equivalent to the 'capture area', while depth may determine the retention of captured material over time. The rims of deeper pools may act as barrier structures to prevent wash-off of captured wrack, with steep or overhanging pool topography likely to be more effective than gently sloped surfaces. Greater water depth in deeper pools may also buffer wave action, thus reducing the hydrodynamic forces acting on material deposited at the pool bottom. Optimizing capture area, depth and interior shape may therefore improve the function of artificial rockpools in retaining detritus (Fig. 3J).

Organic matter accumulation may also be locally enhanced between, or downstream of, protruding, wave energy-dissipating structures, thus increasing sedimentation and benthic-pelagic coupling (Bruschetti, 2019). Such sedimentation is known from mussels (O'Donnell, 2008), oysters (Morris et al., 2019) and polychaetes (Bruschetti, 2019) as well as seagrass meadows, salt marshes and mangroves (Duarte et al., 2013). Aviz et al. (2019) for instance showed that polychaete reefs (*Sabellaria*) contained seven times higher organic matter content than adjacent beaches, while also supporting higher species richness and density.

### 3. Water

Immersion-emersion cycles set intertidal habitats apart from other marine environments. Topographic features can counteract the organismal stress caused by these cycles through water retention in rock pools and void spaces (Southward, 1958; Coombes et al., 2017). From an organismal perspective, water fulfils different ecological functions, such as maintaining hydration, acting as a suspension medium for free-swimming organisms, and buffering light, temperature and hydrodynamic forces. These functions can overlap, for instance in rockpools, where biodiversity patterns are positively correlated with both water availability *per se* (Firth et al., 2014), and pool metrics like area, volume and depth specifically (fish richness; Bugnot et al., 2018). Additional positive biodiversity effects, independent of physical pool features, may be created by algal cover, which can create refugia (for amphipods; Carvalho et al., 2021). Thus, rockpools may provide a variety of ecological functions, with habitat preferences determined by organism-specific needs.

#### 3.1. Hydration

Prevention of organismal desiccation during tidal emersion can occur through water retention. While rockpools (Fig. 4A+B) are obvious water-retaining hotspots of intertidal biodiversity (Chapman and Blockley, 2009; Firth et al., 2013; Bugnot et al., 2018), the roles of humidity in shaded crevices (Fig. 4C), or moisture retention in rugose microtopography and pore spaces (Fig. 4D) are less well understood.

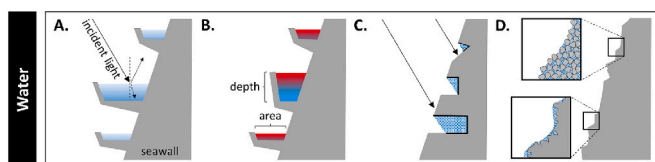


Fig. 4. Effects of artificial topography on water retention in the intertidal. (A, B) Water retention in rock pools with additional ecological effects on (A) light reflection and absorption, and (B) thermal buffering. (C) Humidity retention in shaded crevices of different dimensions. (D) Moisture retention in pore spaces and rugose microtopography.

Strain et al. (2020) reported that humidity in the crevices of artificial settlement tiles (5 cm deep, 1.5–5.0 cm wide) was 5–20 % higher than on flat tile surfaces, with humidity in crevices ranging between 70–90 %. Similarly, Jackson (2010) found higher humidities (60–85 %) in natural and artificial crevices than on emergent surfaces (55–65 %). Rugose and porous topographies can furthermore retain water within their near-surface structure. Coombes and Naylor (2012) for example, showed the porosity of limestone (16 %) to be higher than marine concrete (14 %) and granite (~1 %). Structures with elevated porosity took up and retained higher amounts of water, which was gradually lost during low tide, thereby providing surface moisture and creating evaporative cooling effects (Coombes and Naylor, 2012). Similar to pore spaces, rugose microtopography can also provide moisture during emersion, with Coombes et al. (2017) demonstrating that barnacle matrices (95 % cover) retained up to eight times more water than similarly exposed surfaces without barnacles. Thus, porous and rugose topography at small scales can represent water sources for near-surface biota, alongside larger water-retaining structures such as rockpools. Rugose topography at millimetre to centimetre scales may additionally encourage the settlement of canopy-forming macroalgae (Lubchenco, 1983; Bauer et al., in review), with Coombes et al. (2013) demonstrating that relative humidity was 15 % higher and 71 % less variable underneath dense macroalgal cover.

#### 3.2. Buffering of light, temperature and hydrodynamics

Attenuation and vertical stratification of abiotic environmental factors (e.g., light, temperature, hydrodynamic forces) can partition the rockpool water column into distinct niches, with deeper pools generally expected to buffer ecological stress better and create more stable microclimates (Moschella et al., 2005; Martins et al., 2007; Firth et al., 2014, but see Evans et al., 2016). Reduction of light exposure in rockpools results from light reflection at the water surface, and/or light absorption within the pool (Fig. 4A). Light reflection depends on the light incidence angle, with larger angles leading to increased reflection at the pool surface (e.g., Feynman et al., 2010a, Feynman et al., 2010b). Depending on the time of day, season and latitude, the position of the sun will thus influence light conditions in pools, with reflection rates being highest close to sunrise/sunset, near local winter solstice, and with increasing latitude. For a rockpool on a mid-European shore (48°N), reflection rates of unpolarized sunlight range between 2–100 % (summer solstice) and 16–100 % (winter solstice), fluctuating between daily minimum (solar noon) and maxima (sunrise/sunset) (Feynman et al., 2010a, Feynman et al., 2010b; Jin et al., 2003; Shaw and Vollmer, 2017). Light absorption and backscattering caused by water depth and suspended particles can further contribute to light attenuation. Betancor et al. (2015) found vertical light attenuation to range between 0.14–0.5/m, with up to 50 % of short-wavelength light absorbed or scattered within the upper 1 m of pools. Higher near-surface light attenuation may be found in more turbid systems (Brito et al., 2013). Thus, pool topography may indirectly modulate habitat suitability through the effects of water retention on abiotic resources (e.g., light) and stressors (e.g., temperature).

Rockpools can buffer temperature extremes and fluctuations, with different thermal conditions emerging between pools and surrounding rock (Table 1A), as well as between different pool depth layers (Table 1B). Pool warming and thermal stratification depend on characteristics such as shape (interior topography), dimensions (surface area, volume, depth) as well as their spatial relationships (area-to-volume, area-to-depth ratio) (Fig. 4B) (Daniel and Boyden, 1975). Daytime temperatures are generally lower in rockpools compared to emergent surfaces (Southward, 1958; Chee et al., 2020), while pool depth additionally contributes to temperature buffering, leading to a decrease by 0.3–2.3 °C per 10 cm water depth, relative to surface layers (Daniel and Boyden, 1975; Martins et al., 2007; Speaks et al., 2012) (see Table 1A+B). Temperature decrease with pool depth may however be non-linear, with Daniel and Boyden (1975) showing a stronger decrease

**Table 1**

Summary of observed reductions in temperature driven by water-retaining intertidal pools. Mean  $\Delta^{\circ}\text{C}$  = Difference between mean temperatures. Max.  $\Delta^{\circ}\text{C}$  = Difference between temperature maxima. Where authors measured temperatures over the course of several months, differences are given for the warmest month.

Topographic feature	Comparison	Mean $\Delta^{\circ}\text{C}$	Max. $\Delta^{\circ}\text{C}$	Location	Source
<b>A.</b>					
Natural rock pools (unknown depth)	Emergent rock	1.1	3.8	Plymouth, UK	<a href="#">Southward, 1958</a>
Drill-cored rockpools (5 cm depth)	Emergent rock	1.8	–	Penang, Malaysia	<a href="#">Chee et al., 2020</a>
Drill-cored rockpools (12 cm depth)	Emergent rock	2.0	–	Penang, Malaysia	<a href="#">Chee et al., 2020</a>
Natural rockpool (15 cm depth)	Emergent rock (horizontal)	~2.5	~4.0	Pacific Grove, US	<a href="#">Helmuth and Hofmann, 2001</a>
Water-retaining box (25 cm depth)	Mean annual air temperature	1.1	8.0	Townsville, Australia	<a href="#">Waltham and Sheaves, 2020</a>
<b>B.</b>					
Bottom of natural rockpool (65 cm depth)	Pool surface layer	–	7.5	Wales, UK	<a href="#">Daniel and Boyden, 1975</a>
Bottom of natural rockpool (22 cm depth)	Pool surface layer	–	5.0	Cornwall, UK	<a href="#">Martins et al., 2007</a>
Bottom of natural rockpool (31 cm depth)	Pool surface layer	–	1.0	Florida, US	<a href="#">Speaks et al., 2012</a>
Drill-cored rockpools (12 cm depth)	Drill-cored rockpools (5 cm)	–	0.8	Wales, UK	<a href="#">Evans, 2016 (PhD)</a>
Drill-cored rockpools (12 cm depth)	Drill-cored rockpools (5 cm)	0.2	–	Penang, Malaysia	<a href="#">Chee et al., 2020</a>

in the upper 20 cm (2.8  $^{\circ}\text{C}/10$  cm depth) than in the lower 45 cm (0.6  $^{\circ}\text{C}/10$  cm) of a 65 cm deep pool. Thermal stratification may furthermore differ with solar intensity (tropical vs temperate) and emersion time (low/high shore), with higher, longer solar exposure potentially creating a thicker surface thermal layer ([Speaks et al., 2012](#)). Water temperatures are weakly affected by pool surface area, but strongly affected by shading, with [Daniel and Boyden \(1975\)](#) showing that near-surface temperatures increased by up to 11  $^{\circ}\text{C}$  in sunlit pools, while shaded pools only experienced a  $\leq 1$   $^{\circ}\text{C}$  increase relative to sea temperature. Water temperature may also have secondary effects on other physio-chemical pool parameters, for instance oxygen solubility, which decreases with increasing temperature ([Daniel and Boyden, 1975](#)). Furthermore, pool surface area and depth may impact salinity changes, with shallow pools likely to experience higher water evaporation rates relative to their volume, and consequently stronger salinity increases ([Firth and Williams, 2009](#)). Shallow pools may furthermore be less capable of buffering (i.e., diluting) biota-driven depletion of oxygen (hypoxia) and changes in pH (uptake/production of  $\text{CO}_2$ ) ([Daniel and Boyden, 1975](#)).

Reductions in temperature exposure outside of rockpools can be driven by evaporative cooling. [Coombes and Naylor \(2012\)](#) showed that substrata with porous, rugose microtopography ([Fig. 4D](#)) absorbed more water and showed increased evaporative cooling capacity, with maximum surface temperatures on limestone (16 % porosity) up to 2.4  $^{\circ}\text{C}$  lower than on granite and concrete (1–14 % porosity). These thermal characteristics were attributed to structural differences (pore spaces, roughness) and material properties (discolouration, albedo effects) alike ([Coombes and Naylor, 2012](#)). In subsequent work, [Coombes et al. \(2017\)](#) showed that dense barnacle matrices (empty shells) reduced near-surface temperature maxima by up to 6  $^{\circ}\text{C}$ , driven by water retention and evaporative cooling effects of barnacle topography.

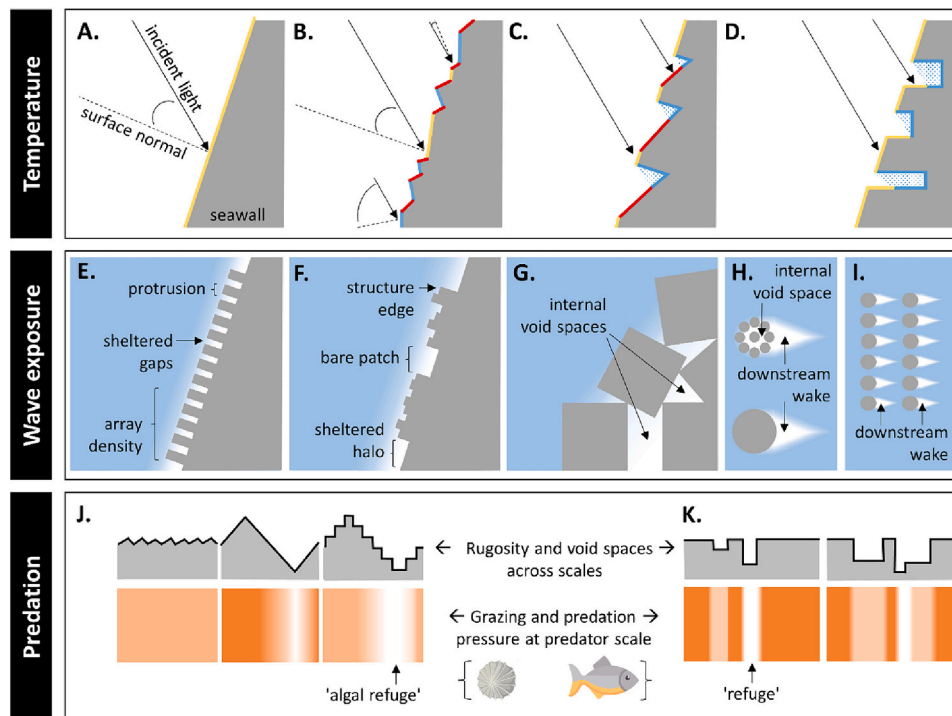
Water bodies in pore spaces, crevices or rockpools additionally buffer hydrodynamic forces due to the viscosity of water and its relative incompressibility. [O'Donnell \(2008\)](#) suggested that topographic features can both retain water and decrease water flowoff between breaking waves, thus creating fluid 'cushions' which can buffer wave-imposed shock pressures. Topography may therefore not only dissipate wave energy through direct interactions between structural elements and hydrodynamics, but the resulting low-energy fluid dynamics may also protect near-surface organisms from high-energy wave exposure.

## 4. Shelter from abiotic stressors and biotic pressures

### 4.1. Temperature

Temperature exposure of intertidal substrata is closely associated with sunlight exposure ([Zhao et al., 2019](#); [Amstutz et al., 2021](#)). Thus, surface temperatures can be affected by substratum orientation (incline and aspect), relative to incident solar irradiation ([Fig. 5A](#)). [Zhao et al. \(2019\)](#) found that temperature maxima decreased with increasing seawall steepness (30 $^{\circ}$  to 90 $^{\circ}$ ) in Singapore. Surface temperatures reached up to 43  $^{\circ}\text{C}$  in a seawall sloped 30 $^{\circ}$ , but only up to 34  $^{\circ}\text{C}$  on a slope of 90 $^{\circ}$ . Slope effects were maximized in the high shore, with a temperature reduction of 9  $^{\circ}\text{C}$  ([Zhao et al., 2019](#)). Thus, high-shore organisms in particular may benefit from alterations in slope angle. However, these findings need to be considered in the context of the near-equator system that [Zhao et al. \(2019\)](#) worked in, with the solar zenith maximizing light exposure of horizontal surfaces throughout the year. At higher latitudes, the light incidence angle is generally greater and more variable. Consequently, thermal mitigation by steep seawall slopes may be reduced and/or fluctuate seasonally. Surface aspect instead gains ecological importance at higher latitudes ([Firth et al., 2016b](#); [Amstutz et al., 2021, 2023](#)), since pole-facing surfaces are exposed to lower incident radiation year-round. As such, temperature buffering due to surface orientation (cooler, pole-facing vs warmer, equator-facing) can exceed seasonal variation, latitude (37–44 $^{\circ}\text{N}$ ) or shore height ([Seabra et al., 2011](#)), while also underpinning thermal refuge availability and organismal heat stress irrespective of latitude (37–55 $^{\circ}\text{N}$ ) ([Lima et al., 2016](#)).

Altered topography may furthermore cause surface temperatures on artificial structures to peak at higher temperatures and later during the day ([Aguilera et al., 2019](#)), with [Cryan et al. \(2021\)](#) showing that west- and south-facing bulkheads exceeded thermal thresholds of  $\geq 28$   $^{\circ}\text{C}$  most frequently. Elevated seawall temperatures in the tropics could be reduced through the integration of step-like structures with 90 $^{\circ}$  verticals ([Zhao et al., 2019](#)) to avoid thermally stressful horizontals ([Helmuth and Hofmann, 2001](#); [Aguilera et al., 2019](#)). In temperate latitudes, shaded microhabitats may be created through pole-facing topography. Alternatively, the integration of small-scale surfaces sloped at different angles (i.e., rugosity) could maximize surface temperature variability in response to diurnal and seasonal changes in light incidence angles ([Fig. 5B](#)). Topographic alterations should be considered relative to the size parameters and material properties of deployed units, since extended surface exposure to high solar irradiation may homogenize microhabitat temperatures due to heat transfer within the substratum.



**Fig. 5.** Effects of topography on shelter from abiotic stressors and biotic pressures. Modulation of seawall surface temperatures (red > yellow > blue) through (A) seawall slope, (B) seawall rugosity, (C) shaded overhangs, and (D) shaded crevices. Formation of hydrodynamically sheltered areas (E) between protruding structural elements, (F) at the structure edges, (G) in void spaces of rock armour, (H) in the downstream wake of, and between, porous cylindrical protrusions (top view, incoming waves from the left, adapted from [Quinones et al., 2022](#)), and (I) in the downstream wake of pole structures (top view, incoming wave from the left, adapted from [Mancheño et al., 2021](#)). Refuge (colour intensity = predation pressure) from (J) grazing, and (K) fish predation through rugosity and void spaces at different spatial scales. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

As such, the scale and complexity of topographic features is crucial, because substratum type, orientation and thickness (scale) can determine how quickly thermal energy is transferred between substratum surfaces.

Heat and desiccation stress can also be mitigated through the creation of shaded overhangs (Fig. 5C) ([Waltham and Sheaves, 2018](#)) and cavities (Fig. 5D) ([Chapman and Blockley, 2009](#); [Jackson, 2010](#)). On a seawall in Hong Kong, [Bradford et al. \(2020\)](#) demonstrated that grooved concrete tiles of 2.5 and 5 cm depth (1.5–5.0 cm width) reduced average crevice temperatures by 0.4 °C and 2 °C, respectively. These effects were limited however to equator-facing surfaces, and did not occur on poleward-facing seawalls ([Bradford et al., 2020](#)), highlighting the importance of seawall aspect. Using the same grooved tiles (5 cm deep, 1.5–5.0 cm wide), [Strain et al. \(2020\)](#) demonstrated that crevices reduced maximum summer temperatures by up to 6.1 °C, while also significantly decreasing temperature fluctuations. Concrete panels with differently sized holes and crevices (<2.5 cm deep) were additionally shown to reduce average temperature by 0.5 °C, with maximum temperatures reduced by up to 10 °C in ‘swim-through’ structures of ≤10 cm depth ([Bishop et al., 2022](#)). Temperature buffering of similar magnitude is also reported from natural structures, such as oyster reefs ([McAfee et al., 2018](#)), with benefits for associated invertebrate communities ([McAfee et al., 2022](#)). Temperatures are generally reduced with increasing crevice depth, with some indications that this relationship may not be strictly linear ([Bradford et al., 2020](#); [Bishop et al., 2022](#)), and that deeper crevices may be disproportionately more efficient at reducing temperatures. It remains unclear what the effect of crevice depth-to-width ratio is on temperature buffering. Narrower, deeper crevices would be expected to have a stronger effect on maintaining low microhabitat temperatures and fluctuations, since a small cavity opening area and large cavity depth (volume) would likely reduce light exposure and air exchange. Conversely, in colder environments, crevices

may retain warmth to buffer cold stress during the winter ([Ng et al., 2017](#)) or at night ([Jackson, 2010](#)), with potential thermal amelioration of frost ([Crisp, 1964](#)) and physical protection of organisms from ice scour ([Scrosati and Heaven, 2006](#)).

#### 4.2. Wave exposure

Hydrodynamic forces have a major structuring role in intertidal communities, limiting macroalgal distribution through wave-induced dislodgement ([Jonsson et al., 2006](#)) while also underpinning negative sedimentation and canopy-sweeping effects on limpets ([Airoldi and Hawkins, 2007](#)) or barnacles ([Jenkins et al., 1999b](#)). Hydrodynamic forces at small scales can be dissipated by roughness elements (Fig. 5E). [Salaudín et al. \(2021\)](#) showed that artificial cylindrical protrusions (1–5 cm length) at different densities (25–98 elements/100 cm<sup>2</sup>) reduced overtopping rates under impulsive wave conditions. This effect was positively related to protrusion length and arrangement density, with a ≥ 90 % reduction in overtopping observed for the longest and densest configurations compared to a plain seawall. [Salaudín et al. \(2021\)](#) also demonstrated that protrusions were better at dissipating wave energy than depressions (0.5 cm depth, 98 holes/100 cm<sup>2</sup>), although the different depth (height) of these structural features makes conclusive comparison difficult. Protruding structural elements that act as barriers also create hydrodynamic shelter nearby, which may benefit organisms living in gaps within the structure or close to the structure edges. [Carrington et al. \(2008\)](#) showed that mussel monolayers (5 cm thickness) reduced free-stream water velocities (10–80 cm/s) by 90–99.9 % within the reef, resulting in flow speeds of <7 cm/s. Reductive effects on flow speeds extended for 5–10 cm above the reef, where flow rates converged with free-stream velocities ([Carrington et al., 2008](#)), indicating that energy dissipation by rough surface topography created a sheltered ‘halo’ of reduced water flow in the



immediate proximity of the structure.

O'Donnell (2008) provided evidence for the spatial extent of this hydrodynamically sheltered area. Using an artificial mussel bed (5 cm thickness) with a bare central patch of different radii (1–30 cm), O'Donnell (2008) demonstrated that the reef structure reduced wave forces on small objects (~1 cm) within the bare patch. Maximum reduction was observed at small patch radii of 1 cm (72–93 % reduction) and 5 cm (30–62 %), but no notable reduction was found at >15 cm radii. Collectively, these findings indicate that rugosity at the scale of mussel reefs diminishes wave exposure, both within the structure gaps and at its outer edges (Fig. 5F), and may thus provide shelter and reduce dislodgment risk. O'Donnell (2008) further suggested that this sheltering effect could be accomplished by any abiotic structure of similar topography to a mussel reef. At different scales, however, hydrodynamic effects of rugosity may differ. In contrast to dense mussel reefs, centimetre-scale rock crevices (5–25 cm wide, 2–15 cm deep) did not reduce wave forces acting on objects of 1 cm size. Rather, wave forces in a large crevice (~25 cm wide, 15 cm deep) were up to twice as high as on neighbouring flat rock (O'Donnell and Denny, 2008). Amplified hydrodynamic forces in crevices may be caused by wave splash (O'Donnell and Denny, 2008) or by fluid compression into narrow gaps, which may lead to flow acceleration (following Bernoulli's principle of fluid dynamics). For an organism, however, the function of a crevice may not solely lie in its hydrodynamic effects. Rather, a structure that closely surrounds the organism can also absorb wave energy, which is transferred directly from the organism (e.g., snail shell; Fig.S1 A + B) onto the surrounding substratum without dislodging the individual (O'Donnell and Denny, 2008).

At the centimetre to metre scale, the porosity of structural elements can also impact hydrodynamic forces and create wave-sheltered environments (Fig. 5G-I). Quinones et al. (2022) simulated the effects of centimetre-scale, porous cylinder arrays ('mangrove roots') on wave velocities and found that 47 % porosity (= void space between cylinders) was similarly efficient at blocking waves and dissipating hydrodynamic energy than a solid, non-porous structure (Fig. 5H). Similarly, Mancheño et al. (2021) studied wave transmission and blockage by metre-scale pole structures ('bamboo poles') in shallow coastal environments and found that pole arrangement in rows with small lateral spacing (high wave blockage) and long streamwise spacing (low sheltering in downstream wake) maximized wave dissipation per pole element (Fig. 5I). Porous structures can create low-energy hydrodynamic environments in their downstream wake (Mancheño et al., 2021; Quinones et al., 2022) as well as in the structure's interior void space (Sherrard et al., 2016; Quinones et al., 2022). Thus, porosity may create hydrodynamically sheltered niches, with species monitoring on the internal surfaces of a porous, wave-exposed groyne for instance showing that wave forces were sufficiently reduced to harbour a biodiverse community (Sherrard et al., 2016).

#### 4.3. Predation pressure

Surface depressions at different spatial scales (i.e., rugosity, void spaces) can reduce grazing (Fig. 5J) and predation pressures (Fig. 5K) due to predator-prey size differences. van Tاملen et al., (1997) found that small-scale crevices ( $\leq 1$  mm width,  $\leq 1.5$  mm depth) enhanced fucoid germling recruitment, with 10 % of germlings surviving in grooves after one year, but none outside of them. Enhanced macroalgal survival in abiotically or biotically formed 'algal refuges' (e.g., rock crevices, mussel beds, tubeworm reefs) may result from protection from desiccation, whiplash and herbivory (Lubchenco, 1983; van Tاملen and Stekoll, 1996; Firth et al., 2021). As such, species-specific snail grazing rates can be affected by substratum topography and spatial heterogeneity (Griffin et al., 2009). Foraging of patellid limpets for instance is highest on flat substrata (Griffin et al., 2009), and patchy substrata with low rugosity (Hawkins and Hartnoll, 1982), but reduced on high rugosity at both millimetre (Hawkins and Hartnoll, 1982) and

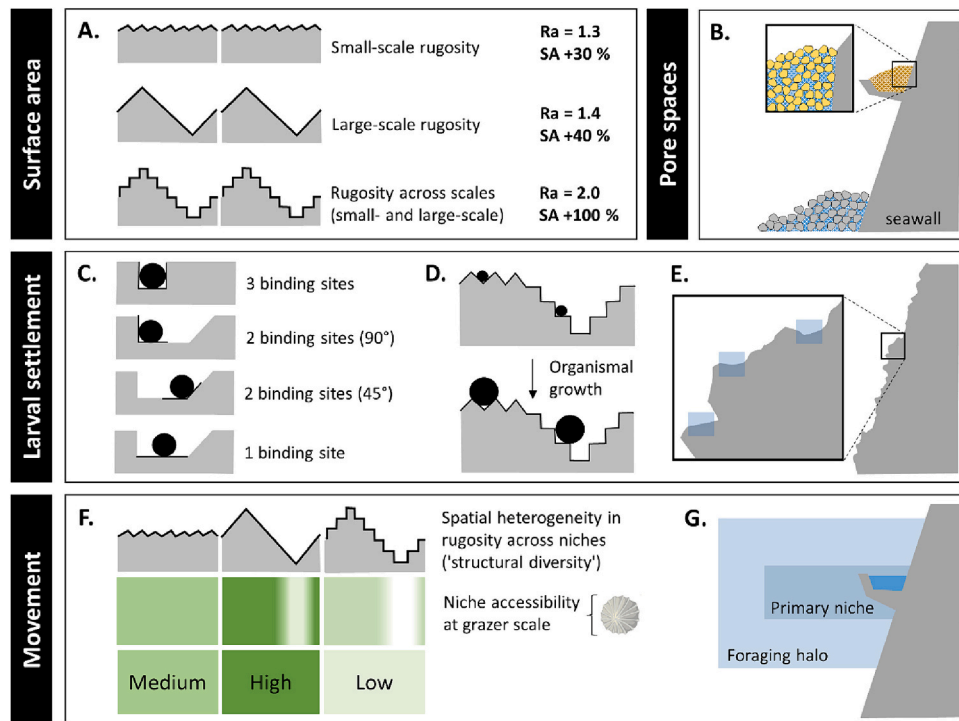
centimetre scales (Griffin et al., 2009). Inaccessibility of small-scale crevices to large-scale grazers may thus protect larvae and germlings from grazing pressure (Fig.S1 C–F), until organisms reach sizes at which they can escape grazing mortality (e.g., >3 cm for fucoids; Lubchenco, 1983). Conversely, rockpools, crevices or bio-eroded pits of sufficiently large-scale dimensions may shelter benthic grazers (e.g., periwinkles, limpets, sea urchins), consequently imposing enhanced grazing pressure on algae near the refugia edges (Fig.S2 A-B) and leading to the formation of grazing halos (Fairweather, 1988; Skov et al., 2010, 2011). The ecological impact of refugia topography is thus dependent on the organism(s) it shelters, which, in turn, can depend on the refuge dimensions (scale).

Spatial dimensions of cavities (e.g., opening area, width, depth, volume) can determine whether a void space can serve as shelter for prey. Cavities that provide ideal shelter for an organism should generally closely match the prey's body size (Strain et al., 2018a). Martins et al. (2010) found that limpet abundance on seawalls increased with artificial pit size (12 and 24 mm diameter) and density, whereby smaller limpets ( $\leq 10$  mm) occupied all pit sizes, while larger limpets ( $\geq 11$  mm) were limited to large pits. Positive effects of pits on limpets were attributed to refuge availability from abiotic (heat, desiccation) and biotic stressors (crab and snail predation) alike (Martins et al., 2010). Likewise, Strain et al. (2018b) found that tiles with crevices of 2.5 and 5.0 cm depth (width 1.5–5.0 cm) reduced fish predation on oysters under elevated predation pressure, with oyster mortality on grooved tiles only half as high (~30 %) as on flat tiles (65 %). Oyster mortality furthermore occurred more frequently on tile ridges than in crevices. Similarly, Hixon and Beets (1989) showed that size and abundance of cavities on artificial reefs correlated with the abundance of small prey fish and larger piscivores. As such, the number of large fish directly increased with the number of void spaces (0, 12, 24) available at their appropriate size (12 × 14 cm). Likewise, small prey fish preferred smaller cavities (4 × 6 cm) and prey abundance declined if only large, predator-sized refugia (12 × 14 cm) were available (Hixon and Beets, 1989). Prey-sized cavities that limit access by larger predators may be particularly important under high predation pressure, while benefits of refugia may disappear where predators are less abundant (Hixon and Beets, 1989; Strain et al., 2018b). Providing a range of cavity sizes close to organismal body sizes ('refuge diversity') has been suggested to mitigate predation pressure, increase species diversity and abundance, and stabilize predator-prey relationships (Hixon and Beets, 1989; Sherman et al., 2002; Komyakova et al., 2019).

## 5. Habitat space

### 5.1. Surface area and pore spaces

Species diversity and abundance generally increase with available substratum area (e.g., Connor and McCoy, 1979). While habitat extent (i.e., geometric surface area) is limited by geographical or ecological boundaries, the available settlement area can be impacted by topography. Topographic surface area is often positively correlated with topographic complexity (e.g., rugosity), which increases the substratum area by creating surface protrusions and depressions (Fig. 6A). While attempts have been made to disentangle biodiversity effects driven by topographic complexity from those of (standardized) surface area (Løke and Todd, 2016; Løke et al., 2019), the combined ecological benefits of surface area and topography may be desirable in practice, as they both promote species richness. Bauer et al. (in review) showed that the rugosity of natural rocky shore substrata increased the geometric surface area within 900 cm<sup>2</sup> quadrats by 28 %. In the same study, artificial concrete substrata increased surface area by only 11 %. At higher spatial scales, rugosity effects on surface area can be expected to exceed these estimates at the decimetre scale (Bauer et al., in review) due to additional topographic complexity, for instance at metre scale. Positive biodiversity effects of surface area are likely to be reduced on artificial



**Fig. 6.** Effects of natural and artificial topography on habitat availability, settlement, and movement. (A) Increase in topographic surface area (SA) relative to a flat surface, due to cumulative effects of substratum roughness (Ra) across spatial scales. (B) Porosity (void spaces) within loose substrata (sediment, gravel). (C) Local binding geometry of propagules (black). (D) Changes in microhabitat conditions (e.g., shelter) with organismal growth. (E) Horizontal microtopography resulting from rugosity within an overall vertically inclined surface. (F) Effect of spatial heterogeneity in rugosity on niche accessibility to a grazer (colour intensity = accessibility). (G) Habitat suitability at two patch scales, with the smooth topography of the wider substratum potentially impairing grazer movement and foraging.

**Table 2**

Summary of propagule settlement and survival observed on different natural or artificial surface topographies. Roughness metrics: Ra = Arithmetical mean roughness. Ry = Maximum peak (used for all authors who reported roughness element size, particle granularity, or crevice depth). Rz = Ten-point mean roughness.

Organism	Roughness with max. recruitment	Range tested	Duration of experiment	Location	Source
<b>A. Algae</b>					
<i>Chondrus crispus</i>	Ry = 1.0–2.0 mm	0.0–2.0 mm	≤15 months	Rhode Island, US	Harlin and Lindbergh, 1977
<i>Corallina officinalis</i>	Ry = 0.1–0.5 mm	0.0–2.0 mm	≤15 months	Rhode Island, US	Harlin and Lindbergh, 1977
<i>Polysiphonia harveyi</i>	Ry = 1.0–2.0 mm	0.0–2.0 mm	≤15 months	Rhode Island, US	Harlin and Lindbergh, 1977
<i>Ulva linza</i> spores	Pit Ø = 5–8 µm	1–10 µm	<1 day	Wales, GB	Xiao et al., 2013
<i>Ulva linza</i> spores	Rz = 25 µm	1–100 µm	<1 day	Plymouth, GB	Granhag et al., 2004
<i>Ulva lactuca</i>	Ry = 1.0–2.0 mm	0.0–2.0 mm	≤15 months	Rhode Island, US	Harlin and Lindbergh, 1977
<b>B. Ascidians</b>					
<i>Botrylloides violaceus</i>	Ra = 7.3–16.1	0.3–16.1	≤10 weeks	New England region, US	Chase et al., 2016
<i>Ciona intestinalis</i>	Ra = 16.1	0.3–16.1	≤10 weeks	New England region, US	Chase et al., 2016
<b>C. Barnacles</b>					
<i>Balanus glandula</i>	Ry = 0.3 mm	0.0–0.3 mm	≤1 month	Oregon, US	Menge et al., 2010
<i>Balanus improvisus</i>	Ry = 1.0 mm	0.0–5.0 mm	1 month	Kiel, DE	Köhler et al., 1999
<i>Balanus improvisus</i>	Ry = 0 µm	0, 64, 352 µm	2 months	Tjärnö, SE	Berntsson et al., 2004
<i>Balanus</i> sp.	Ry = 2.0–5.0 mm	0.6–8.8 mm	2 days	Beaufort, US	Walters and Wethey, 1996
<i>Chthamalus dalli</i>	Ry = 0.3 mm	0.0–0.3 mm	≤1 month	Oregon, US	Menge et al., 2010
<i>Chthamalus</i> spp.	Ra = 1.52	1.09–1.92	4 months	Cornwall, GB	Coombes et al., 2015
<i>Semibalanus balanoides</i>	Ry = 0.1–0.5 mm	0.0–4.0 mm	1 month	Millport, GB	Hills and Thomason, 1998
<i>Semibalanus balanoides</i>	Ry = 5 mm	0–15 mm	≤1.5 months	Capucins/St. Andrews, CA	Chabot and Bourget, 1988
<b>D. Bivalves</b>					
<i>Hiattella arctica</i>	Ry = 1–10 mm	0–100 mm	≤3.5 months	St. Andrews, CA	Bourget et al., 1994
<i>Mytilus edulis</i>	Ry = 1–10 mm	0–100 mm	≤3.5 months	St. Andrews, CA	Bourget et al., 1994
<i>Mytilus edulis</i>	Ry = 5.0 mm	0.0–5.0 mm	1 month	Kiel, DE	Köhler et al., 1999
<b>E. Bryozoans and hydrozoans</b>					
<i>Bugula neritina</i>	Ry = 2.0–5.0 mm	0.6–8.8 mm	2 days	Beaufort, US	Walters and Wethey, 1996
Hydrozoa spp.	Ry = 5.0 mm	0.0–5.0 mm	1 month	Kiel, DE	Köhler et al., 1999
<i>Schizoporella errata</i>	Ry = 2.0–5.0 mm	0.6–8.8 mm	2 days	Beaufort, US	Walters and Wethey, 1996
<i>Tubularia crocea</i>	Ry = 2.0–5.0 mm	0.6–8.8 mm	2 days	Beaufort, US	Walters and Wethey, 1996

structures, with Lawrence et al. (2021) demonstrating that seawalls lacked surface roughness across twelve scales of resolution (1 mm - 10 m). Surface area can be increased through the installation of topographically complex settlement tiles, with panels used by Bishop et al. (2022) providing 56–114 % more substratum area than their planar surface, while other grooved tiles (Vozzo et al., 2021) increased surface area by 44 % (2.5 cm grooves) and 118 % (5 cm grooves). Topographic surface area is expected to change with colonization, thus artificial substrata should be designed in such a way that their area is not disproportionately lost to settlement, as may happen if small crevices are overgrown and internal surfaces lost.

An enhanced substratum area is also found within sediments, gravel or pebbles (Fig. 6B), although the deposition and retention of these loose substrata may fluctuate in time and space (Firth et al., 2016a; Evans, 2016; Chee et al., 2020). Habitat availability within these substrata is furthermore determined by material geometry (e.g., angularity) and matrix formation (e.g., interlocking) (Foss et al., 2023), due to the dependence of organisms on pore space characteristics (e.g., porosity, granularity, void space volume). Thus, structural scales are closely linked to organismal scales (e.g., mobile infauna size). Bone et al. (2022) quantified benthic species in sediment-retaining pools (grain size  $\leq 63 \mu\text{m}$ ) and found total biodiversity to exceed that of local mudflats, with high abundance of mobile species at the millimetre to centimetre scale (annelids, arthropods, snails). Thus, while firm substratum surfaces may benefit sessile species, the pore spaces between loose substrata may favour mobile epifauna or infauna.

## 5.2. Propagule settlement

Fine-scale rugosity ( $\mu\text{m}$ - to mm-scale) can increase the settlement rates of diverse marine taxa such as green algae, red algae, ascidians, barnacles, bivalves, bryozoans and hydrozoans (Harlin and Lindbergh, 1977; Walters and Wethey, 1996; Köhler et al., 1999; Chase et al., 2016). However, ideal roughness conditions for settlement have typically been found to be species-specific (Table 2). Spore settlement and early survival of the green alga *Ulva* is known to be highest in  $\mu\text{m}$ -scale crevices that closely fit the spore diameter (4–5  $\mu\text{m}$ ) (Granhag et al., 2004; Xiao et al., 2013). Similar patterns were exhibited by barnacle cyprids, who settled predominantly on surface roughness that matched their own body size of 0.1–0.5 mm (Menge et al., 2010; Coombes et al., 2015). Larval adhesion often occurs at surface transitions (e.g., corners, edges), since these sites increase the number of available attachment points (Fig. 6C), thus improving local binding geometry (Granhag et al., 2004; Xiao et al., 2013).

Substratum preferences may shift to rugosities at coarser scales as organisms grow and mature, with Harlin and Lindbergh (1977) demonstrating that *Ulva* abundance was three times higher on 1.0–2.0 mm roughness than on 0.1–0.5 mm after  $\leq 15$  months of growth. Likewise, *Mytilus* mussels were observed to migrate from 1 mm to 10 mm deep crevices as they outgrew initial settlement sites (Bourget et al., 1994). Thus, topography at different spatial scales can provide ‘stepping-stones’ for changing ecological needs at different life stages (Fig. 6D).

Settlement site selection can be active or passive. Passive settlement of red algal spores (*Halosaccion*) for instance predominantly occurred on the edges and tips of rugose surface protrusions, likely due to hydrodynamics (Johnson, 1994), while more selective surface exploration and attachment has been reported for other algal spores and faunal larvae (Walters and Wethey, 1996; Xiao et al., 2013; Chase et al., 2016). Active topography selection can be driven by organismal characteristics such as growth form, with Walters and Wethey (1996) demonstrating that solitary or branching organisms often settled at the sheltered base of protruding structures, while encrusting or mat-forming species were generally less vulnerable, and thus more flexible in their site selection. As such, sheltered crevices are commonly considered to create favourable microenvironments for larvae, for instance due to altered

hydrodynamics (Köhler et al., 1999), refuge from desiccation and reduced predator access (Walters and Wethey, 1996; van Tamelen et al., 1997). Consequently, different topographic preferences may reflect species-specific settlement behaviours and ecological needs. Scale-dependent rugosity, which increased both the habitat surface area and the number of surface edges within that habitat (i.e., ridges and crevices), may serve to facilitate organism-specific settlement dynamics, since rugosity at different spatial scales can drive the abundance and topographic diversity of settlement sites (Fig. 6A,C).

Settlement dynamics may furthermore be impacted by substratum slope. *Acropora* coral larvae for instance settled on horizontal surfaces compared to verticals at a ratio of up to 11:1 (Harrington et al., 2004; Yusuf et al., 2019), while recruitment of *Aplidium* ascidians occurred on verticals over horizontals at a ratio of 2:1 (Gotelli, 1987). Topographic settlement preference may prevail even at millimetre scale, with Bauer et al. (in review) showing that mature fucoid macroalgae were often associated with horizontal small-scale surfaces, even within overall vertically inclined large-scale surfaces (Fig. 6E). This topographic effect was attributed to fucoid spore accumulation on horizontals (fluid dynamics) and beneficial abiotic conditions (water retention) (Bauer et al., in review). Varying surface orientations can thus create ecologically different settlement conditions, for instance regarding light and hydrodynamic exposure, particle supply, or water retention.

## 5.3. Movement

Topography and slope can alter movement and foraging behaviours of benthic species. Hawkins and Hartnoll (1982) showed that millimetre-scale topography created by dense barnacle matrices altered limpet foraging activity on vertical surfaces (Fig. 6F). Reduced limpet grazing and predominant tide-out activity were suggested to result from the adverse effects of roughness on movement and attachment (Hawkins and Hartnoll, 1982), with limpets on dense barnacle cover shown to graze for shorter time periods, with a lower number of grazing excursions, as well as shorter grazing distances (Santini et al., 2019). This suggests that limpets minimized their grazing time on rugose surfaces in the face of dislodgement, desiccation and predation risk, but likewise profited from higher microalgal availability in these areas (Santini et al., 2019). Limpet movements have also been shown to increase in tortuosity with increasing surface complexity (Erlandsson et al., 1999; Clubley et al., in prep), indicating that limpets avoid grazing over topographic irregularities. Limpets are generally considered to attach and graze most effectively on flat or low-rugosity surfaces, thus making artificial structures such as seawalls particularly vulnerable to the establishment of ‘limpet barrens’ (*sensu* Firth et al., 2023). These grazing effects may, in turn, be enhanced by low habitat suitability for fucoid macroalgae on smooth verticals (Bauer et al., in review) and potentially reduced bird predation on limpets (e.g., oystercatchers, seagulls). Other snails (genus *Steromphala*) can exhibit high grazing rates on surfaces with centimetre-scale rugosity, suggesting that roughness and spatial heterogeneity can drive grazer-specific movement and habitat use (Griffin et al., 2009). Grazer movements are furthermore impacted by refugia availability and the spatial arrangement of refugia sites, with Cacabelos et al. (2018) showing that gastropod dispersal distances were longer on unmodified seawalls with few refugia, while high refugia density was correlated with shorter movement distances. As such, grazer movements and habitat use may reflect an interplay between organismal morphology and scale-dependent habitat topography and patchiness, with limpet movements for instance constrained by mucous trail deposition (Santini et al., 2019), foot area, and shell shape (Griffin et al., 2009).

Surface orientation at metre scale can furthermore alter movement patterns and connectivity. Chapman and Blockley (2009) observed that starfish and sea urchins did not colonize artificial rockpools within a vertical seawall. They attributed this to the inability of these species to access the pools via the surrounding smooth seawall, in addition to an

elevated dislodgment risk during foraging (Chapman and Blockley, 2009; Chapman and Underwood, 2011). Similar constraints and behavioural effects may be at play in limpet grazing, with limpets on horizontal surfaces predominantly foraging while tidally immersed, whereas on verticals, they exhibit tide-out foraging (Hawkins and Hartnoll, 1982; Santini et al., 2019). This behaviour has been attributed to differences in desiccation, dislodgement and predation risk, which can be underpinned by topographic characteristics such as rugosity and slope-dependent predator access (Hawkins and Hartnoll, 1982; Santini et al., 2019). Thus, when designing topographically complex artificial habitats, it is crucial to ensure that the ecological needs of organisms are met within the niche area accessible to them. If movement and foraging are altered or constrained by the wider arrangement of structural features, habitat suitability and connectivity might be negatively impacted (Fig. 6G).

## 6. Ecological implications of habitat heterogeneity and spatial scale

Habitat heterogeneity (i.e., patch diversity) and spatial arrangement of habitat patches can impact ecological communities, for instance by altering species richness (Loke et al., 2019) and movement patterns (Cacabelos et al., 2018), as well as by enabling stable co-existence of predators and prey (Hixon and Beets, 1989) and preventing resource competition between organisms with similar resource needs (Griffin et al., 2009). Loke et al. (2019) showed that habitat area and spatial arrangement of topographic tiles (habitat patches) affected species assemblages, with richness peaking at the highest habitat area, but at intermediate levels of habitat fragmentation (i.e., patch connectivity). Spatially heterogeneous habitats can furthermore modulate predator-prey relationships and interspecific resource competition through scale-dependent niche partitioning. Hixon and Beets (1989) for example, showed that the abundance and diversity (size range) of void spaces in artificial reefs determined accessibility to small prey fish and large piscivores, with positive effects on fish abundance and community richness. Species-specific gastropod grazing has also been demonstrated to be affected by spatial heterogeneity, with efficient foraging of patellid limpets and trochid snails spatially partitioned between flat and rough topography at the centimetre scale, respectively (Griffin et al., 2009). Thus, within-patch topographic complexity and among-patch habitat heterogeneity is likely to impact assemblage structure, with O'Shaughnessy et al. (2023) showing that topographically complex natural habitats had higher alpha-diversity within sites (~5 m scale) and among sites (habitat scale) than artificial habitats, while artificial habitats however had higher beta-diversity among sites, due to higher topographic heterogeneity among artificial structures.

While natural habitats are typically composed of a spatially heterogeneous mosaic of microhabitat patches, topographically and/or functionally similar patches (e.g., plateaus, crevices, rockpools) can often be found repeatedly throughout these mosaics. Habitat heterogeneity at the patch scale may thus be counterbalanced with a level of habitat homogeneity. While spatial heterogeneity (i.e., the difference in topographic complexity between patches) can impact habitat partitioning and niche formation, overly high heterogeneity ('patchiness') may at the extreme lead to habitat fragmentation, with negative effects on overall community richness (Loke et al., 2019). The repetition of functionally similar topography throughout a habitat may thus facilitate connectivity among (micro-)habitat patches, and associated species distribution and abundance (Borregaard and Rahbek, 2010). Propagules of habitat-forming furoid macroalgae, for instance, have been shown to disperse only over small distances (~50 cm; van Tamen et al., 1997), suggesting that their recruitment may be diminished if the surrounding substratum does not provide suitable topography for settlement (e.g., horizontal surfaces; Bauer et al., in review). Spatially homogeneous topography at metre-scale may furthermore support organismal movement patterns, with patellid limpets (grazing halos ~1 m diameter, Hartnoll and Wright,

1977) known to be effective grazers on patches of low-complexity topography (Griffin et al., 2009). Thus, when eco-engineering artificial habitats, it is important that the substratum topography and its spatial heterogeneity meet organismal habitat requirements at adequate patch scales.

Understanding the scales at which habitats are topographically complex (e.g., rugosity: Lawrence et al., 2021) and spatially heterogeneous (e.g., patch arrangement; Loke et al., 2019), as well as the ecological processes associated, can inform the design and scale at which artificial topography is most effectively implemented. Spatial scale matters, both in topographic complexity and in spatial heterogeneity, because it can for instance determine whether a topographic refugia matches the organismal size (Hixon and Beets, 1989), whether a microhabitat can accommodate organismal growth across different life stages (Bourget et al., 1994), and whether foraging and dispersal movements into the surrounding habitat can occur (Chapman and Blockley, 2009). Likewise, topographic features of different sizes (scales) interact differently with environmental factors such as hydrodynamics, thus impacting species communities through effects on abiotic micro-climate (Guichard et al., 2001; O'Donnell and Denny, 2008). Guichard et al. (2001) showed artificial reefs (cylinders) of different sizes to generate scale-dependent hydrodynamic patterns and turbulence, with associated biological effects on mussel biomass. Similarly, scale-dependent rugosity may either protect algae from large-bodied grazers ('algal refuge', e.g., van Tamen and Stekoll, 1996, van Tamen et al., 1997) or, conversely, may encourage localised grazing around crevices in which smaller grazers are taking shelter ('grazing halo', e.g., Johnson et al., 2008; Skov et al., 2010, 2011). Practical implementation of scale-dependent topography should furthermore be considered relative to biological processes and material properties, since narrow crevices may for instance be overgrown with ongoing colonization, while thin substrata can be prone to fast heat transfer under sun exposure.

## 7. Conclusions

Interactions between intertidal substratum topography and fluctuating environmental factors underpin the formation of distinct micro-environments. Microhabitats can differ from their surrounding habitat abiotically and biotically, and thus alter resource provisioning (e.g., food, water, shelter, habitat space) across organismal sizes and trophic levels. As such, topographic features can fulfil the immediate niche requirements of organisms, but can also facilitate their wider habitat interactions, both spatially (foraging, dispersal) and temporally (succession, growth). Disentangling microhabitat topography from the microenvironmental conditions (micro-climate) that it creates, and thus differentiating structural complexity from 'habitat complexity' in general, may broaden our understanding of the ecological functions and resources that topographic features can provide. Thus, when characterising habitat complexity, structural metrics could be considered alongside functional definitions of ecological conditions (i.e., habitat suitability), since structural parameters alone might not accurately reflect an organism's perception and use of its habitat. Scaling up methodologies to define habitat complexity structurally, abiotically and biotically, may thus enable a more comprehensive understanding of intertidal microhabitat formation.

## CRedit authorship contribution statement

**Franz Bauer:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Antony M. Knights:** Writing – review & editing, Supervision. **Mick E. Hanley:** Writing – review & editing, Supervision. **John N. Griffin:** Writing – review & editing, Supervision. **Andy Foggo:** Writing – review & editing, Supervision. **Austin Brown:** Writing – review & editing, Supervision. **Louise B. Firth:** Writing – review & editing, Supervision, Resources, Project

administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

## Data availability

No novel data was produced for this review.

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## Appendix A. Supplementary data

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