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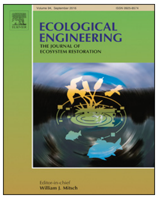

Time-dependent effects of orientation, heterogeneity and composition determines benthic biological community recruitment patterns on subtidal artificial structures

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ABSTRACT

Worldwide, coastlines are becoming increasingly hardened by infrastructure in response to population growth, need for space, and coastal protection. Coastal and marine infrastructure (CMI) supports fewer species and lower abundance and diversity than analogous natural rocky habitats, which can alter community composition and ecosystem functioning. Efforts to develop ecological engineering solutions that offset these negative consequences on biodiversity while retaining engineering function abound, but to date few studies have investigated the role of multiple factors simultaneously driving patterns of biotic colonisation. Here, the role of surface heterogeneity, chemical composition and surface orientation was evaluated over a 6-month period. An increase in habitat heterogeneity, the replacement of shale for ground oyster shell (cue) and downward orientation was predicted to increase species richness, diversity and abundance. Orientation and heterogeneity greatly affected species richness, abundance, and community composition, and the inclusion of ground oyster shell (cue) increased bivalve recruitment but had only a marginal effect on community structure. Community formation was facilitated by low light but inhibited by sedimentation. On upward-facing surfaces, sediment accumulation on high complexity surfaces expanded niche heterogeneity, and supported communities comprised of burrowing polychaetes and predatory species. Surface orientation and heterogeneity are key factors influencing larval recruitment, and in supporting diverse benthic assemblages on artificial structures. These factors should be considered during the design phase of new engineering projects if the negative consequences of artificial structures are to be minimised while ensuring engineering function is maintained.

1. Introduction

Almost half the human population (Crossland et al., 2005) and three quarters of all large cities are located within 100 km of the coast (Firth et al., 2016b; Neumann et al., 2015). With the growing trend of coastal migration and population growth rates expected to exceed 9.5 billion by 2050 (Gerland et al., 2014), anthropogenic pressures are placing increasing demands on coastal marine ecosystems (Airoldi and Beck, 2007; Knights et al., 2015). As a result, increases in coastal and marine infrastructure (CMI), particularly associated with coastal protection and urbanisation (breakwaters, seawalls, piers and pontoons), and marine industry (shipping, renewable energy technologies, aquaculture), are dominating coastlines at the expense of natural habitats (Chapman, 2003; Chee et al., 2017; Firth et al., 2016b).

Coastal hardening – the replacement of soft substrata with hard artificial structures – inevitably provides habitat for benthic communities (Airoldi and Bulleri, 2011; Chapman, 2003; Strain et al., 2018) and are known to alter connectivity patterns (Airoldi et al., 2015; Bishop et al., 2017). Artificial structures typically support lower abundance and richness of species than natural rocky habitats (Connell and Glasby, 1999; Firth et al., 2013; Underwood and Anderson, 1994) and have been reported to facilitate the establishment and spread of non-native species, which can threaten native communities (Airoldi et al., 2015; Bracewell et al., 2012; Glasby et al., 2007). Recent focus has consequently been placed on ecological engineering (eco-engineering) which is the design of sustainable ecosystems for the mutual benefit of society and nature (Mitsch, 2012). Experiments have incorporated natural reef features into CMI design, in attempts to offset the unfavourable impacts of artificial structures on marine ecosystems, whilst retaining structural integrity e.g. (Collins et al., 2002; Firth et al., 2016a; Loke and Todd, 2016).

It has long been known that there is a positive relationship between

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biodiversity and habitat complexity (Hauser et al., 2006; Huston, 1979; Underwood and Anderson, 1994). In the marine environment, natural features, such as crevices, pits and water-retaining features, increase surface area, entrap nutrients, sediments and water and expand the range of niches available for colonisation and shelter (Crisp and Ryland, 1960; Hauser et al., 2006; Loke et al., 2015). This complexity is paramount to supporting a diverse range of organisms. The physical complexity of natural reefs can also alter environmental conditions, such as exposure to light, temperature and water flow rates that result from the orientation of the surface (Thorson, 1964). Shade is increasingly recognised as a key factor in the structure and functioning of intertidal and shallow subtidal benthic communities (Davies et al., 2014; Miller and Etter, 2008; Vermeij and Bak, 2002). Horizontal surfaces exposed to light typically promote algal growth, enhancing primary production but can be negatively affected by high sediment loading (Airoldi, 2003). In contrast, shaded horizontally-oriented surfaces are typically dominated by invertebrates, such as ascidians, barnacles and bryozoans, where there is less competition for space with algae (Anderson and Underwood, 1994; Knott et al., 2004).

The complexity of natural marine features can also alter water flow and boundary layer dynamics, potentially modifying larval supply and settlement (Knights and Walters, 2010; Roberts et al., 1991). Reduced heterogeneity and the reduction in microhabitats provided by CMI may therefore be fundamental in explaining reduced species richness and differences in community composition simply as a result of altered physical drivers, when compared to natural reefs (Firth et al., 2016a; Moschella et al., 2005). An increasing number of studies are showing that CMI material and design modifications, which increase complexity without compromising the primary engineering function of the structure, can enhance recruitment, species richness, and diversity (Chapman and Blockley, 2009; Evans et al., 2016; Firth et al., 2016a, 2014a).

Biogenic habitats are created by oysters, bivalves and polychaete worms (Cole and Knight Jones, 1939; Dubois et al., 2002; Knights et al., 2012). Several factors can influence the settlement of larvae on biogenic habitats, including noise (Lillis et al., 2013), conspecific chemical cues (Browne and Zimmer, 2001; Hadfield and Koehl, 2001; Hay, 2009), biofilms (Barnes et al., 2010; Pawlik, 1992), and proteins and organic compounds in shell matrices (Crisp, 1967; Vasquez et al., 2013). Biofilms are created by the accumulation of micro-organisms on clean surfaces when initially submerged. They coat hard casings and shells of pioneer species such as molluscs and polychaete worms, and significantly contribute to nutrient turnover and productivity (Sawall et al., 2012). Chemicals in the bacteria are strongly depended on for the settlement of larvae, particularly polychaete and mollusc species (Hadfield and Koehl, 2001; Hay, 2009; Pawlik, 1992), and may be almost entirely responsible for the larval attraction of fouling community species (Paul et al., 2011). Bacterial biofilms formed by the bacterium *Alteromonus colwelliana* on oyster shells (Turner et al., 1994), are thought to produce metabolites that induce settlement of oyster larvae, enabling chemically-induced settlement to work on shells of both live and dead oysters (Tamburri et al., 1992). Larvae of many mollusc species will also settle in response to heterospecific cues (Neo et al., 2009; Vasquez et al., 2013), settling on hard shells of other species in the absence of primary hard substrata (Diederich, 2005).

The chemical composition of material used for CMI has potential to influence benthic abundance, richness and diversity (McManus et al., 2017). Substrata comprising differential physical and chemical compositions can affect initial colonisation rates, succession, and subsequent species interactions (Anderson and Underwood, 1994). The most common material used in over 50% of CMI is Portland cement, which offers advantages over other man-made materials, including high porosity, which is favoured by many species (Anderson and Underwood, 1994; Pomerat and Weiss, 1946). It is also easily adaptable to support complex structure designs and desirable habitat features (Firth et al., 2016a, 2014a; Loke and Todd, 2016). However, the lime content found in concrete creates a highly alkaline surface, which is known to be toxic to some marine life upon initial submergence (Lukens and Selberg, 2004). This can reduce initial rates of species colonisation (Nandakumar et al., 2003), such that CMI are not like-for-like substitutes for natural habitats (Sella and Perkol-Finkel, 2015).

This does not mean that CMI does not support life. Concrete is demonstrated to support diverse communities (Firth et al., 2016a; Sella and Perkol-Finkel, 2015). In fact, marine fouling on the surface of concrete has been shown to enhance the structures durability through thermal protection (Coombes et al., 2017) and by slowing down the corrosive effects of chloride ion penetration (Kawabata et al., 2012). Biogenic build-up, such as the deposition of calcium carbonate by calcareous colonisers including serpulid worms and oysters, also offers bio-protection against weathering and erosion, protecting the structure and enhancing its longevity (Coombes et al., 2013). Therefore, efforts to increase the attractiveness of the structure to recruits may be beneficial to both ecosystem services and the longevity of the structure.

On artificial structures, the emergent composition of fouling communities not only depends on the order of larval recruitment and species identity, but also the construction material, its design, and the timing of its placement (Nandakumar, 1996; Underwood and Anderson, 1994). For example, the addition of organic materials can lower the pH of the concrete, and potentially encourage settlement of engineering species such as bivalves, worms and bryozoans (Sella and Perkol-Finkel, 2015). To date, few eco-engineering designs have experimented with the incorporation of organic materials into CMI (but see Neo et al., 2009). The negative implications of creating artificial substrate and its replacement of natural habitats may potentially be offset through novel design and material choice, potentially reducing the negative consequences for biodiversity (Airoldi and Bulleri, 2011) without compromising the original purpose of CMI, but a better understanding of succession and functioning of communities on artificial structures is needed.

Here, we compare recruitment onto concrete tiles manufactured with/without (i) ground oyster shell to replace shale, and (ii) habitat heterogeneity. Tiles were submerged for a period of 6 months and colonisation, succession and diversity assessed using a combination of monthly non-destructive sampling for the first 5 months and destructive sampling after 6 months. We hypothesised that (1) habitat complexity would support greater species richness and diversity; and (2) the replacement of shale with organic replacement would support different taxonomic and community composition compared to standard concrete. A final objective was to test if change in the orientation of the surface (upward or downward-facing used as a proxy for light) would alter recruitment patterns on to tile of different composition and heterogeneity.

2. Materials and methods

2.1. Tile construction and deployment

Individual concrete tiles (15 cm × 15 cm × 1 cm) were constructed with a patterned surface (1 cm wide; 1 cm deep) on one side, and a smooth surface on the other (Fig. 1). This tile size was chosen as it represents a manageable experimental unit in terms of construction, deployment and taxonomic analysis. The block pattern increased surface area by 25% over the smooth tile surface and represents a simple, cheap and easy to implement modification to a standard artificial structure surface. Tiles were made using either: (i) standard concrete mix of 1.5:1.5:1 (sand:shale:Portland cement), or (ii) with complete replacement of the shale component of the mix for ground oyster (*Magallana* (formerly *Crassostrea*) *gigas*) cultch, which may provide an olfactory cue for larval settlement (e.g. O'Connor et al., 2008). Other materials may also provide a cue but are not tested here. All tiles were reinforced with an internal plastic-coated metal mesh grid and cured for 2-wk. Twenty replicates of each tile type were made and randomly