ECO-ENGINEERING OF COASTAL INFRASTRUCTURE:

A DESIGN FOR LIFE

by

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Copyright Statement

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Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment. This study was financed with the aid of a studentship from the University of Plymouth.

Relevant scientific workshops and conferences were attended, at which work from this PhD was presented. Posters were presented at the Marine Biological Association of the UK Postgraduate Conference, the British Ecological Society Annual Symposia and the 5th Eco-Summit Conference. Oral presentations were given at the Marine Biological Association of the UK Postgraduate Conference, the PlyMSEF Postgraduate Conference, the 46th Annual Benthic Ecology Meeting and the 12th International Temperate Reefs Symposium.

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Abstract

Kathryn Anne O’Shaughnessy

Eco-engineering of coastal infrastructure: a design for life.

Coastal urbanisation has driven humans to build artificial defences to protect infrastructure from rising sea level, erosion and stormier seas. Artificial structures are proliferating in the coastal and marine environments (“ocean sprawl”), resulting in a loss of natural habitat, species diversity and ecosystem services. To mitigate the impacts of ocean sprawl, the practice of eco-engineering of coastal infrastructure has been developed. A strong evidence base in support of eco-engineering is growing, yet there remain critical knowledge gaps. This work investigated the ecology of artificial structures and their ability to be enhanced in order to increase species diversity, addressing five knowledge gaps in the eco-engineering literature: (1) understanding of occurrence of non-native species in intertidal natural and artificial habitats along the south coasts of England; (2) looking beyond conventional measures of species diversity to better understand the differences in communities between natural and artificial habitats at multiple spatial scales; (3) comparing how topographic complexity shapes species diversity in both intertidal and subtidal habitats; (4) seeking generality of patterns of eco-engineering interventions across geographic localities; and (5) making the outcomes of eco-engineering research accessible in a practitioner-focused format for stakeholders. To address the first knowledge gap, Rapid Assessment Surveys (RAS) were conducted along the south coast of England. The central region of the south of England supported the most non-native species, while artificial and natural habitats differed in their assemblages of non-native species. Biological surveys in Plymouth Sound (UK) were conducted to address the second knowledge gap. α-diversity (taxon richness) was greater in natural compared to artificial habitats at multiple spatial scales, but β-diversity was greater in artificial compared to natural habitats at the larger spatial scale (m-km). To address the third and fourth knowledge gaps, habitat enhancement eco-engineering trials in Plymouth Sound in intertidal and subtidal habitats were conducted. Results were informally compared to those from equivalent experiments done along the Mediterranean coast of Israel. In general, habitat complexity had an effect on species diversity, but results were dependent on habitat and location. Lastly, an eco-engineering “user-guide” for practitioners was created that can serve as a template for future guides and frameworks as the science evolves and becomes freely accessible to end-users. This thesis evaluates outcomes in the context of their application to the management of eco-engineering in order to mitigate the negative effects of ocean sprawl.

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1. CHAPTER ONE

General Introduction

1.1. Ocean sprawl

The human population continues to grow, exerting pressure on natural resources and transforming landscapes globally (Vitousek et al., 1997; Halpern et al., 2008; Gerland et al., 2014; Cloern et al., 2016). Marine and coastal environments in particular have been drastically modified by global shipping and transport (Halpern et al., 2008; Yigitcanlar et al., 2008), industry (Lin, 1996; Carballo and Naranjo, 2002; Romano et al., 2009), aquaculture (Tovar et al., 2000; Arvanitoyannis and Kassaveti, 2008), overfishing (Parsons, 1996; Jackson et al., 2001) energy extraction (Kingston, 1992; Wiese et al., 2001) and the need to protect coastal infrastructure from rising sea level (Vitousek et al., 1997; Griggs, 2005; Firth and Hawkins, 2011; Stocker et al., 2013; Firth et al., 2016b). Many of these anthropogenic activities have contributed to "ocean sprawl" – a term that was recently coined (Duarte et al., 2012) to describe the proliferation of artificial structures (i.e., seawalls, floating pontoons, breakwaters, oil and gas platforms, groynes, revetment) in marine and coastal environments, and the subsequent modification and loss of natural habitats (i.e., saltmarsh, seagrass, mangroves, sandy beaches, natural rocky shores; Duarte et al., 2012; Firth et al., 2016b; Bishop et al., 2017).

The major anthropogenic threats to the natural environment have been summarised using the acronym, *H.I.P.P.O.*; with *H.* standing for habitat destruction, *I.* representing invasive species, *P.* signifying pollution, *P.* representing population of humans and *O.* standing for over exploitation (Torrance, 2009; UNESCO, 2017). Ocean sprawl is undoubtedly an anthropogenic phenomenon that destroys natural habitat, placing extraordinary stress on estuarine, coastal and marine environments. Ocean sprawl may facilitate overfishing and exploitation of coastal and marine resources by providing transportation hubs for commercial fisherman and structures from which to fish (e.g., jetties and piers). Overexploitation of natural resources alters natural trophic dynamics (Daskalov, 2002; Scheffer et al., 2005), and can even cause a collapse in ecosystems (Jackson et al., 2001; Post, 2013). For example, in the Aleutian Islands, Alaska, sea otters – a keystone species – have traditionally been harvested for their fur. Therefore, since the 1980s, this area saw a drastic decline in otter numbers, which resulted in an increase abundance of their prey – sea urchins – which feed voraciously on kelp (Estes and Palmisano, 1974). Subsequently, the cover of kelp in the Aleutian Islands has declined significantly (Dean et al., 2000; Reisewitz et al., 2006). Human activities in urban ecosystems also affect water quality and pollution load in coastal waters. For instance, impermeable surfaces that are a common feature of urban systems (e.g., roads, buildings, concrete seawalls and bulkheads), increase runoff into adjacent water bodies (Arnold Jr and Gibbons, 1996; Barnes et al., 2001), often facilitating increased input of nutrients and pollutants (e.g., agricultural fertilizers, heavy metals; Arnold Jr and Gibbons, 1996; Wicke et al., 2012), which have the potential to cause red tide events (Hodgkiss and Ho, 1997) and create “dead zones” (Rabalais et al., 2002). Polluted waters can result in the closure of beaches (Rabinovici et al., 2004), decline of recreational activities and investment in coastal development (Ofiara and Seneca, 2006) and closure of fisheries (Lipton and Strand, 1997; Evans et al., 2016), which can have severe implications for fishing- and tourist-dependent communities. Invasive species utilise stationary and mobile artificial structures, such as jetties and sailing vessels, respectively, to establish and spread (Bax et al., 2002; Foster et al., 2016; Johnson et al., 2017), using these structures as stepping stones across otherwise uninhabitable environments (Floerl and Inglis, 2005; Floerl et al., 2009; Sammarco, 2015).

1.2. Coastal artificial structures

Coastal artificial structures are generally built to reclaim land and/or protect it from flooding and erosion (Govarets and Lauwaert, 2009; Dugan et al., 2011; Dafforn et al., 2015b). Artificial coastal structures are often built in sedimentary environments at greater risk of flooding and erosion (Griggs, 2005; Govarets and Lauwaert, 2009; Dugan et al., 2011; Firth et al., 2013a). They can be built along the shoreline, completely separating land from sea (e.g., seawalls, bulkhead, rock revetment; Govarets and Lauwaert, 2009; Dugan et al., 2011), shore-perpendicular and intended to maintain the integrity of a sandy beach (e.g., groynes, jetties; Govarets and Lauwaert, 2009; Dugan et al., 2011) or detached and shore-parallel built with intentions to retard waves reaching the shore and decrease erosion (e.g., breakwaters, low crested structures; Figure 1-1; Airoldi et al., 2005a; Burcharth and Lamberti, 2007; Govarets and Lauwaert, 2009; Dugan et al., 2011; Dafforn et al., 2015b). Coastal artificial structures are now so ubiquitous that in some regions, the extent of artificial coastlines dominates over natural (Dafforn et al., 2015a). For example, > 50% of the Italian North Adriatic shoreline is lined with artificial structures (Airoldi et al., 2005a); 74% of San Diego Bay is armoured with rock revetment (Davis et al., 2002); and nearly 60% of coastal mainland China is now protected by seawalls (Ma et al., 2014).

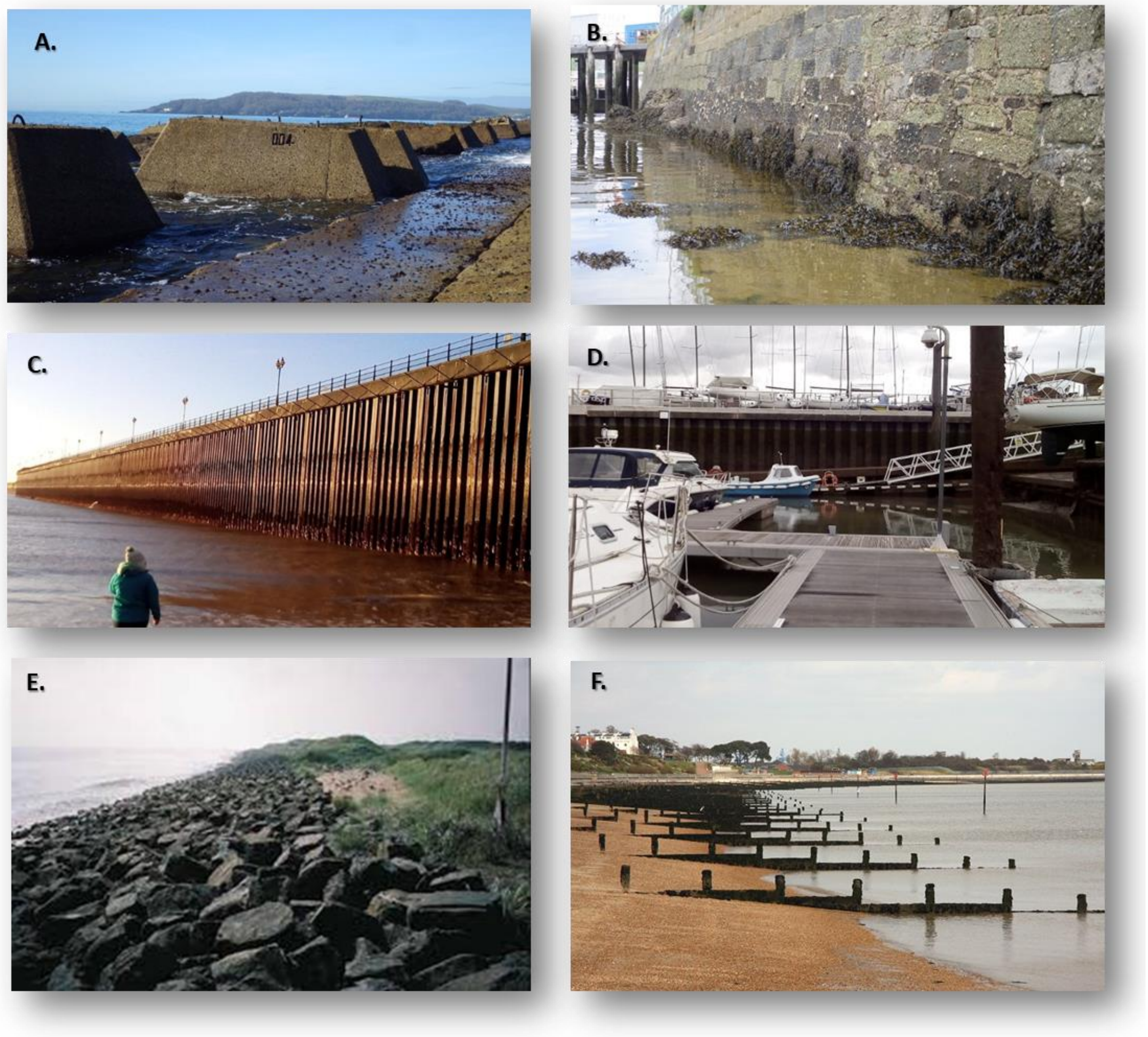


Figure 1-1. Examples of various coastal artificial structures: (A) sacrificial wave-breaker block units placed on the seaward side of Plymouth Breakwater; (B) seawall composed of granite and sandstone separating the land from the sea; (C) metal sheet piling structure making up a protective harbour wall; (D) a recreational marina with metal sheet piling walls for protection from the sea and floating pontoons for vessel docking; (E) rip rap rock revetment is positioned where land meets sea to reduce erosion of land; (F) jetties and groynes are positioned perpendicular to the shore to maintain integrity of a sandy beach.

1.3. Impacts of artificial structures

1.3.1. Environmental impacts

Artificial structures directly replace natural habitat (Airoldi and Beck, 2007; Airoldi et al., 2009; Govarets and Lauwaert, 2009; Dugan et al., 2011); the effects of which are more pronounced in soft bottom habitats because the footprint of an artificial structure completely replaces soft bottom habitat (“placement loss”; Heery et al., 2017).

On sandy beaches, artificial structures such as groynes and jetties alter normal wave activity and subsequently affect longshore transport and sediment deposition on a local and regional level (Dugan et al., 2011). Alongshore structures, such as seawalls, alter the local hydrodynamics, as waves reflecting off vertical seawalls can create turbulence and can interact with incoming waves, causing increased sand scour along the structure; this can cause a loss of beach area in nearby soft-bottom habitats (French, 2002; Bush et al., 2004; Govarets and Lauwaert, 2009; Dugan et al., 2011). Overwater artificial structures such as piers and bridges, can reduce light intensity reaching the sea floor, which can have negative effects on migrating fish species and seagrass communities (Shafer and Robinson, 2001; Shafer, 2002; Ono and Simenstad, 2014; Munsch et al., 2017).

1.3.2. Ecological impacts

1.3.2.1. Biodiversity

Biodiversity of a community changes as organisms colonise available space and biotic succession progresses over time (Bazzaz, 1975; Benedetti-Cecchi, 2000; Noël et al., 2009; Maggi et al., 2011; Bergeron and Fenton, 2012). Biological succession is largely influenced by direct and indirect interactions among species (Connell and Slatyer, 1977; Sousa, 1984; Benedetti-Cecchi, 2000; Benedetti-Cecchi et al., 2000) and the available area of substrate that can be colonised (Sousa, 1984; Benedetti-Cecchi and Cinelli, 1994), as well as the frequency of physical disturbances (Sousa, 1980; McCook and Chapman, 1991). Early colonisers can inhibit or facilitate later colonising species (Connell and Slatyer, 1977; Sousa, 1979), with these interactions typically depending on species life history traits (Sousa, 1980; Tilman, 1985; Walker et al., 1986; Benedetti-Cecchi, 2000). On intertidal rocky shores, for instance, grazing herbivores (e.g., chitons, patellids and littorinids) remove early colonising species, such as ephemeral green algae, facilitating the establishment of other longer-lived, highly seasonal and/or slow-growing species (e.g., corticated red algae, kelp; Connell and Slatyer, 1977; Sousa, 1979; Hawkins et al., 1983; Benedetti-Cecchi and Cinelli, 1994; Anderson and Underwood, 1997; Benedetti-Cecchi, 2000; Aguilera and Navarrete, 2007). In the absence of grazing species, early colonisers inhibit the recruitment of larvae and spores of other species by monopolizing space (Lubchenco, 1983; Geller, 1991; Benedetti-Cecchi, 2000; Benedetti-Cecchi et al., 2000), subsequently keeping biodiversity relatively low over time (Lubchenco and Menge, 1978; Maggi et al., 2011).

Biological succession may initially be influenced by characteristics of the available substrate ('basal' substrate; Marsden and Lansky, 2000; Boyero, 2003; Moschella et al., 2005; Borsje et al., 2011; Coombes et al., 2015). Complex substrate, by design, provides more space for organisms compared to less complex habitat or smaller areas (the 'species-area relationship'; Preston, 1960; Connor and McCoy, 1979; Losos and Schluter, 2000; Chapman and Underwood, 2011; Gatti et al., 2017). A variety of available habitat niches (Whittaker et al., 1973) allows for reduced influence of competition for resources (Schoener, 1989; Dudley and D'Antonio, 1991), thus resulting in an increase in establishment of organisms and thus a diverse assemblage of species surviving in an ecosystem (MacArthur and MacArthur, 1961; Ricklefs, 2010; Pocheville, 2015). Niches can vary throughout time and space (Whittaker et al., 1973; Schoener, 1989; Pocheville, 2015), and can involve more than just ‘habitat’ niche; any type of resource required for survival, such as space (Whittaker et al., 1973; Smith et al., 2014), food (Schoener, 1989) or light availability (Diehl, 1988) can contribute to a niche. The initial colonising community provides biological complexity upon which secondary colonisers will settle, contributing to the process of succession (Turner, 1983; Buhl-Mortensen et al., 2010; Smith et al., 2014). In fact, biological complexity may be more important than basal substrate complexity for determining the biodiversity of a particular substrate, as this new habitat changes as organisms move, die off or are overgrown over time (Benedetti-Cecchi, 2000; Maggi et al., 2011; Smith et al., 2014). As such, available niches temporally change and increase in number with biological succession; niches become more specialized and allow for species coexistence as communities reach maturity (Connell and Slatyer, 1977; Huston and DeAngelis, 1994). In this way, effects of basal substrate complexity may lessen over time due to the original basal complexity being overwhelmed by biotic complexity (Chapman and Underwood, 2011; Smith et al., 2014).

Biodiversity is determined not only by the complexity of a substrate, but also by surrounding environmental factors, often with the suite of species varying over environmental gradients (Heino, 2005; Heino et al., 2007; Dole-Olivier et al., 2009; Gomes-Filho et al., 2010). For example, Gomes-Filho et al. (2010) found that the assemblage of barnacles shifted from dominated by native species to dominated by the non-native barnacle, *Austrominius modestus*, in Plymouth Sound, UK as one moves further up the estuary where salinity values were lower. Similarly, Jenkins and Hartnoll (2001) found that limpet herbivory was greater on exposed intertidal rocky shores than on sheltered shores. Both examples illustrate that environmental gradients can directly and indirectly determine the initial colonising species, as well as the successional communities.

Habitat degradation and destruction is one of the major drivers of biodiversity loss globally (Brooks et al., 2002; Krauss et al., 2010; Mantyka-Pringle et al., 2012). Loss of biodiversity has consequences for ecosystem functioning, such as biofiltration (Hawkins et al., 1992b; Wilkinson et al., 1996) and primary productivity (Costanza et al., 2007). This has knock on effects on ecosystem services such as water quality (Hawkins et al., 1992b; Wilkinson et al., 1996), habitat provision for fisheries (Moyle and Leidy, 1992; Rogers et al., 2014), recreation, tourism and aesthetic appeal (Allen et al., 1992; Hawkins et al., 1992a). Coastal artificial structures are generally considered poor substitutes for their analogous natural rocky shore counterparts (Thompson et al., 2002; Chapman, 2003; Moschella et al., 2005; Geist and Hawkins, 2016; Lai et al., 2018). They are typically characterised by lower species richness (Moschella et al., 2005; Gacia et al., 2007; Firth et al., 2013b), different community composition (Bulleri et al., 2005; Lai et al., 2018), fewer mobile and rare species (Chapman, 2003; Chapman, 2006; Pister, 2009; Chapman and Underwood, 2011) and greater numbers of non-native species (Glasby et al., 2007; Dafforn et al., 2009; Dafforn et al., 2012). In general, many studies agree that artificial and natural habitats support a similar suite of common species, but artificial structures typically have lower abundances of these species (Chapman and Bulleri, 2003; Bulleri et al., 2005; Moschella et al., 2005; Lai et al., 2018).

1.3.2.2. Non-native species

Artificial structures provide hard substrate for attachment of non-native species. Coastal areas characterised by hard built structures, such as international shipping ports, provide a substantial amount of substrate for non-native species colonisation. Global shipping and transportation hubs are often built in heavily urbanised and sheltered estuaries, and as such, typically receive urban and industrial runoff and pollution (Johnston et al., 2017). Ecosystems characterised by lower biodiversity (Stachowicz et al., 1999), sheltered conditions (Bulleri and Airoldi, 2005; Vaselli et al., 2008), greater rates of pollution (Johnston and Roberts, 2009; Johnston et al., 2017) and of which experience disturbance events (Bulleri and Chapman, 2010; Airoldi and Bulleri, 2011) are generally more vulnerable to invasions by non-native species (Arenas et al., 2006b; Dafforn et al., 2012; Mineur et al., 2012). It is commonly accepted that occurrence of non-native species is higher on artificial structures in particular compared to nearby natural habitats (Bulleri, 2005b; Bulleri and Airoldi, 2005; Glasby et al., 2007; Dafforn et al., 2012; Mineur et al., 2012), and many studies have identified artificial structures as the first point of introduction (Griffith et al., 2009; Bishop et al., 2013; Bishop et al., 2015b). Non-native species can negatively affect native biotic communities through competition (Haag et al., 1993; Schloesser and Nalepa, 1994; Blossey and Notzold, 1995), predation (Cohen et al., 1995) and hybridisation (Gray et al., 1991), as well as introduction of new diseases and parasites (Bower et al., 1994; Bishop et al., 2006; Peeler et al., 2011).

Artificial structures provide new hard substrate that can act as ‘stepping-stones’ across sedimentary habitats (Airoldi et al., 2005a; Hawkins et al., 2008; Dafforn et al., 2009; Floerl et al., 2009; Firth et al., 2013a). This effectively increases connectivity (i.e., the facilitation of movement of organisms among habitats and resources through space; Bishop et al., 2017) between isolated or distant hard bottom habitats (Johannesson and Warmoes, 1990; Sammarco et al., 2004; Airoldi et al., 2005a; Dafforn et al., 2009; Mineur et al., 2012; Bishop et al., 2017). This is especially concerning in the context of non-native species, as increased connectivity can promote introduction and spread of new arrivals (Airoldi et al., 2015b; Bishop et al., 2017), thereby facilitating biotic homogenisation (McKinney and Lockwood, 1999; McKinney, 2006). Disturbance events, such as maintenance to a structure (Bulleri and Chapman, 2010; Airoldi and Bulleri, 2011), harvesting organisms (Airoldi et al., 2005b) and docking and tying up of boats (K. O’Shaughnessy, pers. obs.) can often create bare space where dense biological assemblages occurred previously. Consequently, bare space may become colonised by non-native and opportunistic species (Stachowicz et al., 1999; Airoldi and Bulleri, 2011). This may in turn affect the structure and functioning (physical and ecological) of the surrounding environment (McKinney and Lockwood, 1999; McKinney, 2006; Dugan et al., 2011).

Early detection and horizon scanning are key to preventing establishment of non-native species (Manchester and Bullock, 2000; Mehta et al., 2007; Roy et al., 2014;

Kakkonen et al., 2019). Rapid Assessment Surveys (RAS) are a common method used to cover a large number of locations in a reasonable amount of time for documenting distribution of non-native species and detecting new arrivals (Pederson et al., 2005; Arenas et al., 2006a; Bishop et al., 2015a; Bishop et al., 2015b). As densities of new arrivals are typically low in the initial stages of introduction, sampling methods may need to involve surveying multiple different habitats (i.e., subtidal and intertidal) and not focusing only on where non-natives are known to invade (e.g., floating pontoons in marinas; see Chapter 2).

1.4. Characteristics of artificial structures

Coastal artificial structures lack topographic features that are commonly found on natural rocky shores (Chapman, 2003; Moschella et al., 2005; Bulleri and Chapman, 2010; Aguilera et al., 2014). At the smallest scale, these features include millimetre to centimetre size grooves, crevices and cracks (Moschella et al., 2005), while at the medium scale (metres), features include rock pools and gaps between boulders (Chapman, 2017; Liversage et al., 2017). At the largest scale, areas of natural rocky shores vary in complexity at the kilometre scale (Johnson et al., 2003). These complex features are important in providing water and moisture retention (Firth et al., 2013b; Firth et al., 2014b), shade and relief from desiccation (Moschella et al., 2005; Bulleri and Chapman, 2010) and refuge from predation (Fairweather, 1988; Johnson et al., 1998; Skov et al., 2011). Additionally, natural habitats are usually gently sloping, extending the intertidal zone, thereby providing a greater area available for biological recruitment and colonisation (Chapman and Underwood, 2011). Conversely, artificial structures are typically featureless and vertical in design and have a smaller areal extent than natural rocky shores, providing less area for recruitment and colonisation (Chapman and Bulleri, 2003; Moschella et al., 2005; Chapman and Underwood, 2011).

Additionally, the type of material used for construction of artificial structures and the geological origin can influence the colonising communities (Davis et al., 2002; Moschella et al., 2005; Herbert and Hawkins, 2006; Moreira, 2006; Green et al., 2012; Firth et al., 2014b; Dennis et al., 2017).

1.5. Ecological engineering

Ecologists have developed a suite of terms to define and differentiate ecosystems based on their degree of human alteration (Morse et al., 2014). Regardless of whether these ecosystems are defined as “novel” (Hobbs et al., 2006; Morse et al., 2014), “emerging” (Milton, 2003; Hobbs et al., 2006), “impacted” (Morse et al., 2014), “synthetic” (Odum, 1962; Hobbs et al., 2006) or “designed” (Morse et al., 2014), it is clear that human interventions are leading to the development of new ecosystems without natural analogues. In response, some ecologists are calling for a paradigm shift from a focus on the negative impacts of these new ecosystems to considering how to appropriately manage them for ecological and societal benefit (Milton, 2003; Hobbs et al., 2006; Francis, 2014). The design of such sustainable ecosystems which integrate human society with the natural environment for the benefit of both by combining ecological principles with the planning, design and modification of artificial structures, has been labelled “ecological engineering” (or “eco-engineering”; Odum, 1962; Mitsch and Jorgensen, 1989; Mitsch, 1996; Bergen et al., 2001; Odum and Odum, 2003).

Eco-engineering techniques are widely tested and accepted in terrestrial urban ecosystems (e.g., Alberti et al., 2003; Oberndorfer et al., 2007; Francis, 2011; Francis and Lorimer, 2011) and river and wetland ecosystems (e.g., Palmer et al., 2005; Roni et al., 2006; Francis and Hoggart, 2009; Radspinner et al., 2010; Zhang et al., 2010). Application of eco-engineering in the marine and coastal environments, however, has only gained momentum within about the last decade (Strain et al., 2017a). Results from a variety of eco-engineering trials have been contributing to the growing evidence base to support eco-engineering as a sustainable answer to ocean sprawl (e.g., Moschella et al., 2005; Chapman and Blockley, 2009; Martins et al., 2010; Browne and Chapman, 2011; Chapman and Underwood, 2011; Browne and Chapman, 2014; Firth et al., 2014b; Perkol-Finkel and Sella, 2015; Evans et al., 2016a; Perkol-Finkel et al., 2017; Strain et al., 2017a; Strain et al., 2017b). Emerging concepts from these trials show that, generally, effects of interventions are usually positive for local biodiversity. Effects, however, differ based on local conditions, habitat context and specific taxa targeted (Strain et al., 2017a). Whilst extremely informative for the location of interest, most of these experiments have drawn conclusions based on an intervention at only one geographic location at one time point (e.g., Martins et al., 2010; Chapman and Underwood, 2011; Browne and Chapman, 2014; Firth et al., 2014b; Evans et al., 2016a; Strain et al., 2017b; Hanlon et al., 2018; reviewed in Strain et al. 2017a). Thus, there is a clear need to test interventions across multiple geographic locations for ecologically relevant timeframes across seasons and under different environmental conditions to better understand generalities of effects of habitat enhancements (see Chapters 4 and 5).

Artificial structures in the marine environment are not surrogates for the natural habitats they replace, and even the best eco-engineering designs will not replicate nature. The “no active intervention” management policy (Welsh Government, 2011; Environment Agency, 2013) is the best option for maintaining healthy ecosystem functioning (Hoggart et al., 2014). However, the “hold the line” or “advance the line” policies in which existing artificial structures are maintained or new ones are created are currently the most practiced policies in developed nations (Environment Agency, 2013; Hoggart et al., 2014). There is emerging concern that the promise of eco-engineering to deliver beneficial ecological benefits might be used to facilitate harmful activities and developments in coastal environments where development would not otherwise be approved (Firth et al., in prep). It is important, therefore, for ecologists to be aware that the way they communicate eco-engineering information to managers, decision-makers and the general public should be without exaggeration or promise of desired results, and recognise that the best advice might be to do nothing or implement soft or hybrid eco-engineering approaches.

1.5.1. Hard approaches to eco-engineering

Although soft approaches (using vegetation, ecosystem engineering organisms or sand fills for coastal protection; Morris et al., 2018a) and hybrid designs (combination of soft and hard techniques; Bilkovic and Mitchell, 2013) for eco-engineering of coastal structures are preferred (Morris et al., 2018a), quite often in urbanised areas, the only feasible approach is to build hard structures due to lack of space and the immediate need to protect valuable coastal infrastructure (Borsje et al., 2011; Chee et al., 2017; Morris et al., 2018a). This thesis focuses only on hard approaches to eco-engineering of coastal structures to provide secondary ecological benefits.

Eco-engineering of artificial structures in coastal environments typically involves adding topographic complexity to encourage biological recruitment and colonisation in order to increase biodiversity (Moschella et al., 2005; Borsje et al., 2011; Chapman and Underwood, 2011; Firth et al., 2014b; Evans et al., 2016a; Loke and Todd, 2016; Martins et al., 2016; Strain et al., 2017a) and discourage non-native species (Paalvast et al., 2012; Sella and Perkol-Finkel, 2015; Morris et al., 2017b). Designs can add complexity in the form of microscale texture (< 1 cm) such as grooves and pits, fine scale (1 - 100 cm) and larger scale (1 - 100 m) habitats such as crevices, rock pools and gaps between boulders (Moschella et al., 2005; Firth et al., 2013b; Coombes et al., 2015; Liversage et al., 2017). At the smallest scale (millimetres), incorporating microtexture into built structures has been shown to increase larval recruitment and survival of barnacles (Coombes et al., 2015). Medium scale interventions (centimetres to metres) have included drilling pits (Chapman and Underwood, 2011; Firth et al., 2014b; Martins et al., 2016; Hall et al., 2018), creating water-retaining features (Chapman and Underwood, 2011; Browne and Chapman, 2014; Evans et al., 2016a; Firth et al., 2016a), manipulating wet mortar to create pits during the construction phase of a seawall (Firth et al., 2014b; Jackson, 2015) and attaching complex tiles or panels (Toft et al., 2014; Cordell et al., 2017; Perkol-Finkel et al., 2017) onto artificial structures to enhance species diversity. Larger scale interventions (> 1 m) involve placement of precast habitat-enhancement units within the existing structure or during construction (Firth et al., 2014b; Perkol-Finkel and Sella, 2015; Sella and Perkol-Finkel, 2015). If eco-engineering is incorporated during the construction phase, designs can be more creative, less expensive and implemented on a much larger scale than if fitted retrospectively (Firth et al., 2014b; Sella and Perkol-Finkel, 2015).

Eco-engineering interventions can also involve the use of habitat-forming organisms, such as macroalgae and calcifying organisms, in order to achieve a variety of desired secondary ecological benefits. For example, past trials have involved transplantation of target species onto artificial structures to rehabilitate the population (Marzinelli et al., 2009; Campbell et al., 2014) or for conservation or habitat functioning purposes (Perkol-Finkel et al., 2012; Ng et al., 2015; Ferrario et al., 2016). Abundances of filter feeding and photosynthesising organisms, such as mussels and algae, can vary greatly on artificial structures (Hawkins et al., 1992a; Layman et al., 2014; Ferrario et al., 2016). These organisms provide habitat and improve water quality (Russell et al., 1983; Allen et al., 1992; Layman et al., 2014), and thus are desirable species to incorporate into eco-engineering interventions. For example, corals and sponges have been transplanted onto artificial structures to enhance habitat and provide food to fish and gastropods (Ng et al., 2015), and mussel cultivation operations have been set-up in urban docks to improve water quality (Allen et al., 1992; Hawkins et al., 1992a; Wilkinson et al., 1996). Chapter 6 of this thesis provides a review of hard eco-engineering designs representing a range of interventions in a variety of habitats and geographic locations.

An emerging trend in eco-engineering is the utilisation of natural materials in concrete to replace standard Portland cement, which may help mitigate the negative effects of concrete structures in the marine environment (Meyer, 2009; Neo et al., 2009; Perkol-Finkel and Sella, 2013; Perkol-Finkel and Sella, 2015; The World Harbour Project, 2018; ECOncrete Inc., 2019; Seattle Office of the Waterfront and Civic Projects, 2019). Perkol-Finkel and Sella (2013) tested the effects of a range of concrete matrices compared to standard Portland cement on biological recruitment, and found that ecosystem engineers such as oysters, serpulid worms, barnacles and corals were more abundant on the innovative concrete matrices and contributed to the strength of the structure. Novel experiments have found that ground-up crustose coralline algae, molluscs and hemp fibres can also be used as aggregate replacement to attract larvae and increase native species richness, respectively (Neo et al., 2009; Dennis et al., 2017; Hanlon et al., 2018).

The majority of hard eco-engineering interventions to date have been tested in the intertidal zone (but see Sella and Perkol-Finkel, 2015; Perkol-Finkel et al., 2017), yet many structures in urbanised harbours are located within shallow subtidal habitats (National Institute of Coastal and Marine Management of the Netherlands, 2004). Since diversity tends to be greater at lower tidal heights (Saier, 2002; Chapman and Bulleri, 2003; Bulleri et al., 2005; Moschella et al., 2005; Chapman and Blockley, 2009; Firth et al., 2013a; Firth et al., 2013b) and non-native species tend to be more abundant in subtidal compared to intertidal habitats (Dafforn et al., 2012), trials in subtidal habitats are urgently needed (see Chapter 5).

1.5.2. Artificial reefs and lessons learned

Artificial reefs are created from the placement of non-natural substrate in the sea intended to mimic characteristics of natural habitat, and which have traditionally been used to aggregate or produce marine biomass (e.g., fish) for human benefit (Bohnsack, 1991; Carr and Hixon, 1997; Baine, 2001). Any hard substrate placed in the sea will inevitably become colonised by marine life through the artificial reef effect (Langhamer et al., 2009). This concept holds true even for structures that unintentionally become artificial reefs, such as oil and gas platforms (Stephan et al., 1990; Kaiser and Pulsipher, 2005; Kaiser, 2006a; Langhamer, 2012; Ajemian et al., 2015), sunken ships (Stephan et al., 1990; Arena et al., 2007), piers and jetties (Hueckel and Stayton, 1982; Coleman and Connell, 2001).

Artificial reef research and design started in Japan (Bohnsack and Sutherland, 1985), but to date, artificial reefs have been utilised worldwide for a myriad of purposes (Lima et al., 2019), including water quality improvement (Antsulevich, 1994; Falcão et al., 2009), habitat mitigation for human impacts, nursey habitat (West et al., 1994; Patranella et al., 2017) and recreational purposes such as SCUBA diving (Wilhelmsson et al., 1998; Stolk et al., 2007), surfing (Jackson et al., 2005; Rendle and Rodwell, 2014; Herbert et al., 2017) and angling (Milon, 1989; Hooper et al., 2017). The infancy of artificial reef design was often less ‘design’ and more often involved the dumping of indiscriminate materials of opportunity (Harris et al., 1996), such as tyres (Stephan et al., 1990; Collins et al., 2002; Sherman and Spieler, 2006; Morley et al., 2008) and bridge rubble (Stephan et al., 1990; Harris et al., 1996; Bortone et al., 1998; Harris and Pardee Woodring, 2003). The dumping of these materials has led to complications with waterway safety and navigation (Stephan et al., 1990; Challinor and Hall, 2008), fishing line entanglement (Stephan et al., 1990), inaccessible fishing sites and expensive hazard markings (Stephan et al., 1990). The objectives of artificial reefs have not always been defined at the onset of creation and many structures have actually failed to function as fish enhancement structures (Baine, 2001), and thus, there has been much scrutiny over their effectiveness (Stephan et al., 1990).

Creating artificial reefs from decommissioned oil and gas platforms was first explored in the late 1970s and early 1980s in the Gulf of Mexico with the reefing of a subsea production system, and shortly following, the reefing of an oil platform jacket (Dauterive, 2000). Since then, the concept and methods have evolved to maximise cost savings, minimise environmental disruption and boost angling and SCUBA diving opportunities (Stephan et al., 1990; Kaiser and Pulsipher, 2005; Twomey, 2011; Kaiser et al., 2019). Government bodies from the Gulf of Mexico, in particular, are active in transforming platforms into reefs, as thousands of current platforms are nearing the end of their functional life and oil and gas exploration is moving into deeper offshore waters (Stephan et al., 1990; Dauterive, 2000; Macreadie et al., 2011).

Recently, research and design development has shifted to multifunctional artificial reefs that are purposefully designed to provide multiple benefits for humans and nature on a variety of coastal and marine structures such as coastal defence structures (Challinor and Hall, 2008; Cordell et al., 2017), wave and tidal energy devices (Callaway et al., 2017) and offshore wind devices (Langhamer and Wilhelmsson, 2009; Lacroix and Pioch, 2011). As the research and design of ecologically engineered coastal structures are similar to that of artificial reefs, it is imperative that researchers involved in the development of multifunctional coastal structures be knowledgeable on the decades of research into the effectiveness of intentionally built artificial reefs, as well as the policy and management of these structures. For example, artificial reef projects traditionally go through environmental and archaeological assessments, as well as permitting and siting processes that may involve reviewing hydrological, geographical, geological, biological, ecological, economic and social criteria before material can be placed in the sea (Stephan et al., 1990; Kaiser, 2006a; Kaiser et al., 2019); all these processes involve multiple parties and many years to complete. In locations where artificial reefs are common, policies are in place (NEFA, 1984; Stone, 1986), and guidance manuals (Atlantic and Gulf States Marine Fisheries Commission, 2004; US DoC and NOAA, 2007; Rousseau, 2008) are available concerning the planning, design, siting and materials that should be used for artificial reef construction. In the Gulf of Mexico, government legislators and state agencies closely regulate the planning, management and monitoring of artificial reefs (Stephan et al., 1990; Kaiser, 2006a; Kaiser et al., 2019).

Ecologists leading eco-engineering projects can learn from the decades of research and development, successes and failures and immense scrutiny that artificial reefs have experienced. Although the field of eco-engineering has not seen the same of criticism that artificial reefs have, it is important for eco-engineering projects to consider these potential criticisms early on in order to push the field forward with little resistance from the public, conservation groups, economists and government bodies. Artificial reefs have been blamed for mortality of sea turtles (Barnette, 2017; Texas Parks and Wildlife Artificial Reefs Program, pers. comm.), interference in shrimping and other trawling and bottom-fishing activities (Texas Parks and Wildlife Artificial Reefs Program, pers. comm.) and influencing the adjacent soft sediment habitat (Ambrose and Anderson, 1990; Stephan et al., 1990; Danovaro et al., 2002; Langhamer, 2012; Heery et al., 2017). There remains a contentious debate over the ability of artificial reefs to produce organisms rather than simply concentrate the already existing biomass in a region (Bohnsack and Sutherland, 1985; DeMartini et al., 1994; Grossman et al., 1997; Pickering and Whitmarsh, 1997; Shipp, 1999; Brickhill et al., 2005; Smith et al., 2015). Some studies argue that artificial reefs increase catch rates by aggregating recreational fish, thereby creating a situation in which previously unexploited populations are now available to be fished (and thus overexploited; Polovina, 1989; Grossman et al., 1997). Other studies have shown that the addition of essential hard substrate to a habitat facilitates the addition of new individuals with an increase in overall abundance and biomass (Claisse et al., 2014; Claisse et al., 2015; Smith et al., 2015; Smith et al., 2016; Streich et al., 2017). Popular game fish are known residents and visitors to artificial reefs (Stephan et al., 1990; Bohnsack et al., 1994; Streich et al., 2017), with these fisheries attracting anglers and SCUBA divers, boosting tourism, and representing a vital source of income for local communities (Stephan et al., 1990; Adams et al., 2006; Stolk et al., 2007; Rendle and Rodwell, 2014). Reviews on the production versus attraction debate have concluded that carefully controlled studies with high replication, adequate temporal sampling capturing all life history stages and analysis of fish age and length data over time are necessary to resolve this contentious issue (Bohnsack and Sutherland, 1985; Brickhill et al., 2005), and that clearly defined management strategies are vital in assessing the success of an artificial reef (Pickering and Whitmarsh, 1997).

1.6. Measuring biodiversity

The current biodiversity crisis (Singh, 2002; Koh et al., 2004; Monastersky, 2014) has caused a growing need for efficient and cost-effective sampling methods to quantify biodiversity for a variety of purposes such as environmental impact assessments (Michelsen, 2008; Koellner et al., 2013), monitoring biotic responses to anthropogenic change (Chapman, 2003; Sattler et al., 2010) and tracking range expansions of climate migrants (Herbert et al., 2003; Mieszkowska et al., 2006; Hawkins et al., 2009). Biodiversity is the variety of life within and between species and of ecosystems; it considers genetic diversity, species diversity and ecosystem diversity (Convention on Biological Diversity, 2006; Colwell, 2009). Species diversity is only a part of biodiversity, composed of species richness (number of different species present in a given area regardless of identity) and relative abundance (number of individuals of each species; Colwell, 2009; Tuomisto, 2010b). Ecologists and conservationists have traditionally labelled “species diversity” as “biodiversity”, neglecting the other components of biodiversity (Colwell, 2009). Moreover, total and mean species richness are often used as the only response variables in habitat assessment studies in terrestrial, freshwater and marine systems (e.g., Brönmark, 1985; Kohn and Walsh, 1994; Chapman, 2003; Sattler et al., 2010; Nielsen et al., 2011; Firth et al., 2013b; Firth et al., 2014a). It is a concern that mean species richness may not be sensitive enough to detect important differences between habitats of interest or levels of factors in an experiment, and therefore may overlook ecological information necessary for conservation and management decisions (Warwick and Clarke, 1998; Chapman et al., 2009; Winfree et al., 2015; Hillebrand et al., 2018). Information concerning abundances of species in particular has been recognised as more valuable in assessing ecosystem functioning compared to species richness alone (Yee and Juliano, 2007; Dirzo et al., 2014; Winfree et al., 2015). Furthermore, biodiversity assessments that consider multiple spatial scales may be more valuable for landscape scale management decisions compared to focussing on biodiversity at a single scale (Legendre et al., 2005; Devictor et al., 2010; Socolar et al., 2016), as response of taxa can differ across spatial scales (Terlizzi et al., 2008; Morris et al., 2018c; Porter et al., 2018). The use of β-diversity – the variation in identities of species among sampling units in a given area (Anderson et al., 2011) – has been shown as an effective measure to detect differences in species diversity at multiple spatial scales (Terlizzi et al., 2008; Bevilacqua et al., 2012; Barros et al., 2014; Porter et al., 2018; see Chapter 3).

1.7. Policy drivers and potential for application of eco-engineering in coastal development

Throughout this section, the potential of applying eco-engineering in coastal developments as routine practice are discussed, and two barriers to eco-engineering designs becoming part of real practice are introduced: (1) policy concerning the use of nature-based solutions (e.g., eco-engineering) during coastal development in the UK is non-statutory (UK Parliament, 2009; HM Government, 2011; Welsh Government, 2017b; Welsh Government, 2017a); and (2) evidence supporting eco-engineering is locked away in academic literature – the synthesis of research into a practitioner-focused format is lacking (McNie, 2007; Holmes and Clark, 2008; Evans et al., 2019). In this chapter and Chapter 7, relevant policies in the UK are discussed, but more specifically, policies from a Welsh perspective are highlighted.

Despite the mounting evidence supporting eco-engineering as a sustainable option to mitigate the effects of ocean sprawl (Strain et al., 2017a) and increasing government and stakeholder awareness of the ecological benefits of eco-engineered structures (Evans et al., 2017; Evans et al., 2019), consideration of eco-engineering at the policy level in Wales and the wider UK is still non-statutory (Table 1-1; UK Parliament, 2009; HM Government, 2011; Welsh Government, 2016; Welsh Government, 2017a). There has been recent progress, however, in shifting perceptions from traditional hard built structures to nature-based solutions for flood and coastal erosion management in the UK and Wales (HM Government, 2011; Naylor et al., 2012; Evans et al., 2017; Welsh Government, 2017a; Welsh Government, 2017b) and around the world (Dafforn et al., 2015a; Dafforn et al., 2016; Mayer-Pinto et al., 2017). In the 2011 National Strategy for Flood and Coastal Erosion Risk Management in Wales, there was no mention of working with natural processes for coastal adaptation (Welsh Government, 2011). Although still in the development stage, the 2019 National Strategy for Flood and Coastal Erosion Risk Management has an entire section dedicated to nature-based solutions, in which the concept is introduced, recommendation for application is put forward and case studies are presented (WG FCERM team, pers. comm.). The 2017 Draft Welsh National Marine Plan (due to be released summer 2019) and the Marine Policy Statement (UK) encourage innovative coastal developments that restore marine habitats and build resilient ecosystems by increasing biodiversity and supporting ecosystem services. The 2017 Draft Welsh National Marine Plan in particular highlights the need to build with alternative substrate that favours biotic settlement and colonisation and encourages incorporation of additional habitat complexity to support a more biodiverse community (Table 1-1). Although these policies are far from statutory requirements, they are undoubtedly setting the stage for future obligatory regulations for sustainable coastal development in Wales and the wider UK.

In Wales, polices such as the Well-Being of Future Generations Act and the Environment (Wales) Act (Table 1-1) have helped foster support (albeit theoretical) for using nature-based solutions as an alternative to traditional building in both terrestrial and coastal systems. Although this is encouraging, the WG FCERM team has expressed concern over access to evidence supporting eco-engineering as a useful tool for coastal adaptation, as most research is locked away in inaccessible academic journals. Even if this information were made freely available to government bodies and practitioners, the overwhelming amount of literature at hand would probably discourage them from pursuing these options. Thus, there is a clear need to provide practitioners with the appropriate evidence and guidance on using eco-engineering as a sustainable alternative to traditional hard engineering of coastal structures (Evans et al., 2019; see Chapter 6).

Table 1-1. Current environmental policy relevant to sustainable coastal development in the EU, UK and Wales.

Policy	**Relevant sections**	**Relevant key points**	**Steered by/product of**
EU and UK			
The Marine Strategy Framework Directive (2008)	-	One of the main aims is the "achievement of good environmental status in our marine and coastal waters" by 2020.	European Commission
Habitats Directive 92/43/EEC (1992)	-	Advises "on the conservation of natural habitats and of wild fauna and flora" and "aims to promote the maintenance of biodiversity, taking account of economic, social, cultural and regional requirements."	European Commission
Water Framework Directive (2000)	-	Aims to achieve "good ecological status" in all European waterbodies.	European Commission
Convention on Biological Diversity (CBD) (1992)		The main aims include "the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources."	United Nations Environment Programme (UNEP)
Environment Act (1995)	-	Promotes the "conservation of natural resources and the conservation or enhancement of the environment." Creation of the Environment Agency (EA).	UK Parliament (implementation of EU Directive)
Marine and Coastal Access Act (2009)	-	Policy to oversee marine functions and activities. Creation and protection of Marine Conservation Zones (MCZ) and national nature reserves. Creation of the Marine Management Organisation (MMO).	UK Parliament (implementation of EU Directive)
Marine Policy Statement (2011)	2.6.1. Marine ecology and biodiversity	"Development proposals may provide, where appropriate, opportunities for building-in beneficial features for marine ecology, biodiversity and geodiversity as part of good design; for example, incorporating use of shelter for juvenile fish alongside proposals for structures in the sea."	Marine and Coastal Access Act 2009

Wales

Draft Welsh Marine Plan (2017)	General policy – Living within environmental limits; Protection, restoration and enhancement of marine ecosystems	"When developing proposals, the sensitivities of marine ecosystems should be taken into account and where possible, proposals should demonstrate how they will contribute to their protection." More specifically, by "using different substrates for building on the foreshore that are favourable to post-construction colonisation by a range of species. Small changes to intertidal structures that allow the formation of crevices in walls or pools at low tide as opposed to the structure drying out entirely can provide an additional environment for rock pool species that would otherwise be unable to exist there."	Marine and Coastal Access Act 2009 (UK)
The Well-Being of Future Generations (Wales) Act (2015)	Part 2: Improving Well-Being; Sustainable development and well-being duty on public bodies	A resilient Wales means "a nation which maintains and enhances a biodiverse natural environment with healthy functioning ecosystems that support social, economic and ecological resilience and the capacity to adapt to change (for example climate change)."	Welsh Government
The Environment (Wales) Act (2016)	Section 6: Biodiversity and resilience of ecosystems duty Section 7: Biodiversity lists and duty to take steps to maintain and enhance biodiversity	Requires that "public authorities must seek to maintain and enhance biodiversity so far as consistent with the proper exercise of their functions and in so doing promote the resilience of ecosystems." The Welsh Government must publish "lists of priority habitats and species that it considers 'of principal importance for the purpose of maintaining and enhancing biodiversity in relation to Wales'."	Well-Being of Future Generations Act (2015)
Sustainable Management of Natural Resources (SMNR) (2018)	-	The SMNsssR aims to deliver "a strategy on the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way."	Part 1: Environment (Wales) Act 2016
The Natural Resources Policy (NRP) (2016)	Section 4.3: Nature-based solutions and maximising our contribution across the well-being goals	The NRP guilds the delivery of nature-based solutions with a particular focus on the following: • Developing resilient ecological networks • Increasing green infrastructure in and around urban areas • Coastal zone management and adaptation	Part 1: Environment (Wales) Act 2016

1.8. Overview and aims of the thesis

The overall aim of this thesis was to investigate the ecology of artificial structures and their ability to be enhanced in order to increase species diversity, with the view to enhancing ecosystem functioning, offsetting the establishment of non-native species and promoting ecosystem services. This research addressed five knowledge gaps in the current eco-engineering literature: (1) understanding of occurrence and patterns of non-native species in intertidal natural and artificial habitats along the south coasts of England (Chapter 2); (2) looking beyond conventional measures (α-diversity) of species diversity to better understand the differences in communities between natural and artificial habitats at multiple spatial scales (Chapter 3); (3) comparing how topographic complexity shapes species diversity in both intertidal and subtidal habitats (Chapters 4 and 5); (4) seeking generality of patterns of eco-engineering interventions across geographic localities (Chapters 4 and 5); and (5) making the outcomes of eco-engineering research accessible in a user-friendly and practitioner-focused format for stakeholders and end-users (Chapter 6). Each knowledge gap is addressed in detail in Chapters 2 - 6.

Chapter 2: Occurrence of non-native species recorded from Rapid Assessment Surveys (RAS) in natural and artificial intertidal habitats

Coastal artificial structures may facilitate the spread of non-native species (Airoldi et al., 2015b; Bishop et al., 2017), thus, one of the goals of eco-engineering is to encourage native assemblages, thereby offsetting non-natives (Paalvast et al., 2012; Firth et al., 2014b; Dafforn et al., 2015b; Chapman et al., 2018). Therefore, providing a baseline of current non-native species occurrence and abundance in the geographic region of interest is necessary for monitoring success of eco-engineering designs (Dafforn et al., 2015b; Mayer-Pinto et al., 2017). Moreover, patterns of occurrence and observed differences in non-native species assemblages between natural and artificial habitats can inform eco-engineering designs in order to discourage non-native species colonisation. The south coast of England is well studied in regards to occurrence of subtidal non-native species in marinas, but comprehensive records from intertidal habitats, especially natural rocky shores, are lacking. Rapid Assessment Surveys (RAS) in harbours along the south coast of England were conducted to quantify intertidal non-native species on artificial structures and compare assemblages between natural and artificial habitats. Information from this chapter will contribute to a more comprehensive view of non-native species present in the south of England to provide an "intertidal baseline" and allow for the predictive capability to identify harbours at high risk of invasion, which can aid in effective horizon scanning.

Chapter 3: Impacts of coastal urbanisation on species diversity are scale and metric dependent

Species diversity (usually measured as mean taxon richness) is often the response variable of choice for measuring success of eco-engineering interventions or monitoring community composition among habitats (e.g., Chapman, 2003; Firth et al., 2013b; Firth et al., 2014a). Moreover, measurements are often done at one spatial scale and using one metric of analysis, which can sometimes overlook valuable ecological information. To better understand differences in biotic communities between natural and artificial habitats, intertidal natural rocky shores and artificial structures in Plymouth Sound were surveyed. Plymouth Sound was used because it is an ideal model system due to its mosaic of natural and artificial habitats. Data were analysed at two spatial scales and using multiple measures of species diversity in order to capture as much ecological information as possible. Results from this chapter can inform future monitoring practices and analyses.

Chapter 4: Effects of habitat complexity and mussel seeding on species diversity in intertidal habitats across two geographic locations

Experiments for this chapter were part of the Sydney Institute of Marine Science's World Harbour Project (World Harbour Project, 2019) – a global initiative aimed at building ecologically-stable and resilient harbours in urbanised port cities around the world. The project consisted of 15 partner cities from across the globe running the same experiment to test the effects of eco-engineering techniques in enhancing native biodiversity in intertidal habitats. To investigate effects of added complexity on species diversity, tiles of various topographic complexities and mussel seeding were attached to intertidal seawalls. Although data collected from these experiments contributed to the global analysis done by Sydney Institute of Marine Science, statistical analysis of these data were done on their own to draw conclusions at a local level. Additionally, informal comparisons were made of local results with those obtained from similar intertidal eco-engineering trials conducted at a marina in the Mediterranean Sea in order to understand the generality of patterns of effects across two geographic locations.

Chapter 5: Effects of habitat complexity, mussel seeding and shade on species diversity in subtidal habitats across two geographic locations

The majority of eco-engineering studies to date have been trialled in intertidal habitats (Strain et al., 2017a), with very few subtidal examples (but see Sella and Perkol-Finkel, 2015; Perkol-Finkel et al., 2017). To address the knowledge gap concerning the potential of eco-engineering to enhance species diversity in subtidal habitats, tiles of various levels of topographic complexity and mussel seeding as well as tiles that were shaded or unshaded were deployed subtidally off floating pontoons.

Results from these experiments were informally compared to those from similar eco-engineering subtidal trials conducted at a marina in the Mediterranean Sea. The rationale for this comparison was to address the knowledge gap concerning comparison of results across geographic localities for generality of patterns.

Chapter 6: Design catalogue for eco-engineering of marine and coastal artificial structures: a multifunctional approach for stakeholders and end-users

This chapter addressed the need for a practitioner-focused and structured "user guide" for eco-engineering in marine, coastal and estuarine environments. It is presented as an accessible review and catalogue of possible eco-engineering options and a summary of guidance for a range of different structures tailored for practitioners. It includes an introduction to eco-engineering in marine, coastal and estuarine environments, provides a step-by-step approach to choosing the appropriate eco-engineering intervention, broadly describes different types of eco-engineering and concludes with a photographic catalogue of a range of examples. This work can serve as a template for future eco-engineering guides that should evolve in tandem with emerging proof-of-concept evidence.

Chapter 7: General Discussion

This chapter is a synthesis of major findings from the PhD set in the context of potential application and current policy. This section concludes with recommendations for future work.

2. CHAPTER TWO

Occurrence of non-native species recorded from Rapid Assessment Surveys (RAS) in natural and artificial intertidal habitats

Abstract

Loss of natural habitat from ocean sprawl coupled with non-native species (NNS) introductions are among the top threats to marine biodiversity globally. Effective methods of early detection and eradication of NNS are urgently needed. Rapid Assessment Surveys (RAS) combining both quantitative and semi-quantitative techniques were conducted to compare NNS richness and assemblage composition on both intertidal natural rocky shores and artificial structures along the south coast of England. Additionally, surveys were conducted to assessed NNS richness and assemblage composition on groynes that retained a constant connection to the sea at low water compared with those that were exposed at low water. Overall, 26 NNS were found, with two species discovered in new localities (the carpet sea squirt, *Didemnum vexillum* Kott, 2002 and the red alga, *Chrysymenia wrightii* (Harvey) Yamada, 1932. NNS assemblage composition varied significantly between natural and artificial habitats, with artificial habitats supporting greater numbers of NNS only when quantitative data were analysed. Assemblage composition differed among harbours and regions (West, Central, East), with the Central region supporting the greatest number of NNS. There was a positive relationship between NNS richness and average number of vessels arriving to each region. Groynes that maintained a constant connection to the sea at low water supported significantly more NNS and different NNS assemblage composition compared to “unconnected” groynes. Overall, semi-qualitative sampling techniques detected more NNS than quantitative techniques, but neither method captured all NNS recorded on their own, highlighting the importance of a combined

sampling approach for early detection of new arrivals. Results indicate that international transport and artificial structures likely play important synergistic roles in the introduction and spread of NNS into harbours.

2.1 Introduction

The world is experiencing a biodiversity crisis (Singh, 2002; Monastersky, 2014). Natural habitat loss and the introduction and spread of non-native species (NNS) are modifying natural ecosystems and threatening global biodiversity (Manchester and Bullock, 2000; Bax et al., 2003; Simberloff, 2005; Brooks et al., 2006). “Ocean sprawl” – the proliferation of artificial structures (e.g., seawalls, groynes, piers, floating pontoons, offshore platforms) in coastal and marine environments is leading to the replacement of natural habitats with a variety of hard engineered structures built to support human activities (e.g., aquaculture, transportation, industry, shipping, energy extraction) and stabilise and protect shorelines from rising seas (Griggs, 2005; Duarte et al., 2012; Firth et al., 2016b; Bishop et al., 2017). Ocean sprawl provides substrata for attachment of NNS, facilitating ecological connectivity among global transportation and shipping hubs (Bishop et al., 2017) and aiding the spread of cryptogenic (i.e., it is unclear whether the species is native or introduced; Kinzie, 1984; Carlton, 1996a), opportunistic (i.e., a species adapted to exploit new or disturbed habitats; Whitlatch and Zajac, 1985) and non-native species (Carlton and Geller, 1993; Cohen and Carlton, 1997; Ruiz et al., 1997; Dafforn et al., 2009; Firth et al., 2016b). Artificial structures facilitate the homogenisation of biological communities, supporting species assemblages not encountered in natural habitats and affecting the structure and functioning (physical and ecological) of the surrounding environment (McKinney and Lockwood, 1999; McKinney, 2006; Dugan et al., 2011).

NNS can have detrimental impacts on the receiving natural environment through competition and predation with native species (Blossey and Notzold, 1995; Cohen et al., 1995; Lengyel et al., 2009), as well as introduction of new diseases and parasites (Bower et al., 1994; Bishop et al., 2006; Peeler et al., 2011), with consequences for local biodiversity and ecosystem structure and functioning (Mack et al., 2000; Molnar et al., 2008; Dafforn et al., 2012). As such, NNS can affect local and regional economies (Pimentel et al., 2005; Williams et al., 2010). For example, the carpet sea squirt, *Didemnum vexillum* Kott 2002, is considered a global invader (Osman and Whitlatch, 2007; Herborg et al., 2009; Lambert, 2009). It is known to smother native sessile communities (Griffith et al., 2009; Lengyel et al., 2009) and foul marina equipment and boat hulls in great abundances (Coutts and Forrest, 2007). The European zebra mussel, *Dreissena polymorpha* (Pallas), was introduced to the US Great Lakes in the mid-1980s via ballast water discharged from ships travelling from Europe and has since spread to adjacent aquatic waterways (Hebert et al., 1989; O'Neill Jr and Dextrase, 1994; Benson and Boydstun, 1995; Pimentel et al., 2005). *D. polymorpha* outcompetes native molluscs and clogs water filtration systems, intake pipes and electric generating plants, costing US $1 billion per year in control measures (Stein and Flack, 1996; Pimentel et al., 2005).

The importance of horizon scanning (i.e., investigating future potential NNS threats; Roy et al., 2014; Gallardo et al., 2016) and regular monitoring (Eno et al., 1997; Manchester and Bullock, 2000; Mehta et al., 2007; Kakkonen et al., 2019) for preventing establishment and/or spread of NNS (Witte et al., 2010; McDonald, 2012; Gallagher et al., 2017) cannot be overstated. As many NNS are rare/low in numbers or are cryptogenic during initial introduction (Mehta et al., 2007; Rees et al., 2014; Bishop et al., 2015b), approaches that utilise multiple measures and are sensitive enough to detect low species densities (e.g., eDNA; Rees et al., 2014; Klymus et al., 2015; Xia et al., 2018) are necessary for early detection and prevention of establishment (Mehta et al., 2007; Kakkonen et al., 2019). For example, the Asian green mussel, *Perna viridis* (Linnaeus, 1758), has invaded marine waters around the world (Baker et al., 2007), fouling artificial structures such as intake pipes (Benson et al., 2001). A horizon scan determined that *P. viridis* was a non-native species of high priority in Australian waters (Hayes et al., 2005). Subsequently, potential receiving habitats and pathways of introduction (hulls and ballast water of foreign vessels) have been meticulously monitored (Stafford et al., 2007; Wells, 2017) and legally binding conditions have been set out that require developers to make efforts to minimise NNS introductions (Wells, 2017). These early detection methods were vital when a small population of *P. viridis* was found in 2011 in Western Australia, as immediate response and thus eradication was possible (McDonald, 2012).

The rise in global shipping and transportation has meant that harbours have become characterised by a range of different artificial structures, with many harbours seeing an extraordinary amount of shipping traffic from around the world every day (Seebens et al., 2013; Marine Traffic, 2019; World Port Source, 2019). Mobile vectors (e.g., small leisure craft to large commercial tankers) are facilitated by static structures (i.e., artificial structures; e.g., breakwaters, groynes and offshore oil and gas platforms) in acting as stepping-stones or reservoirs contributing to the introduction and spread of NNS globally (Floerl and Inglis, 2005; Clarke Murray et al., 2011; Mineur et al., 2012). The primary vectors of initial introduction are typically transoceanic ships, barges and floating platforms (i.e., mobile vectors) that dock in large international harbours (Carlton and Geller, 1993; Ruiz et al., 1997). These vessels transport species in two main ways: (1) as larvae in ship ballast water and (2) as adults fouling ship hulls (Gollasch, 2002; Gollasch, 2008; Molnar et al., 2008). Thus, initial NNS colonisation and settlement tend to be highest within major shipping ports compared to surrounding areas (Eno et al., 1997; Molnar et al., 2008; Keller et al., 2011; Wood et al., 2015; Foster et al., 2016). Secondary spread of NNS is likely through a combination of mobile vectors and artificial structures (Carlton and Geller, 1993; Sammarco et al., 2004; Clarke Murray et al., 2011; Airoldi et al., 2015b). NNS can hitchhike on smaller local vessels, such as leisure craft and fishing boats, that travel amongst multiple ports regionally; they can then break off or spawn in the visited locations (Floerl and Inglis, 2005; Clarke Murray et al., 2011). Planktonic larvae of NNS can also be carried away from the port of introduction by wave-driven currents (McQuaid and Phillips, 2000), settling on artificial structures along the coast (Wasson et al., 2001). For example, in a study investigating dispersal of mussel larvae, propagules travelled up to nearly 100 km from the source population, but dispersal was highly dependent on local hydrography and time of year (McQuaid and Phillips, 2000). In this way, artificial structures act as ‘stepping stones’, allowing non-natives to persist or spread by provision of hard substrate amongst otherwise uninhabitable habitats (e.g., 'soft bottom' sediment habitat; Apte et al., 2000; Floerl et al., 2009; Airoldi et al., 2015a; Sammarco, 2015; Bishop et al., 2017).

Artificial structures are a common feature of heavily urbanised harbours, necessary for supporting industry, commercial and naval shipping, cruise liners and ferry traffic (Mineur et al., 2012). Biotic communities on artificial structures are typically less diverse with greater numbers of non-native species than comparable natural rocky shore habitat (Glasby et al., 2007; Vaselli et al., 2008; Airoldi et al., 2015a). This disparity has been attributed to the physical design of artificial structures; they typically have steep profiles and reduced surface area and limited topographic complexity compared to their natural analogues (Moschella et al., 2005; Chapman and Underwood, 2011). Human activities in harbours (e.g., vessel docking, fishing, maintenance work) can exacerbate effects of artificial structures on the biotic communities by physically dislodging communities from substrate, creating bare space for new colonisers to exploit and thereby influencing successional dynamics of the community (e.g., removal of predators, loss of canopy algae; Stachowicz et al., 1999; Byers, 2002). Additionally, ports are usually located within sheltered bays or estuaries, which by nature, experience greater fluxes in temperature and salinity (Whitehead et al., 2009), nutrients (Statham, 2012) and pollution (Stark, 1998; Johnston et al., 2017; Hitchcock and Mitrovic, 2019) compared to open coasts. Additionally, shipping activities introduce pollutants from waste discharges (Butt, 2007), fuel spillages (Walkup, 1971; Simpson et al., 1995) and anti-fouling paints (Floerl and Inglis, 2005; Turner, 2010). These physical and chemical stressors may synergistically interact, leaving severely disturbed areas vulnerable to more resilient and opportunistic invaders (Stachowicz et al., 1999; Piola and Johnston, 2008; Airoldi and Bulleri, 2011; Johnston et al., 2017).

Depending on their primary function, artificial structures in intertidal habitats can be built in the low-, mid- or high-shore (Dugan et al., 2011). For example, seawalls are shoreline structures built directly abutting land so as to separate land and water, primarily functioning to retain land and prevent erosion (Govarets and Lauwaert, 2009; Chapman and Underwood, 2011; Dugan et al., 2011). They can be placed in mid- or upper-intertidal habitats, or span the entire intertidal zone, remaining connected to the sea at low tide (Dugan et al., 2011). Shore-perpendicular groynes however are built to preserve the width of sandy beaches by preventing sediment transport away from the concerned area (Dugan et al., 2011). These structures can reach into the lower intertidal or shallow subtidal zones, retaining a constant connection to the sea even at extreme low water. There is general agreement that biodiversity is greater in the lower compared to the upper intertidal zone on artificial structures (Moschella et al., 2005; Chapman and Underwood, 2011; Dugan et al., 2011; Firth et al., 2016a), likely due to longer immersion periods which is when structures are exposed to the pool of colonising species. Little research, however, has been done to investigate occurrence of NNS on structures that maintain a constant connection to the sea compared to structures that are completely exposed at low water. Such research may inform the study of artificial structures as ‘stepping stones’ for NNS spread between distant locations (Floerl and Inglis, 2005; Airoldi et al., 2015b; De Mesel et al., 2015), which may disrupt natural ecological connectivity (Trakhtenbrot et al., 2005; De Mesel et al., 2015; Bishop et al., 2017). Providing additional hard substrate where it is naturally absent represents a potential pathway by which opportunistic and non-native fouling species can proliferate in an otherwise uninhabitable environment (Sammarco et al., 2004; Floerl et al., 2009; De Mesel et al., 2015; Bishop et al., 2017). This knowledge will be critical as coastal urbanisation continues and decisions will be made regarding coastal development to work with nature and support native biotic communities (Dafforn, 2017; Mayer-Pinto et al., 2017).

Interest in the field of urban ecology is growing, as humans are increasingly aware of their impact on the natural environment and realising the value of natural capital (i.e., essential ecosystem services for humans; Schultz et al., 2015; Norton et al., 2016; Ouyang et al., 2016). Urban ecology strives to understand the relationship between living organisms and the surrounding urban environment, in particular, examining anthropogenic effects on biological communities (Collins et al., 2000; Alberti et al., 2003; Alberti, 2005). In urbanised coastal environments, there have been a multitude of surveys conducted to investigate the differences in biodiversity between natural and artificial intertidal habitats (Chapman, 2003; Bulleri and Chapman, 2004; Knott et al., 2004; Airoldi et al., 2005a; Bulleri et al., 2005; Moschella et al., 2005; Firth et al., 2016c; Mayer-Pinto et al., 2018b). Information from these studies should serve as a benchmark against which to measure change to biotic communities over time, and is essential in informing management decisions concerning ecological engineering of artificial coastal structures. Ecological engineering (or “eco-engineering”) is an approach that combines ecology and engineering techniques to manage hard engineered structures for ecological and societal benefits (Odum, 1962; Mitsch and Jorgensen, 1989; Mitsch, 1996; Milton, 2003; Odum and Odum, 2003). Increasing interest in eco-engineering of coastlines in urbanised harbours (Cordell et al., 2017; World Harbour Project, 2018; Living Seawalls, 2019) has heightened the need for a variety of ecological survey information at local and regional scales (Mayer-Pinto et al., 2017).

Studies investigating the distribution and assemblage of NNS on artificial structures in intertidal habitats are lacking (but see Arenas et al., 2006a; Ashton et al., 2006; Bishop et al., 2013; Bishop et al., 2015a; Bishop et al., 2015b for studies in subtidal habitats), and even less attention has been paid to understanding differences in NNS assemblages between natural and artificial intertidal habitats (but see Glasby et al., 2007; Dafforn et al., 2012 for natural and artificial comparison in subtidal habitats). It has been well documented that NNS invade and proliferate on subtidal artificial structures (i.e., floating pontoons; Arenas et al., 2006a; Ashton et al., 2006; Glasby et al., 2007; Dafforn et al., 2012; Bishop et al., 2015a; Bishop et al., 2015b; Wood et al., 2015; Foster et al., 2016). This should not mean, however, that surveys focus on these structures alone, as there have been documented cases of NNS ‘spill over’ into natural habitats (Coutts and Forrest, 2007; Valentine et al., 2007; Carman and Grunden, 2010; Epstein and Smale, 2018). Understanding the mechanisms underpinning the diversity deficit and difference in NNS assemblages between natural and artificial habitats is critical to develop a robust foundation of evidence upon which to base eco-engineering and coastal management decisions.

Initial records of introduction to the British Isles are often from the south coast of England due to its proximity to Europe and high volume of local (usually recreational) and international traffic (Fletcher and Manfredi, 1995; Arenas et al., 2006a; Minchin et al., 2013; Defra, 2015; Foster et al., 2016; Defra, 2019). The south coast of England can be separated into three regions: West, Central and East (Bishop et al., 2015b). International shipping, industry, and cruise traffic is greatest in the Central region (i.e., Poole, Southampton and Portsmouth [the Solent]; Marine Traffic, 2019) . In the East, Dover is UK's closest connection to France, and thus supports cargo and passenger ships from Calais (Marine Traffic, 2019). In the West, there is less international shipping than in the Central region, but two of the harbours support military bases (i.e., Falmouth and Plymouth; Marine Traffic, 2019). Previous surveys in subtidal habitats in these areas have found higher occurrences of NNS in the Central region compared to the other two regions (Bishop et al., 2015b; Foster et al., 2016), suggesting that shipping patterns may influence the number of NNS found in each of the three regions. Moreover, it is likely that NNS which have become established in Europe have crossed the English Channel from Europe to the UK (Eno et al., 1997). One study found that marinas in the north of France shared a similar suite of NNS to marinas in the southwest of England, with higher abundances of NNS in France (Bishop et al., 2015a). This suggests the general movement of NNS has been from France across the Channel to England. For example, the orange-tipped sea squirt, *Corella eumyota* Traustedt, 1882, was first recorded in Gosport (Portsmouth area) in 2004, but has been known in France since 2002 (Bishop et al., 2015b). Similarly, the red ripple bryozoan, *Watersipora subatra* (Ortmann, 1890), was first discovered in Plymouth and Poole in 2008, but was already established in France since 1999 (Bishop et al., 2015a; Bishop et al., 2015b). The current study builds on existing background knowledge from previous studies conducted in subtidal habitats along the south coast of England (i.e., Arenas et al., 2006a; Minchin et al., 2013; Bishop et al., 2015a; Bishop et al., 2015b).

Rapid Assessment Surveys (RAS) are used as a practical method of covering a large number of locations in a reasonable amount of time, being particularly useful in detecting new arrivals of non-native species and tracking their spatio-temporal spread (Pederson et al., 2005; Arenas et al., 2006a; Bishop et al., 2015a; Bishop et al., 2015b). RAS are typically a qualitative approach, involving timed searches of targeted areas and habitats (i.e., undersides of floating pontoons). In biodiversity surveys, however, the most common means of gathering data is predominantly through quantitative quadrat sampling (Chapman, 2003; Chapman, 2006; Airoldi and Bulleri, 2011; Lai et al., 2018), often avoiding topographically complex surfaces (Bulleri et al., 2005; Dafforn et al., 2012; Firth et al., 2016c). Recording of species using the latter strategy, however, depends entirely on where the quadrats fall, and most likely fails to capture presence of rare species and/or species that live in complex and hidden habitats such as cracks, rock pools and the undersides of boulders. To address the current knowledge gaps concerning occurrence of NNS on natural rocky shores and artificial structures in intertidal habitats, we conducted Rapid Assessment Surveys of NNS in intertidal natural and artificial habitats using both qualitative and quantitative techniques within 11 harbours along the south coast of England to test the following hypotheses:

1. Total and mean NNS richness will be greater, and NNS assemblage composition will be different in artificial compared to natural habitats (Study 1).
2. Total and mean NNS richness and NNS composition in artificial habitats will differ among harbours and regions; specifically, total and mean richness will be highest in the Central region (Study 2).
3. The number of NNS per harbour and region will be positively correlated with average number of arriving vessels (Study 2).
4. Artificial structures that maintained a connection to the sea at low water will support greater total and mean NNS richness, and different assemblage

composition, compared to structures that were not connected to the sea at low water (Study 3).

2.2 Materials and methods

2.2.1 Study region

The harbours along the south coast of England are ideally positioned in the English Channel for supporting international and regional shipping traffic, military traffic and ferries to continental Europe. Major international shipping ports along the south coast include Southampton, Portsmouth and Dover, while major cross-channel ferry terminals are located in Plymouth, Poole, Southampton, Portsmouth and Dover (Table 2-1; Figure 2-1; Marine Traffic, 2019). This area has a long history of supporting wartime activities, and many of these ports still support active military bases (i.e., Falmouth, Plymouth, Poole and Portsmouth; The Royal Navy, 2019). At the nearest point between England and France, the distance is only 33 km (i.e., the Straight of Dover; Sea Routes, 2019). Plymouth, Southampton and Portsmouth are major hubs for yachting enthusiasts from around Europe and the world, while Poole and Southampton are proximal to shellfish aquaculture sites which have had a history of international shellfish translocation (Arenas et al., 2006a); an activity that is known to be a major pathway for the introduction of NNS (Minchin, 1996; Ruesink et al., 2005; Molnar et al., 2008). Consequently, the south coast of England has traditionally been susceptible to invasions and is known as the point of introduction for many NNS from Europe and around the world (Farnham et al., 1973; Fletcher and Manfredi, 1995; Eno et al., 1997; Bishop et al., 2015a; Bishop et al., 2015b).

In this study, harbours were grouped into geographic regions following Bishop et al. (2015b). Harbours in the ‘West’ are located west of Portland Bill. ‘Central’ harbours are located within the Solent region, including Poole Harbour. ‘East’ harbours are located east of the Solent (Table 2-1). All harbours had artificial substrata, but only harbours in the West had natural rocky shore (contained within the larger natural harbour) for comparison. Therefore, sites east of Portland Bill were not included in the natural and artificial comparison study (Study 1; Appendix 1).

Table 2-1. Details for NNS RAS conducted along the south coast of England, including survey details, type of vessels by harbour and harbour characteristics. Natural and artificial habitat comparisons were only done in the West region (FAL, LOE, PLY, SAL, TOR). Vessel information was obtained from Marine Traffic (2019) and World Port Source (2019). *Continental passenger ferries travel from south England to northern Europe. †Dominant natural habitat is rocky shore ('RS') or soft bottom ('SB') habitat. ‡Main features include [a]size of harbour ('v. sm' = very small, 'sm' = small, 'med' = medium and 'lg' = large); [b]type of harbour (natural coastal inlet, coastal breakwater); [c]freshwater input; [d]depth of main channel ('shallow' = < 5 m, 'average' = 5-9 m and 'deep' = > 9 m) and [e]average tidal range as recorded in July 2018 from Tide Plotter (v. 5.8, Belfield Software Ltd). Information on size and type of harbour, as well as depth of main channel were obtained from World Port Source (2019).

Survey details			***Type of vessels***					***Harbour characteristics***	
Har code	**Harbour/ city**	**Region**	**Int'l shipping (types of destinations)**	**Cont'l passenger ferry (no. of destinations) ***	**Int'l cruise lines (types of destinations)**	**Military**	**Fishing vessels & leisure craft**	**Dom nat hab†**	**Main features‡**
FAL	Falmouth	West	0	0	0	✓	✓	RS	med[a]; natural coastal inlet[b]; moderate input[c]; average[d]; 3.6 m[e]
LOE	Looe	West	0	0	0	0	✓	RS	v. sm[a]; natural coastal inlet[b]; major input[c]; shallow[d]; 3.5 m[e]
PLY	Plymouth	West	Global	2	0	✓	✓	RS	med[a]; natural coastal inlet[b]; moderate input[c]; deep[d]; 3.6 m[e]
SAL	Salcombe	West	0	0	0	0	✓	RS	v. sm[a]; natural coastal inlet[b]; minimal input[c]; shallow[d]; 3.3 m[e]
TOR	Torbay	West	0	0	0	0	✓	RS	v. sm[a]; coastal breakwater[b]; no input[c]; average[d]; 3.0 m[e]
POL	Poole	Central	0	1	0	0	✓	SB	sm[a]; natural coastal inlet[b]; limited input[c]; shallow[d]; 1.0 m[e]
SHN	Southampton	Central	Global	0	Global	0	✓	SB	lg[a]; natural coastal inlet[b]; moderate input[c]; average[d]; 2.9 m[e]
PMH	Portsmouth	Central	0	6	0	✓	✓	SB	med[a]; natural coastal inlet[b]; limited input[c]; average; deep[d]; 3.1 m[e]
SHM	Shoreham	East	0	0	0	0	✓	SB	v. sm[a]; natural coastal inlet[b]; major input[c]; shallow[d]; 4.5 m[e]
FOL	Folkestone	East	0	0	0	0	✓	SB	v. sm[a]; coastal breakwater[b]; no input[c]; average[d]; 5.2 m[e]
DOV	Dover	East	European	2	European	0	✓	SB	sm[a]; coastal breakwater[b]; no input[c]; average[d]; 4.7 m[e]

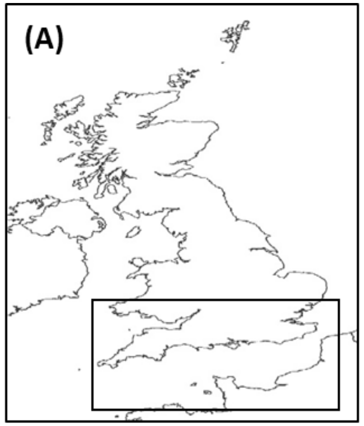
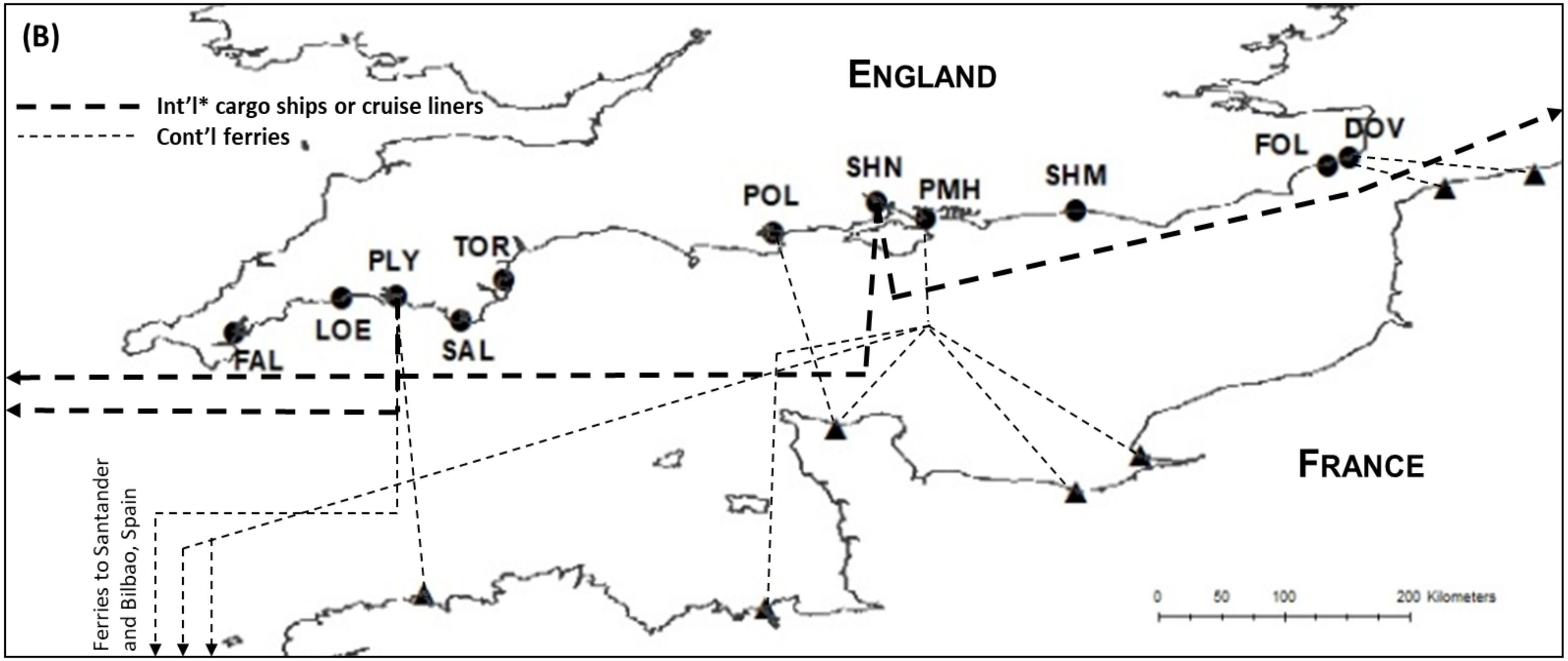


Figure 2-1. (A) Map of the British Isles, with the English Channel indicated in the black box. (B) Continental ferry routes across the English Channel are shown by the light dashes and internationally sailing vessels (cargo ships or luxury cruise liners) are shown by the dark dashes. Lines representing shipping routes do not reflect the numbers of vessels arriving and departing. *International cargo ships and cruise liners include only those vessels that travel outside of northern Europe (e.g., Dover supports cargo-shipping activities, but these ships regularly sail only to European destinations). Southampton and Plymouth are the only harbours with ships that sail internationally on a regular basis (dark dashes). Harbours within the West region include Falmouth, Looe, Plymouth, Salcombe and Torbay. Harbours within the Central region include Poole, Southampton and Portsmouth. Harbours within the East region include Shoreham, Folkestone and Dover. See Table 2-1 for Harbour codes. Information was obtained from Marine Traffic (2019) and World Port Source (2019).



2.2.2 Sampling methods

2.2.2.1 Study 1: NNS richness and assemblage composition in natural compared to artificial habitats

To investigate differences of occurrence of NNS between natural and artificial habitats, 10 surveys (‘Sites’) in natural habitats (i.e., rocky shores) and 11 surveys (‘Sites’) in artificial habitats (artificial structures) in the West region were conducted (Appendix 1; Table 1, 2) between May and July 2018. Natural sites were chosen based on location to closest harbour and were as sheltered as possible to reduce the influence of wave exposure gradients on assemblage composition. Water temperature and salinity were recorded at each site during time of sampling (low water of spring tides). Artificial structures surveyed included seawalls composed of locally sourced rock. There was no restriction placed on size of structure.

To capture NNS richness and abundance, a combined approach that consisted of employing quantitative and semi-quantitative techniques was used; native biota were not quantified. Quantitative techniques involved haphazardly placing 20 quadrats (25 x 25 cm) in the lower intertidal within a 10 x 10 m area. Often, this area was condensed because the steeper slope of artificial structures resulted in reduced area available to survey. All NNS visible to the naked eye within the quadrats were identified and quantified. The surveyor was trained by expert taxonomists who specialise in NNS identification. Voucher specimens and photographs were transported back to the laboratory where experts confirmed the identities of NNS. To positively identify and quantify the non-native barnacle, *Austrominius modestus* (Darwin, 1854), 5 x 5 cm photo-quadrat images ($n = 20$) were taken in the densest barnacle zone and photographs were later analysed using ImageJ (Schneider et al., 2012). Slope and substrate were standardised by surveying vertical or sloping substrate ($\geq 45°$ angle) and avoiding topographically complex surfaces (i.e., gaps, grooves, pits, crevices, rock pools). To locate rare species, a 30-minute timed search was conducted across the study area, including complex surfaces and microhabitats that were avoided during the quantitative assessment. A semi-quantitative assessment of overall abundance of each NNS was made on a scale of 0-3 (0 = absent, 1 = rare-occasional, 2 = frequent-common, 3 = abundant-superabundant; Bishop et al., 2015b). Thus, the quantitative method produced 20 quadrat replicates per site, while the semi-quantitative technique produced one abundance score for each NNS per site. Species that could not be identified in the field (e.g., bryozoans such as *Tricellaria inopinata* (d'Hondt & Occhipinti Ambrogi, 1985) and *Bugulina* spp.) were preserved in 70% ethanol and transported back to the laboratory where they were examined using microscopy.

2.2.2.2 Study 2: Comparison of NNS richness and assemblage composition among harbours and regions and general description of NNS present on artificial structures

Eleven harbours spanning three regions across the south coast of England were surveyed (West: Falmouth, Looe, Plymouth, Salcombe, Torbay; Central: Poole, Southampton, Portsmouth; East: Shoreham, Folkestone, Dover) between May and October 2018. As many artificial structures (‘Sites’) as possible with public access were surveyed in each harbour, with no restriction on size of structure. Artificial structures surveyed extended into the lower intertidal zone when low water was ≤ 1 m, and included seawalls, breakwaters, groynes, discharge pipes and piers. Some of these structures extended into the subtidal zone. The same sampling methodologies used for Study 1 were also followed for Study 2.

2.2.2.3 Study 3: NNS richness and assemblage composition on groynes constantly connected to the sea compared to groynes not constantly connected to the sea

To determine if there was a difference in NNS richness and assemblage composition between artificial structures with a constant connection to the sea compared to structures that are exposed at low water, eight rock armour groynes were surveyed on Sandbanks Beach just outside Poole Harbour (50.686761, -1.938103) during mean low water spring tides (approx. 0.3 m above CD) in September 2018. Four of these groynes retained a connection to the sea even at extreme low water, while the other four were fully exposed at low water (Figure 2-2). The same sampling methodologies used for Study 1 were also followed for Study 3. Quadrats were placed at the same tidal height across all groynes (i.e., lower intertidal). Comparable tidal heights on each groyne were determined by moving between structures and noting the position of the receding water on groynes. Groynes were positioned perpendicular to the beach, therefore both sides of the structures were sampled using both sampling techniques.

Figure 2-2. Example of an “unconnected” groyne that becomes exposed at low water (foreground) compared to a “connected” groyne that retains a constant connection with the sea even at low water (background).

2.2.3 Statistical analyses

2.2.3.1 Study 1: NNS richness and assemblage composition in natural compared to artificial habitats

To compare NNS richness and assemblage composition between natural and artificial habitats, comparisons were made between 10 natural sites and 11 nearby artificial sites. NNS richness and assemblage composition were assessed using quantitative and semi-quantitative data. Two-way nested designs with fixed factor Habitat (2 levels: natural, artificial) and random factor Site (nested in Habitat) were employed. PERMANOVA tests were based on 9999 permutations of residuals under a reduced model. Tests for differences were conducted in PRIMER v6 with the PERMANOVA+ add-on using the PERMANOVA routine (PRIMER-E Ltd, Plymouth, UK; Anderson et al., 2008), and ordination of samples were visualised using two-dimensional non-metric multidimensional scaling (nMDS) plots. Contributions to dissimilarities among regions from each species was determined using the similarity percentages routine (SIMPER).

2.2.3.2 Study 2: Comparison of NNS richness and assemblage composition among harbours and regions and general description of NNS present on artificial structures

Differences in NNS richness and assemblage composition among harbours and regions were assessed using data from both the quantitative and semi-quantitative surveys. For both sampling methods, where abundance information was used, data were fourth-root transformed to down-weight the influence of very abundant species (Anderson et al., 2008). Bray-Curtis dissimilarly matrices were then computed, and permutational multivariate analysis of variance tests (PERMANOVA; Anderson, 2001) were used to test for differences in species richness and assemblage composition. For quantitative data, a three-way nested design was used for each test with random factor Site (number of levels depended on number of surveys done in each harbour) nested in fixed factor Harbour (10 levels: Falmouth, Looe, Plymouth, Torbay, Poole, Southampton, Portsmouth, Shoreham, Folkestone, Dover) nested in fixed factor Region (3 levels: West, Central, East). As quantitative sampling was not undertaken in Salcombe, only 10 harbours were included in quantitative analyses. Because there was not replication at the ‘Site’ level when semi-quantitative data were analysed (i.e., there was one abundance value per site), two-way nested designs with fixed factor Harbour (11 levels: Falmouth, Looe, Plymouth, Salcombe, Torbay, Poole, Southampton, Portsmouth, Shoreham, Folkestone, Dover) nested in fixed factor Region (3 levels) were used. Correlations between NNS richness and number of vessels per harbour and region were assessed using Spearman Rank-order correlations in SigmaPlot v13. Information about vessel type and the average number of vessels per harbour over a 60-

day period as a proxy for boat traffic in general was obtained from the Marine Traffic website (Marine Traffic, 2019).

2.2.3.3 Study 3: NNS richness and assemblage composition on groynes constantly connected to the sea compared to groynes not constantly connected to the sea

Differences in NNS species richness and assemblage composition between “connected” and “unconnected” groynes were analysed using data from both the quantitative and semi-quantitative surveys. One-way permutational multivariate analysis of variance tests (PERMANOVA; Anderson, 2001) were used to test for differences in species richness and assemblage composition between “connected” and “unconnected” groynes with fixed factor Connection (2 levels: connected, not connected) after Bray-Curtis dissimilarity matrices were computed. Where abundance information was used, data were square root transformed to down-weight the influence of very abundant species (Anderson et al., 2008).

2.3 Results

2.3.1 General overview

Water temperature and salinity collected during surveys ranged from 12.5-25.2 °C and 29-35 psu, respectively (Appendix 1, Table 2). In Study 1, a total of 15 NNS were recorded across artificial and natural habitats, with artificial habitats supporting more NNS (12 taxa) than natural habitats (9 taxa). In Study 2, a total of 26 NNS were recorded in surveys conducted on artificial structures (Table 2-2), with Poole and the Central region supporting the greatest mean and total NNS richness. In Study 3, a total of 13 NNS were recorded, with 13 NNS found on groynes with a constant connection to the sea, while only 3 NNS were found on groynes that were not connected at low water.

Table 2-2. Summary table of NNS recorded during the quantitative and semi-quantitative surveys, and within natural and artificial habitats, as well as the number of harbours occupied. NNS included under the 'Artificial' column are species recorded in all artificial habitats during Study 1 and 2, but asterisks (*) indicate NNS that were also recorded on artificial structures in the natural and artificial habitats comparison study (Study 1). †Botrylloides sp. indet. represents a species of Botrylloides that is likely either *B. diegensis* or *B. violaceus* but could not be positively distinguished between the two (Bishop et al., 2015b). ††*Crepidula fornicata* was regularly observed at the base of artificial structures amongst rock rubble; it was rarely seen directly on artificial structures. *C. fornicata* was included in all analyses.

	Total no. of harbours	**Quantitative**	**Semi-quantitative**	**Natural**	**Artificial**
Bryozoa					
Watersipora subatra (Ortmann, 1890)	7	✓	✓	✓	✓*
Tricellaria inopinata d'Hondt & Occhipinti Ambrogi, 1985	5	✓	✓		✓*
Bugulina stolonifera (Ryland, 1960)	2	✓			✓
Bugulina simplex (Hincks, 1886)	1		✓		✓
Bugula neritina (Linnaeus, 1758)	3	✓	✓		✓
Ascidian					
Didemnum vexillum Kott, 2002	2	✓	✓		✓
Botrylloides diegensis Ritter & Forsyth, 1917	3	✓	✓		✓
Botrylloides violaceus Oka, 1927	3	✓	✓		✓*
Botrylloides sp. indet.†	3	✓	✓		✓*
Aplidium cf. *glabrum* (Verrill, 1871)	2	✓	✓		✓
Styela clava Herdman, 1881	6	✓	✓		✓*
Corella eumyota Traustedt, 1882	1		✓		✓
Mollusca					
Magallana gigas (Thunberg, 1793)	10	✓	✓	✓	✓*
Crepidula fornicata (Linnaeus, 1758) ††	5	✓	✓		✓*
Cnidaria					
Diadumene lineata (Verrill, 1869)	1		✓		✓

Arthropoda					
Austrominius modestus (Darwin, 1854)	11	✓	✓	✓	✓*
Annelida					
Ficopomatus enigmaticus (Fauvel, 1923)	2		✓		✓
Ochrophyta					
Undaria pinnatifida (Harvey) Suringar, 1873	2	✓	✓	✓	✓
Sargassum muticum (Yendo) Fensholt, 1955	6	✓	✓	✓	✓*
Colpomenia peregrina Sauvageau, 1927	4	✓	✓	✓	✓*
Rhodophyta					
Grateloupia turuturu Yamada, 1941	2	✓	✓	✓	✓
Chrysymenia wrightii (Harvey) Yamada, 1932	1		✓		✓
Caulacanthus okamurae Yamada, 1933	8	✓	✓	✓	✓*
Bonnemaisonia hamifera Hariot, 1891	1		✓		✓*
Asparagopsis armata Harvey, 1855	1		✓	✓	
Chlorophyta					
Codium fragile subsp. fragile (Suringar) Hariot, 1889	1		✓		✓
Total number of species	**26**	**18**	**25**	**9**	**25**

2.3.2 Study 1: NNS richness and assemblage composition in natural compared to artificial habitats

Of the 15 NNS that were recorded along the southwest coast of England (Table 2-2), nine and 12 were recorded in natural (60% of total) and artificial habitats (80% of total), respectively. Species that were unique to natural habitat included the brown alga, *Undaria pinnatifida* (Harvey) Suringar, 1873 and the red algae, *Grateloupia turuturu* Yamada, 1941 and *Asparagopsis armata* Harvey, 1855. Species unique to artificial habitat included the erect bryozoan, *T. inopinata*, the orange cloak sea squirt, *Botrylloides violaceus* Oka, 1927, an unidentified Botrylloides species, *Botrylloides* sp. indet. (Bishop et al., 2015b), the leathery sea squirt, *Styela clava* Herdman, 1881, the slipper limpet, *Crepidula fornicata* (Linnaeus, 1758) and the red alga, *Bonnemaisonia hamifera* Hariot, 1891 (Figure 2-2). The artificial structures sampled in this study consisted of ten seawalls composed of medium to large natural stone and one seawall composed of large Portland concrete blocks. The seawalls made of natural stone supported more NNS (10 species) compared to the seawall composed of Portland concrete (8 species). Semi-quantitative techniques found 15 NNS across natural and artificial habitat, while quantitative techniques yielded only eight species. The use of quantitative techniques alone failed to record *B. violaceus*, *C. fornicata*, *U. pinnatifida*, *G. turuturu*, *A. armata*, *B. hamifera* and the brown alga, *Sargassum muticum* (Yendo) Fensholt, 1955.

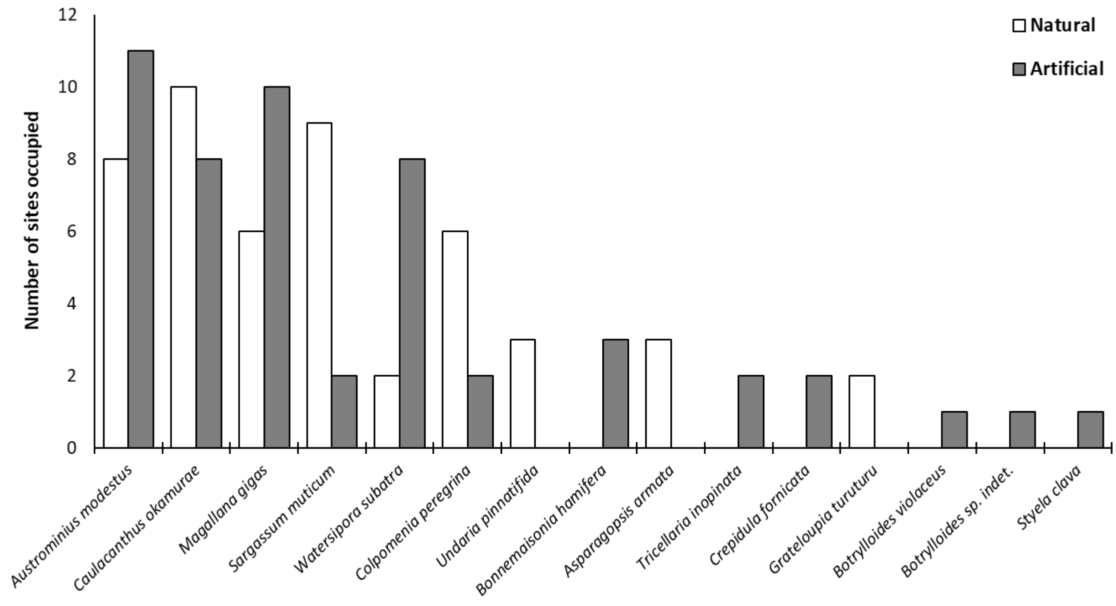


Figure 2-3. The number of sites occupied by non-native species along the southwest coast of England within natural and artificial habitats.

Statistical analysis of the quantitative data found that mean NNS richness per site was significantly greater in artificial compared to natural habitats (Table 2-3a, Figure 2-4a), and similarly, assemblage composition of NNS varied significantly between natural and artificial habitats (Table 2-3a). Statistical analysis of the semi-quantitative data showed that the mean number of NNS per site did not differ significantly between habitats (Table 2-3b, Figure 2-4b), although community assemblage did differ (Table 2-3b, Figure 2-5). SIMPER analysis of quantitative data showed that over 80% of dissimilarity in assemblage composition between natural and artificial habitats was attributed to *A. modestus* (32.6%), *W. subatra* (30.9%) and the red alga, *Caulacanthus okamurae* Yamada, 1933 (23.1%), with all three species more abundant in artificial habitats (Table 2-4a). SIMPER analysis of semi-quantitative data revealed that over 50% of dissimilarity in assemblage composition between natural and artificial habitats was attributable to four species: *S. muticum* (17.3%), the red ripple bryozoan, *W. subatra* (14.5%), the brown alga, *Colpomenia peregrina* Sauvageau, 1927 (12.4%) and the Pacific oyster, *Magallana gigas* (Thunberg, 1793) (11.8%). *S. muticum* and *C.*

peregrina were more abundant in natural habitats, while *W. subatra* and *M. gigas* were more common in artificial habitats (Table 2-4b).

Table 2-3. PERMANOVA results comparing NNS richness and assemblage composition between natural and artificial habitats using (a) quantitative data and (b) semi-quantitative data. Significant p-values are bolded.

(a) Quantitative data

Two-way PERMANOVA comparing species richness between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	18976	18976	7.1199	**0.0009**
Site(Habitat)	18	47985	2665.8	33.327	**0.0001**
Residual	380	30396	79.989		
Total	399	97274			
Transformation:	pres/abs				

Two-way PERMANOVA comparing assemblage composition between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	24297	24297	6.3912	**0.0006**
Site(Habitat)	18	68443	3802.4	16.724	**0.0001**
Residual	380	86397	227.36		
Total	399	179000			
Transformation:	fourth root				

(b) Semi-quantitative data

One-way ANOVA comparing species richness between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	94.912	94.912	0.59709	0.4781
Residual	19	3020.2	158.96		
Total	20	3115.1			
Transformation:	pres/abs				

One-way PERMANOVA comparing assemblage composition between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	4854.7	4854.7	9.041	**0.0001**
Residual	19	10202	536.96		
Total	20	15057			
Transformation:	fourth root				

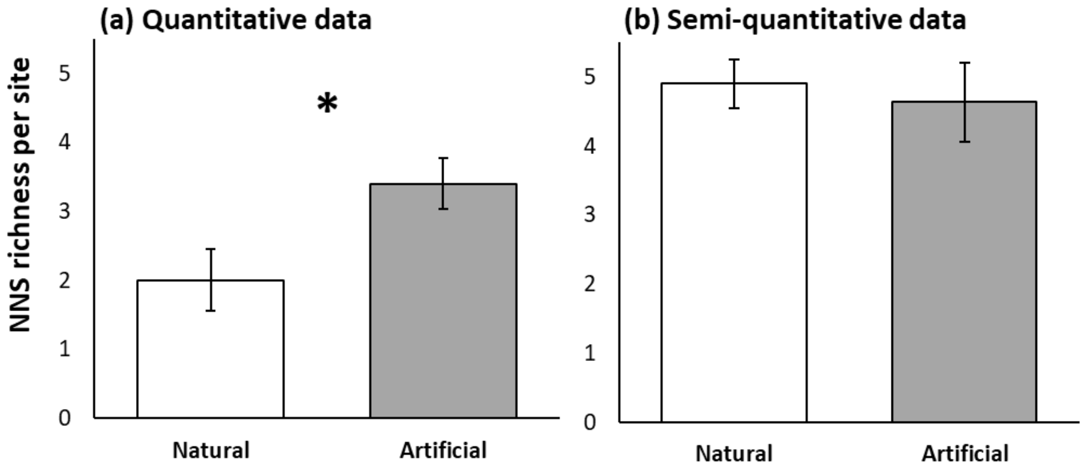


Figure 2-4. Comparison of mean number of NNS per site in natural and artificial habtitat using (a) quantitative and (b) semi-quantitative sampling techniques. NNS richness was significantly greater in artifical compared to natural habitats using quantitative techniques (p = 0.0009) but not using semi-quantitative methods (natural sites, n = 10; artificial sites, n = 11). Error bars show standard error.

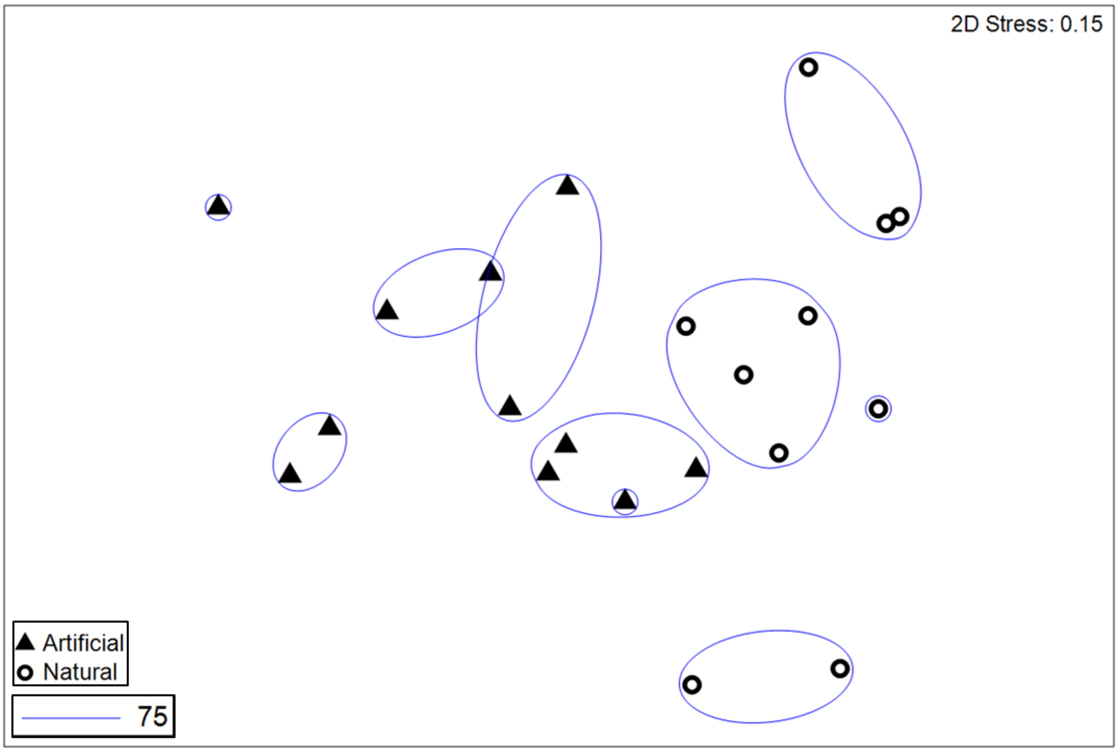


Figure 2-5. Non-metric multi-dimensional scaling plot (nMDS) showing significant variation in assemblage composition of NNS between natural and artificial habitats recorded from Rapid Assessment Surveys (RAS). Assemblage composition between the two habitats varied significantly (p = 0.0001). The blue envelopes indicate that the assemblages within the envelopes are 75% similar.

Table 2-4. Differences in average abundances (indicated by > or <) and contributions (%) of individual species to assemblage composition dissimilarities between natural and artificial habitats using (a) quantitative and (b) semi-quantitative techniques. Consistency of contribution is shown by 'Diss/SD', which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(a)	**Average dissimilarity = 42.0%**	**Natural**	**>/<**	**Artificial**	**Contr%**	**Diss/SD**
	Austrominius modestus (%)	0.8	<	1.0	32.6	0.4
	Watersipora subatra (%)	0.0	<	0.5	30.9	0.6
	Caulacanthus okamurae (%)	0.2	<	0.3	23.1	0.5

(b)	**Average dissimilarity = 50.0%**	**Natural**	**>/<**	**Artificial**	**Contr%**	**Diss/SD**
	Sargassum muticum (%)	1.0	>	0.2	17.3	1.7
	Watersipora subatra (%)	0.2	<	0.8	14.5	1.3
	Colponemia peregrina (%)	0.7	>	0.2	12.4	1.1
	Magallana gigas (%)	0.6	<	1.0	11.8	1.0
	Caulacanthus okamurae (%)	1.1	>	0.8	7.3	0.8
	Asparagopsis armata (%)	0.3	>	0.0	6.6	0.6
	Undaria pinnatifida (%)	0.3	>	0.0	5.5	0.6

2.3.3 Study 2: Comparison of NNS richness and assemblage composition among harbours and regions and general description of NNS present on artificial structures

Overall, 26 NNS were recorded on artificial structures across 11 harbours along the south coast of England (Table 2-2). The barnacle, *A. modestus*, had the highest frequency of occurrence (43 sites), while the erect bryozoan, *Bugulina simplex* (Hincks, 1886), *C. eumyota*, the red alga, *Chrysymenia wrightii* (Harvey) Yamada, 1932, the green alga, *Codium fragile subsp. fragile* (Suringar) Hariot, 1889 and *U. pinnatifida* were only found at a single site each (Figure 2-6). Groynes composed of large natural boulders (n = 4) supported the greatest number of NNS at 17, while seawalls composed of Portland cement mixed with stone (n = 2) supported the fewest number of NNS at 6 species. Metal pipes and piers (n = 5) supported 14 NNS, seawalls composed of medium and large natural stone (n = 12) supported 13 NNS, wave breaker walls composed of metal sheet piling (n = 5) and reinforced concrete structures (n = 3) both supported 12 NNS, wooden structures that included wave break walls and piers (n = 7) supported 11 NNS and structures composed of concrete, which included bridge support structures and old boat ramps (n = 5), supported 10 NNS. Results are reported from both sampling methods, but only the semi-quantitative data are used to produce figures.

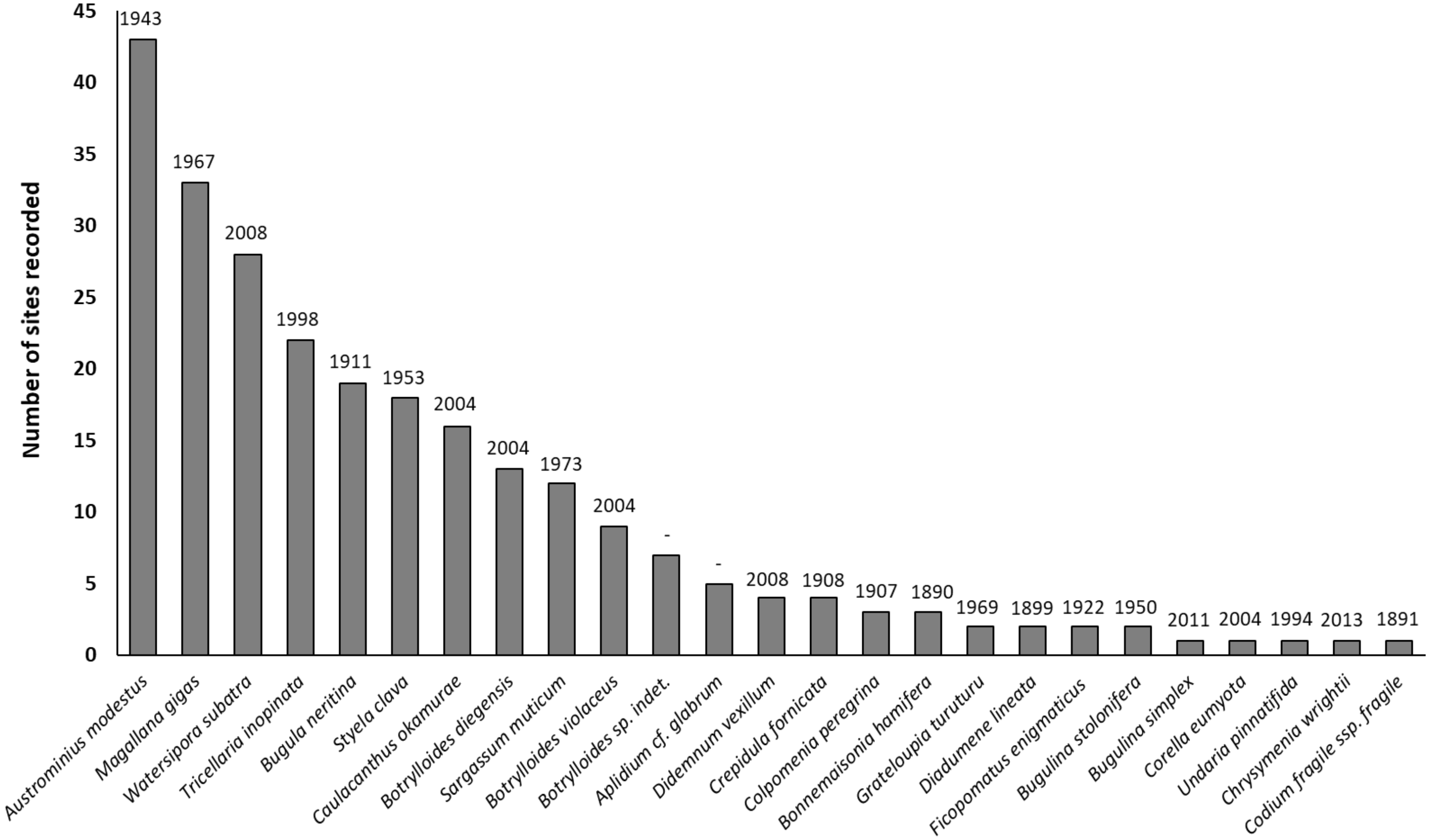


Figure 2-6. Frequency of occurrence of NNS recorded from Rapid Assessment Surveys (RAS) on artificial structures along the south coast of England, with year of first record in the British Isles indicated above the bar. A dash above the bar indicates where dates could not be found or are not applicable (i.e., *Botrylloides* sp. indet. represents a *Botrylloides* spp. that is likely either *B. diegensis* or *B. violaceus* but could not be positively distinguished between the two).

Quantitative sampling found that the greatest total number of NNS was in Poole, while Looe and Folkestone supported the fewest NNS. The total number of NNS was greatest in the Central region and lowest in the West (Table 2-5). Statistical analysis of the quantitative data revealed that mean NNS richness and assemblage composition were significantly different among harbours and regions (Table 2-6a). For NNS richness, post-hoc pairwise comparisons showed significantly greater numbers of NNS in Torbay compared to Looe ($p = 0.0084$) in the West, Southampton compared to Portsmouth ($p = 0.003$) in the Central region and Shoreham compared to Folkestone ($p = 0.0045$) in the East. On average, significantly more NNS were found in the Central region compared to the West and East regions. For NNS assemblage composition, post-hoc pairwise comparison tests revealed significant variation between Falmouth and Looe ($p = 0.0232$), Falmouth and Plymouth ($p = 0.0292$), Falmouth and Torbay ($p = 0.0244$) and Looe and Torbay ($p = 0.0073$) in the West, Poole and Southampton ($p = 0.0090$) and Southampton and Portsmouth ($p = 0.0002$) in the Central region and Shoreham and Folkestone ($p = 0.0034$) in the East. Post-hoc pairwise tests for NNS assemblage composition comparing regions showed that the West and Central ($p = 0.0012$) and the Central and East ($p = 0.0012$) regions differed significantly. SIMPER analysis found that the average dissimilarity in assemblage composition was 54.5% between West and East regions, 60.0% between West and Central regions and 68.5% between Central and East regions (Table 2-7a). The erect bryozoan, *Bugula neritina* (Linnaeus, 1758) contributed the most to the dissimilarity between West and Central (15%; greater in Central), while *W. subatra* contributed the most to dissimilarities between West and East (37.3%; greater in West) and Central and East regions (22.1%; greater in Central).

Statistical analysis of semi-quantitative data revealed a significant difference in mean NNS richness among regions, with Central supporting more NNS, on average and in total, per harbour compared to West and East (Table 2-5, 2-6b; Figure 2-7). There were no significant differences, however, in mean NNS richness among harbours within regions (Table 2-6b). Assemblage composition varied significantly among both harbours and regions (Table 2-6b; Figure 2-8). Post-hoc pairwise comparisons revealed significant variation in assemblage composition between Falmouth and Plymouth (p = 0.0355) in the West region and Poole and Portsmouth (p = 0.0131), Poole and Southampton (p = 0.0014) and Portsmouth and Southampton (p = 0.0013) in the Central region. Post-hoc pairwise tests comparing regions showed that the West and Central (p = 0.0144) and Central and East assemblage compositions (p = 0.0326) differed significantly (Figure 2-8). SIMPER analysis showed that the average dissimilarity in assemblage composition was 38.5% between West and East, 57.0% between West and Central and 64.9% between Central and East regions (Table 2-7b). *W. subatra* contributed the most to the dissimilarity between West and East regions (25.4%; greater in West), while *C. okamurae* contributed the most to dissimilarities between West and Central (11.4%; greater in West) and Central and East regions (1.6%; greater in East).

Table 2-5. Summary of NNS found using the quantitative and the semi-quantitative techniques by harbour and region. A dash (-) represents no survey undertaken.

		Total no. NNS			
Harbour	**Region**	**Quantitative**		**Semi-quantitative**	
		harbour	region	harbour	region
FAL	West	7	8	9	12
LOE	West	1		3	
PLY	West	4		4	
SAL	West	-		4	
TOR	West	5		7	
POL	Central	14	17	15	22
SHN	Central	11		12	
PMH	Central	12		17	
SHM	East	3	5	5	6
FOL	East	1		2	
DOV	East	3		6	

Table 2-6. PERMANOVA results for comparison of NNS richness and assemblage composition using (a) quantitative data and (b) semi-quantitative data among harbours and regions. Significant p-values are bolded.

(a) Quantitative data

Three-way PERMANOVA comparing species richness among regions, harbours and sites.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	60707	30354	7.0537	**0.0025**
Harbour(Region)	7	118340	16905	3.9287	**0.0019**
Site(Harbour(Region))	30	118340	4303.2	15.623	**0.0001**
Residual	760	118340	275.44		
Total	799	118340			
Transformation:	pres/abs				

Three-way PERMANOVA comparing assemblage composition among regions, harbours and sites.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	75905	37953	4.5881	**0.0040**
Harbour(Region)	7	221400	31628	3.8236	**0.0001**
Site(Harbour(Region))	30	248160	8272	11.922	**0.0001**
Residual	760	527330	693.85		
Total	799	1155800			
Transformation:	fourth root				

(b) Semi-quantitative data

Two-way PERMANOVA comparing non-native species richness among regions and harbours.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	4014	2007	7.0275	**0.0012**
Harbour(Region)	8	2399.2	299.9	1.0501	0.4183
Residual	33	9424.5	285.59		
Total	43	18170			
Transformation:	pres/abs				

Two-way PERMANOVA comparing non-native assemblage composition among regions and harbours.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	12842	6420.9	7.586	**0.0001**
Harbour(Region)	8	15168	1896	2.24	**0.0028**
Residual	33	27931	846.41		
Total	43	65127			
Transformation:	fourth root				

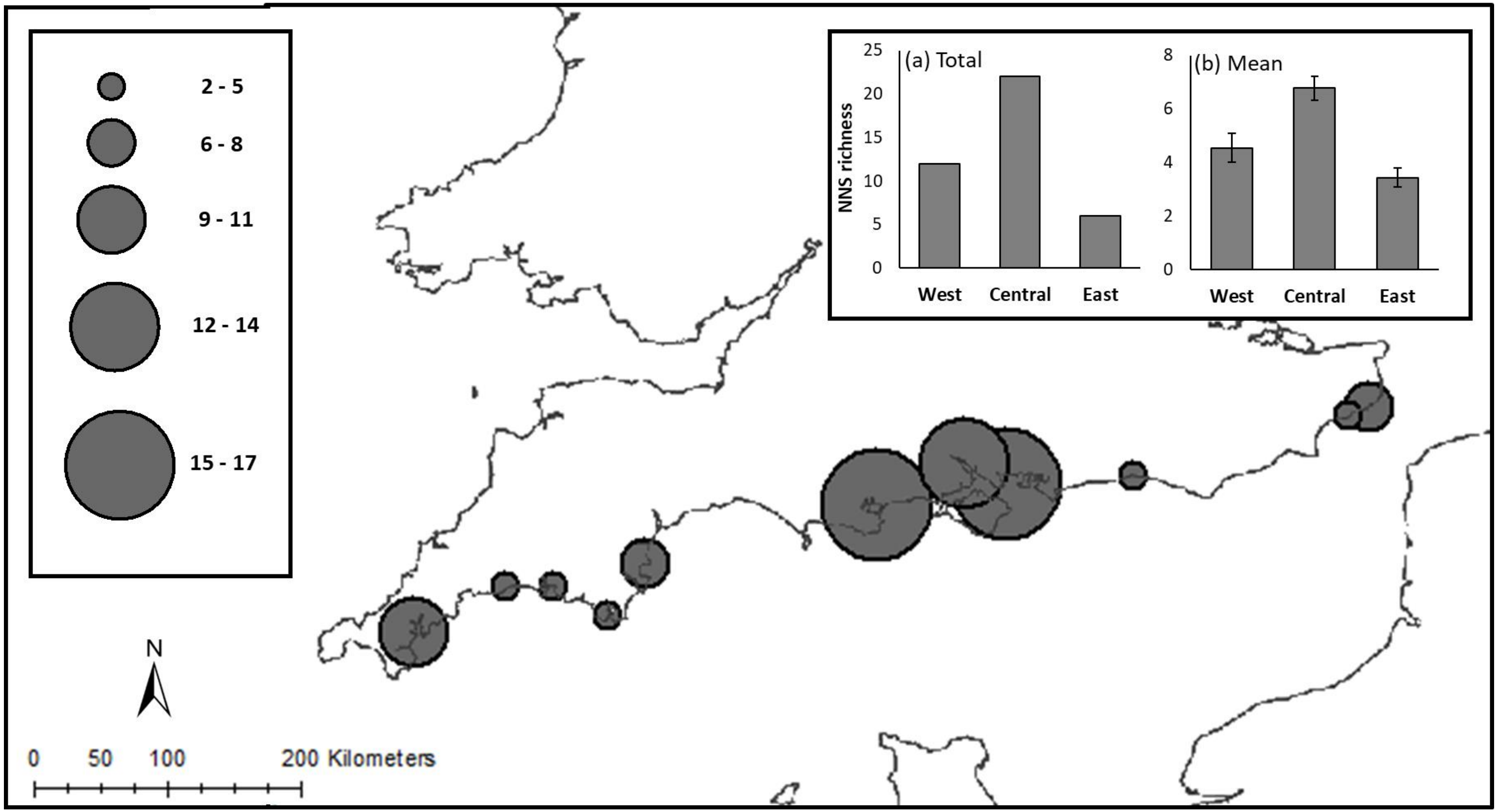


Figure 2-7. The number of NNS recorded per harbour along the south coast of England ranged from 2-17. Size of circles represents the total number of species recorded per harbour. Harbours from West to East: Falmouth, Looe, Plymouth, Salcombe, Torbay (West region), Poole, Southampton, Portsmouth (Central region), Shoreham, Folkestone and Dover (East region). The bar charts in the upper right corner show (a) total NNS richness and (b) mean (± 1 SE) NNS richness by region.

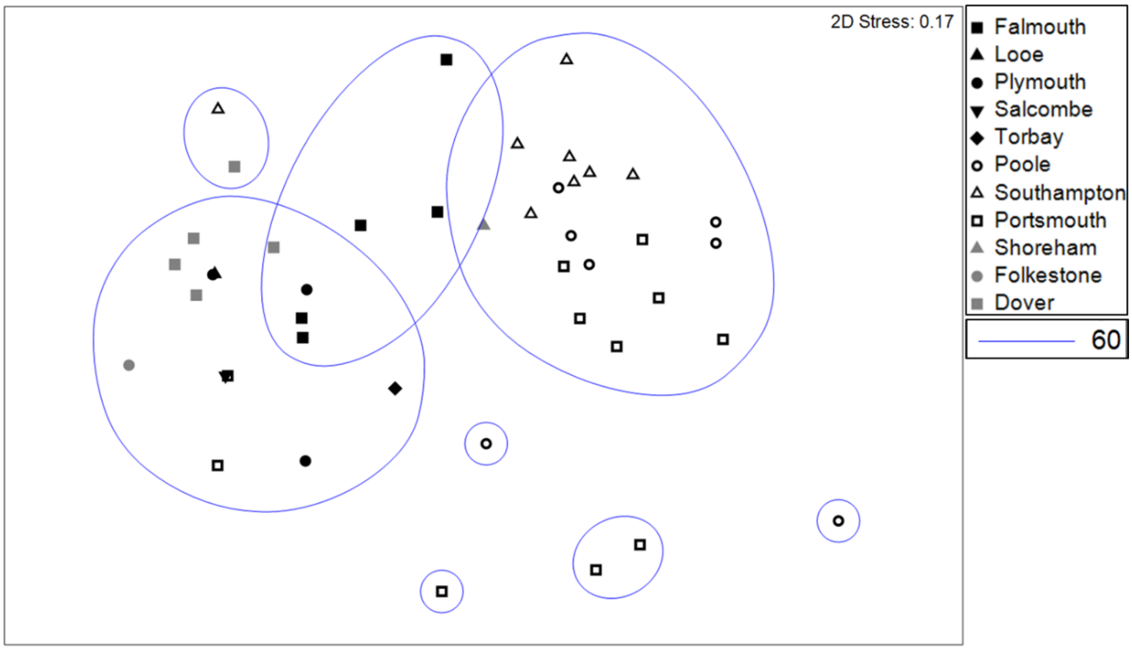


Figure 2-8. Non-metric multi-dimensional scaling plot (nMDS) showing significant variation in NNS assemblage composition from Rapid Assessment Surveys (RAS) on artificial structures among harbours (p = 0.0028) and regions (p = 0.0001) along the south coast of England. Dark shapes represent harbours in the West region, open shapes indicate harbours in the Central region and grey shaded shapes represent harbours in the East. The blue envelopes indicate that the assemblages within the envelopes are 75% similar.

Table 2-7. Differences in average abundances (indicated by > or <) and contributions (%) of individual species to assemblage composition dissimilarities between regions for West versus East, West versus Central and Central versus East using (a) quantitative data and (b) semi-quantitative data. Consistency of contribution is shown by ‘Diss/SD’, which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(a) Quantitative data

Average dissimilarity = 54.5%	**West**	**>/<**	**East**	**% Contr.**	**Diss/SD**
Watersipora subatra (%)	1.1	>	0.0	37.3	1.7
Caulacanthus okamurae (%)	0.8	>	0.0	29.1	1.1
Magallana gigas (%)	0.5	>	0.1	18.3	0.9

Average dissimilarity = 60.0%	**West**	**>/<**	**Central**	**% Contr.**	**Diss/SD**
Bugula neritina (%)	0.0	<	1.1	15.0	1.3
Caulacanthus okamurae (%)	0.8	>	0.0	13.9	1.0
Watersipora subatra (%)	1.1	<	1.2	13.6	1.1
Tricellaria inopinata (%)	0.2	<	0.9	11.9	1.4

Styela clava (%)	0.1	<	0.8	10.6	1.1
Magallana gigas (%)	0.5	>	0.4	10.3	1.0

Average dissimilarity = 68.5%	**Central**	**>/<**	**East**	**% Contr.**	**Diss/SD**
Watersipora subatra (%)	1.2	>	0.0	22.1	1.5
Bugula neritina (%)	1.1	>	0.0	17.1	1.3
Tricellaria inopinata (%)	0.9	>	0.0	13.6	1.4
Styela clava (%)	0.8	>	0.0	11.9	1.1
Magallana gigas (%)	0.4	>	0.1	6.8	0.7

(b) Semi-quantitative data

Average dissimilarity = 38.5%	**West**	**>/<**	**East**	**% Contr.**	**Diss/SD**
Watersipora subatra (%)	0.8	>	0.0	25.4	1.5
Caulacanthus okamurae (%)	0.8	<	0.9	13.9	0.8
Magallana gigas (%)	1.0	>	0.8	12.8	0.8
Bonnemaisonia hamifera (%)	0.3	>	0.0	7.3	0.6
Styela clava (%)	0.1	<	0.2	6.4	0.5
Crepidula fornicata (%)[†]	0.1	<	0.2	6.3	0.5

Average dissimilarity = 57.0%	**West**	**>/<**	**Central**	**% Contr.**	**Diss/SD**
Caulacanthus okamurae (%)	0.8	>	0.1	11.4	1.3
Bugula neritina (%)	0.0	<	0.8	10.8	1.4
Tricellaria inopinata (%)	0.2	<	0.8	10.5	1.4
Styela clava (%)	0.1	<	0.6	8.7	1.1
Watersipora subatra (%)	0.8	=	0.8	8.0	0.9
Magallana gigas (%)	1.0	>	0.7	7.9	0.9
Sargassum muticum (%)	0.2	<	0.4	6.9	0.8
Botrylloides diegensis (%)	0.0	<	0.5	6.7	0.9

Average dissimilarity = 64.9%	**Central**	**>/<**	**East**	**% Contr.**	**Diss/SD**
Caulacanthus okamurae (%)	0.1	<	0.9	1.6	12.2
Watersipora subatra (%)	0.8	>	0.0	1.5	11.9
Tricellaria inopinata (%)	0.8	>	0.0	1.6	11.5
Bugula neritina (%)	0.8	>	0.0	1.4	10.8
Styela clava (%)	0.6	>	0.2	1.1	8.6
Magallana gigas (%)	0.7	<	0.8	0.8	6.8
Botrylloides diegensis (%)	0.5	>	0.0	0.9	6.7
Sargassum muticum (%)	0.4	>	0.0	0.7	6.3

[†] *Crepidula fornicata* was regularly observed at the base of artificial structures amongst rock rubble; it was rarely seen directly on artificial structures. *C. fornicata* was included in all analyses.

Two NNS were discovered in new localities: the carpet sea squirt, *Didemnum vexillum* Kott, 2002 was found in Poole and Portsmouth, and the red alga, *Chrysymenia wrightii* (Harvey) Yamada, 1932 was found in Portsmouth. Colonies of *D. vexillum* within Poole Harbour were found on the seaward side of a wooden wave breaker wall (50.688439, -1.9456) and a metal pipe positioned perpendicular to the shore (50.702722, -1.944408). Colonies in Portsmouth were both located on concrete fishing piers perpendicular to the shore (50.789144, -1.106972; 50.788917, -1.028583). *C. wrightii* was found in a small water-retaining pool along a stepped seawall in Portsmouth (50.777714, -1.086403). The only previously confirmed record of *C. wrightii* was from marinas in Falmouth (Wood et al., 2015).

Portsmouth and Southampton supported the greatest average number of vessel arrivals per day at 86.4 and 83.1, respectively, while Folkestone supported the fewest (0.4; Figure 2-9). Spearman Rank-order correlations using semi-quantitative methods revealed a significant positive relationship between average number of vessel arrivals per region and NNS richness ($r_s = 0.502$, $p < 0.001$). There was, however, no significant relationship between average number of vessel arrivals per harbour and non-native species richness ($r_s = 0.213$, $p = 0.171$).

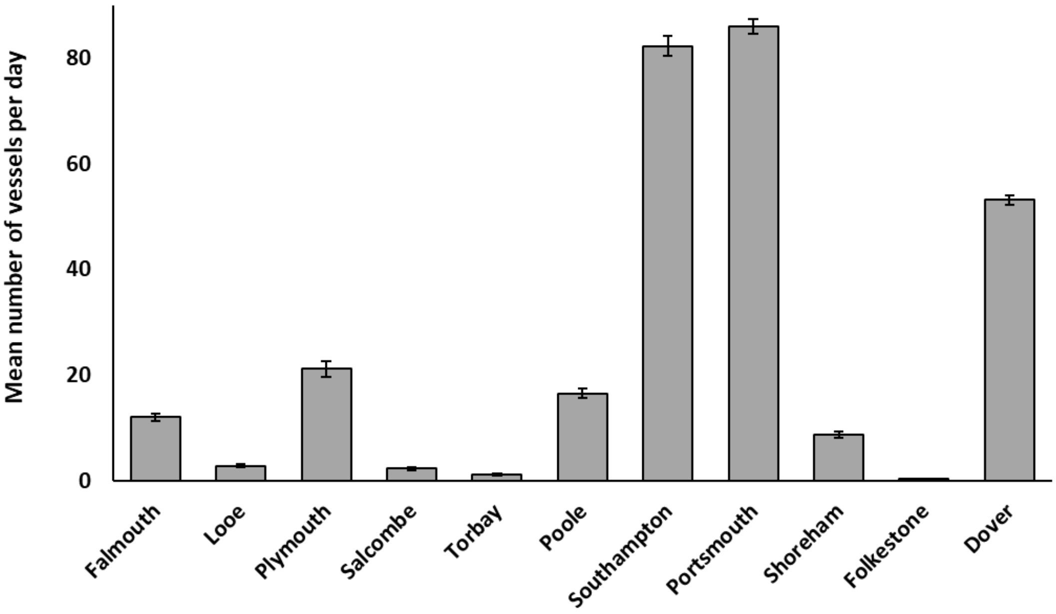


Figure 2-9. Mean number of vessels per day averaged over 60 days. Data was obtained from Marine Traffic (2019).

2.3.1 Study 3: NNS richness and assemblage composition on groynes constantly connected to the sea compared to groynes not constantly connected to the sea

Overall, 13 NNS were recorded across all groynes at Sandbanks (Table 2-8). All 13 NNS were present on groynes connected to the sea, while only three NNS were present on groynes unconnected to the sea. The three species recorded on “unconnected” groynes were *T. inopinata*, *G. turuturu* and *A. modestus*. The quantitative technique captured 10 NNS, while the semi-quantitative method captured 12 NNS. *B. violaceus* was unique to the quantitative technique, while *M. gigas*, the erect bryozoa, *Bugulina stolonifera* (Ryland, 1960) and *S. muticum* were unique to the semi-quantitative techniques. Data from both sampling methods were analysed but only semi-quantitative data was used for figures, as the semi-quantitative method found more NNS.

Table 2-8. Summary table for NNS recorded from groynes with a constant connection to the sea and groynes without a connection to the sea at low water. Numbers are included for both quantitative and semi-quantitative sampling techniques.

	Connected	**Unconnected**	**Quantitative**	**Semi-quantitative**
Bugulina stolonifera (Ryland, 1960)	✓			✓
Bugula neritina (Linnaeus, 1758)	✓		✓	✓
Botrylloides diegensis Ritter & Forsyth, 1917	✓		✓	✓
Botrylloides violaceus Oka, 1927	✓		✓	
Watersipora subatra (Ortmann, 1890)	✓		✓	✓
Tricellaria inopinata d'Hondt & Occhipinti Ambrogi, 1985	✓	✓	✓	✓
Magallana gigas (Thunberg, 1793)	✓			✓
Austrominius modestus (Darwin, 1854)	✓	✓	✓	✓
Codium fragile subsp. fragile (Suringar) Hariot, 1889	✓		✓	✓
Grateloupia turuturu Yamada, 1941	✓	✓	✓	✓
Sargassum muticum (Yendo) Fensholt, 1955	✓			✓
Colpomenia peregrina Sauvageau, 1927	✓		✓	✓
Undaria pinnatifida (Harvey) Suringar, 1873	✓		✓	✓
Total number of species	**13**	**3**	**10**	**12**

The results differed with sampling method. Groynes with a constant connection to the sea supported significantly greater mean NNS richness using semi-quantitative (Table 2-9b; Figure 2-10) but not quantitative techniques (Table 2-9a). NNS assemblage composition was significantly different between "connected" and "unconnected" groynes using both sampling methods (Table 2-9a, b; Figure 2-11). SIMPER analysis showed that, when analysing quantitative data, the average dissimilarity between "connected" and "unconnected" groynes was 97.4%, of which over 75% of those differences were attributed to *T. inopinata* (63.5%) and *W. subatra* (15.0%). Abundances of *T. inopinata* were greater on "unconnected" groynes, while *W. subatra* abundances were greater on "connected" groynes (Table 2-10a). SIMPER analysis of semi-quantitative data revealed that NNS assemblage compositions on "connected" and "unconnected" groynes were 83.7% dissimilar, with over a third of the dissimilarity attributable to *G. turuturu* (12.5%), *T. inopinata* (12.2%) and *A. modestus* (11.5%), with all species more abundant on "connected" groynes (Table 2-10b).

Table 2-9. PERMANOVA results for NNS richness and assemblage composition using (a) quantitative data and (b) semi-quantitative data between structures connected to the sea compared to structures not connected to the sea. Where unique permutations were < 100, Monte Carlo tests were run and P(MC) values were used to determine significance. Significant p-values are bolded.

(a) Quantitative data

One-way ANOVA comparing NNS richness between structures connected and not connected to the sea.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Connection	1	141.03	141.03	0.61079	0.4368	68	0.4477
Residual	158	36483	230.91				
Total	159	36624					
Transform	pres/abs						

One-way PERMANOVA comparing NNS assemblage composition between structures connected and not connected to the sea.

Source	df	SS	MS	Pseudo-F	P(perm)
Connection	1	1688.7	1688.7	6.1388	**0.0008**
Residual	158	43464	275.09		

Total	159	45153
Transform	square root	

(b) Semi-quantitative data

One-way ANOVA comparing NNS richness between structures connected and not connected to the sea.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Connection	1	5514	5514	8.6482	0.0591	18	**0.0123**
Residual	6	3825.5	637.59				
Total	7	9339.5					
Transform	pres/abs						

One-way PERMANOVA comparing NNS assemblage composition between structures connected and not connected to the sea.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	(MC)
Connection	1	5318.1	5318.1	4.6495	0.0572	25	**0.0323**
Residual	6	6862.7	1143.8				
Total	7	12181					
Transform	square root						

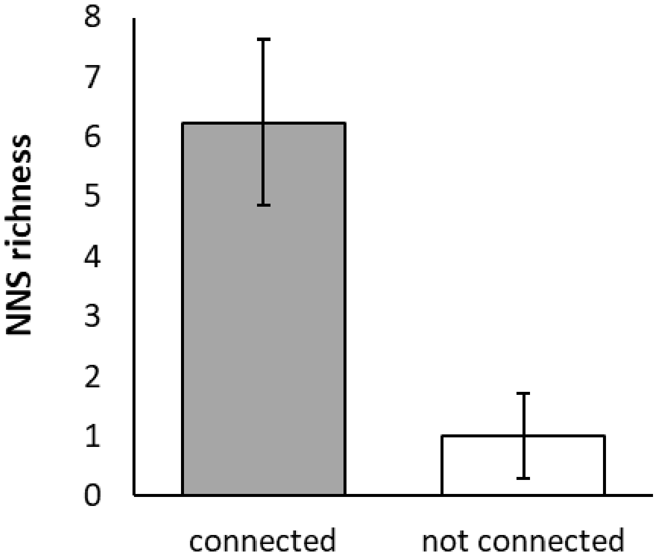


Figure 2-10. Comparison of NNS richness between structures connected to the sea and structures not connected to the sea. Numbers of NNS were significantly greater on “connected” structures compared to “unconnected” structures (semi-quantitative data; connected, n = 4; not connected, n = 4; p = 0.0123).

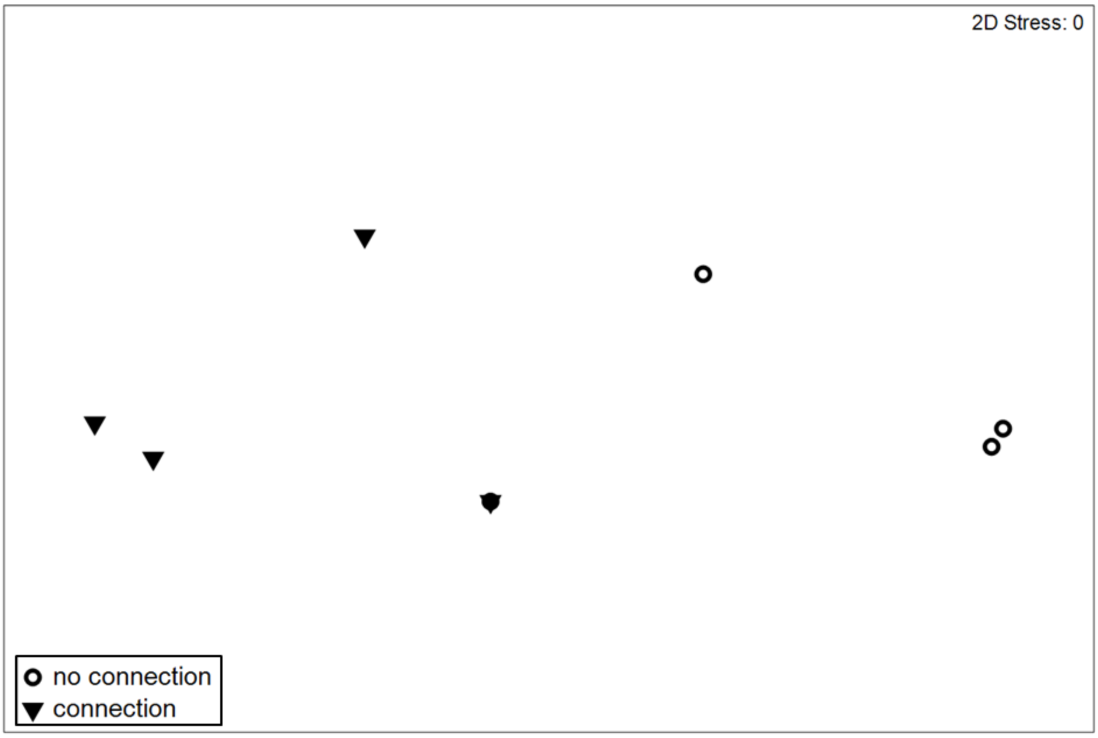


Figure 2-11. Non-metric multi-dimensional scaling plot (nMDS) showing significant variation in NNS assemblage composition on structures connected to the sea compared to structures not connected to the sea (semi-quantitative data; connected, n = 4; not connected, n = 4; p = 0.0323).

Table 2-10. Differences in average abundances (indicated by > or <) and contributions (%) of individual species to assemblage composition dissimilarities between "connected" and "unconnected" groynes using (a) quantitative data and (b) semi-quantitative data. Consistency of contribution is shown by ‘Diss/SD’, which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(a) Quantitative data

Average dissimilarity = 97.4%	**No connection**	**>/<**	**Connection**	**% Contr.**	**Diss/SD**
Tricellaria inoptinata (%)	0.2	>	0.1	63.5	1.4
Watersipora subatra (%)	0.0	<	0.1	15.0	0.5

(b) Semi-quantitative data

Average dissimilarity = 83.7%	**No connection**	**>/<**	**Connection**	**% Contr.**	**Diss/SD**
Grateloupia turuturu (%)	0.3	<	0.8	12.5	0.9
Tricellaria inopinata (%)	0.6	<	0.8	12.2	0.9
Austrominius modestus (%)	0.3	<	0.7	11.5	1.0
Watersipora subatra (%)	0.0	<	0.8	10.9	1.5
Botrylloides diegensis (%)	0.0	<	0.8	10.9	1.5
Undaria pinnatifida (%)	0.0	<	0.8	10.9	1.5
Codium fragile ssp. *fragile* (%)	0.0	<	0.5	10.9	0.8

2.4 Discussion

This study addressed knowledge gaps concerning occurrence of NNS in natural and artificial intertidal habitats along the south coast of England. The surveys found that artificial structures supported different assemblage compositions of NNS compared to natural rocky shores. Differences in NNS richness, however, depended on sampling method used: quantitative methods detected significantly greater numbers of NNS in artificial compared to natural habitats, while semi-quantitative methods found no differences. NNS assemblage composition was significantly different among regions and harbours within regions. NNS richness among regions was significantly different, while differences among harbours within regions depended on sampling technique: quantitative sampling showed significant differences among harbours, but semi-quantitative did not show differences. Artificial structures in the Central region supported the greatest number of NNS compared to the West and East regions, and this was positively correlated with the average number of vessel arrivals per day. Finally, as predicted, groynes with a constant connection to the sea at low water supported greater numbers and different NNS assemblage compositions compared to “unconnected” groynes.

Artificial structures supported more NNS than natural rocky shores and the suite of species varied markedly when quantitative data were analysed, corroborating results from previous studies (Glasby et al., 2007; Tyrrell and Byers, 2007; Dafforn et al., 2012). However, semi-quantitative methods, which involved timed searches of entire sites, did not detect significant differences between habitats. This is because the semi-quantitative method allowed complex habitats, such as rock pools and undersides of boulders, to be searched for presence of NNS. The algae, *U. pinnatifida*, *G. turuturu* and *A. armata*, were present only in natural habitats; *C. peregrina* and *S. muticum* were more abundant in natural compared to artificial habitats. These algae were only found in rock pools (and in the case of artificial habitats, water-retaining gaps in the structures), implying that if quantitative measures were to have been used alone, this suite of NNS would have been almost entirely overlooked.

The jump from artificial structures to natural habitats is not uncommon for NNS (Floc'h et al., 1991; Connell, 2001; Coutts and Forrest, 2007; Dafforn et al., 2012; Heiser et al., 2014; Epstein and Smale, 2018). In the southwest of England, *U. pinnatifida* in particular is commonly found attached to floating pontoons in marinas in a state of continuous immersion (Fletcher and Manfredi, 1995; Arenas et al., 2006a; Epstein and Smale, 2018), but information about its abundance in intertidal natural and artificial habitats is lacking (but see Heiser et al., 2014). A recent report found *U. pinnatifida* in the intertidal to shallow subtidal fringe on natural rocky shores in harbours in the southwest of England (Epstein and Smale, 2018). Results from Epstein and Smale (2018) suggested that the natural rocky shore populations were a result of a ‘spillover’ from populations in marinas, as there was a positive correlation between proximity to marinas supporting *U. pinnatifida* and its abundance on natural shores. The current study found *U. pinnatifida* on natural rocky shores in Plymouth and Torbay, both sites of which are adjacent to marinas where *U. pinnatifida* has been recorded (Arenas et al., 2006a; Farrell and Fletcher, 2006; Epstein and Smale, 2018). Findings from natural habitats surveyed in this study support results from previous studies and emphasize the high probability of NNS spread out from artificial into natural habitats.

Results from the current study found that NNS richness among regions was significantly different, with the Central region supporting the greatest number of NNS. This result supports those from previous surveys (Bishop et al., 2015b; Wood et al., 2015; Foster et al., 2016), which found the greatest number of NNS in marinas within the Central region of England. Similar to results from the current study, Bishop et al. (2015b) recorded the fewest numbers of NNS in the eastern English Channel compared to the central and western English Channel. Although a relative paucity of suitable sites limited the number of potential sample sites available for this study and Bishop et al. (2015b), the close similarity of NNS richness in our study suggests that NNS richness is actually lower in the East (6 NNS found in this study; 5 NNS found in Bishop et al. 2015b). As the Central region sees the most vessels per day by a significant amount, it is no surprise that this area supports the greatest number of NNS. Dover (East region), however, sees a relatively large amount of vessel traffic, yet counter to what would be expected, NNS richness was relatively low here. Variation in local environmental conditions and estuary morphology might explain these biological differences. For example, previous studies have shown that industrial and urban runoff adversely affects native composition and ecological functioning of marine communities (Johnston and Roberts, 2009; Burton and Johnston, 2010), and that species response (recolonisation) can vary depending on exposure to particular contaminants (Trannum et al., 2004). Additionally, NNS have been shown to tolerate contaminants and pollution while abundances of native species decline under the same conditions (Crooks et al., 2011; Dafforn et al., 2011; McKenzie et al., 2011). Thus, a decline in native biotic communities can easily give NNS a competitive advantage where conditions are unfavourable for native species (Johnson et al., 2017). Southampton in particular is characterised by commercial shipping and industry. The western bank of the River Test has a large industrial park that houses a power station, which intakes local water for coolant and discharges much warmer water relative to ambient conditions (~5 °C; K. O’Shaughnessy, pers. obs; Appendix 1, Table 2). These unnatural conditions undoubtedly affect the biotic communities on structures adjacent to the power plant, with potential effects downstream. The relatively high number of NNS in Poole (considering the low occurrence of vessel traffic) compared to neighbouring harbours might be explained by differences in estuary morphology and hydrography. Poole has been described as a “lagoon-like” harbour, as it is a shallow and warm body of water with a narrow estuary mouth and a small tidal range (approx. 1.8 m; Humphries, 2005; May, 2005; World Port Source, 2019). A double high water holds water above mean tide for up to 16 hours (May, 2005), and slow flushing times allow for retention of water and particles, including metal and organic pollutants (May, 2005; May and Humphreys, 2005). Compared to the larger and deeper harbours in the Central region that support larger and more vessels – Southampton and Portsmouth – Poole would logically support many fewer NNS. It is possible that more NNS are found in Poole Harbour relative to other Central harbours because the warm conditions are favourable to NNS that originate from subtropical waters (Walther et al., 2009), such as the carpet sea squirt, *D. vexillum*. Moreover, slow and incomplete flushing of the harbour means larvae of NNS are present in the water for long periods of time, potentially allowing increased settlement compared to harbours with faster flushing times. Findings from these surveys therefore highlight the difficulty in teasing apart potential factors driving NNS colonisation on artificial structures in a variety of harbours and regions.

Observed variation in NNS assemblage composition among harbours and regions is probably linked to the numbers and types of vessels arriving in harbours and the subsequent secondary destinations to which species can be transported, facilitating immigration and spread of NNS (Carlton, 1996b; Floerl and Inglis, 2005; Defra, 2015). For example, Portsmouth and Southampton (Central region) are, on average, the busiest harbours along the south coast of England (Associated British Ports, 2019), but the types of vessels, and their embarkation ports, vary greatly. The Port of Southampton is unique in our survey in being one of the largest cruise ship and container ports in the UK, accommodating vessels that travel worldwide (Associated British Ports, 2019). Additionally, it hosts one of the largest oil refineries in the UK, which sees over 2,000 vessels annually (Exxon Mobile, 2019). Consequently, many more vessels sail internationally from here compared to other ports along the south coast of England. Southampton also has significant recreational marinas adjacent to the port in former commercial docks, with a large concentration of marinas in Southampton Water and the Solent more generally. By contrast, the majority of passenger vessels in Portsmouth and Poole are ferries sailing no further than Northern France, and most other traffic (excluding the naval ships at Portsmouth) being local fishing and pleasure craft. Therefore, at least two invasion scenarios are possible: (1) international container ships and cruise liners transport NNS as fouling adults or as planktonic larvae in ballast water into the Port of Southampton (Ruiz et al., 2000); or (2) trans-channel vessels carry NNS (originating from Europe or introduced from other parts of the world) from the north of France and Spain into Portsmouth and Poole Harbours (Bax et al., 2002; Bishop et al., 2013). Species originating in the Pacific (i.e., *B. violaceus*, *M. gigas*, *D. vexillum*) were most likely introduced to the British Isles by way of vessel traffic from Europe (Eno et al., 1997; Bishop et al., 2015a; Defra, 2015; Foster et al., 2016). In both scenarios, NNS then probably spread to neighbouring ports via local vessel traffic (Clarke Murray et al., 2011; Zabin et al., 2014; Roche et al., 2015) and/or using artificial structures (e.g., groynes; Mineur et al., 2012; Airoldi et al., 2015a) as ‘stepping stones’ (Floerl and Inglis, 2005; Bishop et al., 2017; Johnson et al., 2017). It is likely that both scenarios act in synergy to create a constant influx of hitchhiking species on large trans-channel and international vessels into ports along the south coast of England.

Artificial structures are characterised by low species diversity compared to natural rocky shores (Chapman, 2003; Bulleri and Chapman, 2010), which means they are less resilient to colonisation by NNS (Maron and Vilà, 2001; Stachowicz et al., 2002). They endure regular disturbances from human trampling, maintenance (Airoldi and Bulleri, 2011), vessel docking (K. O’Shaughnessy, pers. obs.) and wash from propellers on large vessels. Moreover, their proximity to transoceanic vessels means artificial structures endure increased propagule pressure and repeated introductions. For example, an average of over 80 vessels per day dock in Portsmouth Harbour, which is likely to cause dislodgement of species fouling docks, chains and other equipment. This opens up bare space for opportunistic and NNS to colonise (Airoldi and Bulleri, 2011; Bracewell et al., 2012). Smaller harbours with less vessel traffic and fewer artificial structures, such as Salcombe and Looe, experience fewer disturbances and have less hard substrate present, contributing to lower invasion success.

Artificial structures may play an important role in the introduction, establishment and spread of NNS. They are typically built in soft sediment habitats because of the lack of hard substrate that naturally protects the coastline against flooding and erosion (Dugan et al., 2011; Firth et al., 2013a). On a regional scale, artificial structures provide new substrata for the spread of opportunistic and NNS by acting as ‘stepping stones’ across soft sediment habitat (Floerl and Inglis, 2005; Coutts and Forrest, 2007; Dafforn et al., 2009; Bishop et al., 2017). In so doing these structures may increase connectivity between distant or isolated ‘hard bottom’ habitats (Sammarco et al., 2004; Airoldi et al., 2005a; Mineur et al., 2012). In this study, harbours east of Torbay (Central and East regions) were dominated by soft sediment habitats, thus fouling organisms typical of natural rocky shores were only able to survive by colonising hard artificial substrate in these harbours (e.g., floating pontoons, seawalls, groynes). It is therefore possible that artificial structures in soft sediment habitats act as simplified surrogates of natural rocky shore (Thompson et al., 2002; Moschella et al., 2005), in that NNS would not have otherwise been able to become established without these structures in place.

Groynes that retained a constant connection to the sea at low tide supported greater numbers of NNS compared to groynes that did not retain a connection at low tide. This result was not surprising, as structures in subtidal habitats are continually exposed to a pool of colonising species throughout the entire tidal cycle. These results agree with past reports of greater species diversity in lower intertidal to subtidal habitats (Saier, 2002; Moschella et al., 2005; Burcharth and Lamberti, 2007; Chapman and Underwood, 2011; Dugan et al., 2011; Firth et al., 2016a). Even though sampling was conducted at about the same tidal height for both “connected” and “unconnected” groynes, the differences in NNS richness might be due to the susceptibility of the structure to invasion. For example, it is possible that once a structure is colonised, species will reproduce and spread across the structure where physical conditions allow. And since subtidal structures are more likely to be colonised (Moschella et al., 2005;

Chapman and Underwood, 2011; Dugan et al., 2011), the connected structures are more susceptible to NNS colonisation in general. Additionally, "connected" groynes are exposed to frequent wave action, and therefore will experience more disturbances (Griggs, 2005; Dugan et al., 2011), which create bare space for NNS colonisation (Airoldi and Bulleri, 2011). NNS recorded on "unconnected" groynes might be regarded as high-risk species, as they are able to take advantage of substrate regardless of connection to a constant supply of propagules, allowing for their proliferation and spread. More importantly, groynes placed along a sandy beach that extend into subtidal habitats are likely to act as corridors or 'stepping stones' for NNS between distant areas (Floerl and Inglis, 2005; Airoldi et al., 2015b; Bishop et al., 2017). This may be of particular concern in situations where groynes are built along a sandy beach adjacent to a major international shipping harbour that is known to support an abundance of NNS. Potential implications of increased connectivity (i.e., presence of artificial structures) between international ports and distant habitats might involve increased facilitation of NNS spread from these ports – 'hot spots' for ecological invasion (Carlton and Geller, 1993; Ruiz et al., 1997; Drake and Lodge, 2004) – to natural habitats (Epstein and Smale, 2018), where the new species may outcompete or smother native biota (e.g., the carpet sea squirt, *D. vexillum*; Lengyel et al., 2009).

Study 3 (comparison of "connected" versus "unconnected" groynes) was an opportunistic and preliminary study done on a small-scale with few replicates. Tidal height was determined by estimating similar shore heights from observations of the tide receding. Methods to determine exact tidal height on each structure did not utilise beach profiling equipment, thus the established tidal height on each groyne was not precise. This may be an important consideration because this study was conducted in Poole, which is a microtidal environment (1.8 m tidal range); therefore, the differences in physical and biological factors between mid- and lower intertidal are minimal and difficult to determine without appropriate scientific equipment. Therefore, further surveys with precise measurements of tidal height on groynes that incorporate many replicates are still needed.

Horizon scanning, early detection measures and continual monitoring are key to preventing the establishment of NNS (Eno et al., 1997; Manchester and Bullock, 2000; Mehta et al., 2007). Horizon scanning identifies potential future invaders, assesses the impact they may have on the receiving ecosystem and develops a management plan so that action can be taken in the early stages of introduction (Eno et al., 1997; Manchester and Bullock, 2000; Coutts and Forrest, 2007). Management plans should take a joined-up approach, in which all interested and responsible parties (e.g., stakeholders, scientists, government, permitting bodies) are included throughout the planning process for rapid response (Bax et al., 2002; Wotton et al., 2004; Anderson, 2005), as delays in action can compromise the eradication process (see Coutts and Forrest, 2007). Successful eradication or control is dependent on early detection of NNS, which is difficult due to low densities during initial introduction stage (Mehta et al., 2007; Rees et al., 2014). This means that detection by traditional methods is often ineffective (Mehta et al 2007). Traditional methods of detection involve visual surveys usually conducted by expert taxonomists in marinas known to be hotspots for invasion (e.g., the Solent region in southern England; Tidbury et al., 2014; Bishop et al., 2015b; Defra, 2015; Foster et al., 2016). The high numbers and abundances of NNS recorded from intertidal surveys during the current study, however, demonstrate that surveys should be conducted in a range of different habitats (e.g., low-, mid- and high-intertidal, subtidal; artificial, natural), and not confined to the most common structures known to support NNS (i.e., marina pontoons). This is because vital information about NNS introduction and distribution could be overlooked if some habitats are neglected. For example, some NNS, such as *S. muticum*, were actually first recorded in the British Isles from natural habitats (Farnham et al., 1973; Boalch and Potts, 1977). Moreover, the current study showed that *S. muticum* was more abundant in natural habitats, arguably posing a threat to natural ecosystems, as they may facilitate biotic homogenization of natural rocky shores (McKinney and Lockwood, 1999; McKinney, 2006). As demonstrated in the current study, a combined approach to sampling may be most effective in capturing all NNS present. For example, *S. muticum* and *C. peregrina* were rarely detected by quantitative measures in natural habitats, despite their abundances being relatively large. This was due to the ability of semi-quantitative methods to capture species in complex habitats, such as crevices, rock pools and undersides of boulders, which were the favourable habitats of these NNS. Although using combined sampling techniques in a variety of habitats may be the best traditional approach, these certainly are not the most efficient means of detection. Non-traditional methods for detecting NNS have recently included employing eDNA techniques (Valentin et al., 2018; Xia et al., 2018). This novel method identifies presence of all species within a single sample of material (e.g., soil, permafrost, snow) or water (freshwater, saltwater) and is a more sensitive and less destructive alternative to traditional monitoring (Takahara et al., 2013; Rees et al., 2014; Klymus et al., 2015). Unfortunately, there is not a “one size fits all” approach for early detection of NNS, thus, a range of different approaches employed in a variety of habitats may be the most comprehensive option.

Eradication and control of NNS are more effective if managed from the early stages of introduction before the NNS establishes a reproducing population and becomes widely distributed (Eno et al., 1997; Coutts and Forrest, 2007; Mehta et al., 2007). Methods of eradication and control can be physical (Coutts and Forrest, 2007; Guy and Roberts, 2010), biological (Atalah et al., 2016) or chemical (Coutts and Forrest, 2007) in nature. Physical techniques involve mechanical removal or smothering of the NNS. For example, a cull on the non-native Pacific oyster, *M. gigas*, in Northern Ireland involved destroying oysters with hammers, reducing the population by nearly 100% (Guy and Roberts, 2010). Subsequently, similar eradication techniques have been implemented in the southeast of England (Herbert et al., 2012). Coutts and Forrest (2007) wrapped pilings infected with *D. vexillum* in polyethylene to reduce water flow to the animal and cause anoxic conditions. Removal of any space-occupying organism, however, puts the bare substrate at risk of being recolonised by NNS. Biological control, or “biocontrol” uses native enemies or parasites (use of NNS is highly discouraged; Atalah et al., 2015) to reduce or control the density-dependent adverse effects of NNS or pests (Atalah et al., 2015; Great Britain Non-Native Species Secretariat, 2019) . While biocontrol methods are widely used to control NNS in terrestrial systems, there are few marine examples that have been tested *in situ* (Secord, 2003) and considerable knowledge gaps exist which need addressing before biocontrol can be used as a reliable NNS management tool in the marine environment (Secord, 2003; Atalah et al., 2016). Chemical controls utilise substances such as chlorine to kill NNS (Coutts and Forrest, 2007; Sambrook et al., 2014) or copper to discourage settlement of fouling organisms (i.e., anti-fouling paints; Eno et al., 1997; Maréchal and Hellio, 2009; Lindgren et al., 2018). Copper-based anti-fouling paints have been shown to be toxic to native biotic communities (Eno et al., 1997; Maréchal and Hellio, 2009; Piola et al., 2009; Dafforn et al., 2011), and some NNS actually show resistance to these paints (Piola et al., 2009). Regulatory bodies have responded by increasing regulations on biocides (i.e., copper; Dafforn et al., 2011), which has subsequently prompted research and development into non-toxic alternatives (Maréchal and Hellio, 2009; PML Applications Ltd, 2019). One such alternative mimics the characteristics of natural physical surface topography of marine organisms (e.g., molluscan shells, crustose coralline algae, marine mammal skin, shark skin) – which are often naturally free of fouling organisms – to discourage settlement (Scardino, 2009; "bio-inspired antifouling"; Kirschner and Brennan, 2012; Nir and Reches, 2016; Pradhan et al., 2019). Bio-inspired anti-fouling techniques are still to a large extent in the experimental phase (Damodaran and Murthy, 2016; Pradhan et al., 2019); however, future application may help aid in NNS management, especially if used in concert with traditional techniques.

Results from these surveys clearly demonstrate that eco-engineering designs must consider the potential for colonisation by NNS (Sella and Perkol-Finkel, 2015; Dafforn, 2017; Strain et al., 2017a). This is of particular concern when designs involve adding new hard substrate to an existing structure, as any substrate placed in the sea is a blank canvass for opportunistic and NNS colonisation (Airoldi, 2000; Bulleri and Airoldi, 2005; Airoldi and Bulleri, 2011). Results from Study 3, testing the effects of groyne connection to the sea on NNS occurrence, can inform eco-engineering decisions regarding placement of interventions in relation to tidal height. As biodiversity in general is greater in lower compared to upper intertidal habitats (Moschella et al., 2005; Dugan et al., 2011), eco-engineering intervention outcomes would likely be maximised with placement in the lower intertidal (Chapman and Underwood, 2011; Firth et al., 2016a); yet interventions placed here run the risk of facilitating spread of NNS. Additionally, NNS may have different reproductive seasons than their native counterparts, meaning there is less competition for space when larvae settle. For example, in the British Isles, the native barnacle, *Semibalanus balanoides* (Linnaeus, 1767), reproduces in the spring (Barnes and Barnes, 1968), while reproduction of the non-native barnacle, *A. modestus*, is year-round with a peak in the autumn (O'Riordan and Murphy, 2000; Gallagher et al., 2015). Therefore, the timing (Airoldi and Bulleri, 2011; Evans, 2016) and placement (Chapman and Underwood, 2011; Firth et al., 2016a) of artificial structures and eco-engineering interventions may be important (but difficult to achieve in practice) in allowing native communities to develop, thereby discouraging settlement of NNS.

There are considerations that should be noted for future rapid assessment surveys of NNS. In these studies, sampling effort among harbours was not equal in Study 1 (comparing occurrence of NNS between natural and artificial habitats) and Study 2 (comparing occurrence of NNS among harbours and regions along the south coast of England). For example, more surveys were done in larger harbours such as Portsmouth (n = 11), while fewer surveys were conducted in smaller harbours such as Folkestone (n = 1). The rationale for varying the number of surveys by harbour was to reflect the size of the harbour so as to not oversample small harbours. Chapman et al. (2018) noted that species are more likely to be sampled in a smaller area where there is a more intense sampling effort. The goal of the current methods was to keep the ratio of surveys to available habitat fairly constant (i.e., fewer number of surveys in small harbours and greater number of surveys in large harbours). Future rapid assessment surveys should ensure that sampling effort is appropriate for hypotheses posed. Also, as artificial structures are often located in difficult to access areas that pose safety hazards, no restriction on type and size of structure was imposed during these studies in order to ensure an adequate sampling effort (i.e., many structures could not be safely accessed so they were removed from the list of potential sampling sites from the onset of the study). Therefore, criteria for structures surveyed was ease of access to structure and the structure reaching into the lower intertidal. Thus, structures of different types (e.g., rip rap revetment, groynes, seawalls) and composition (e.g., wood, rock) were sampled without consideration of differences. These may be important considerations (Connell, 2001; Hanlon et al., 2018), as Hall (2018) demonstrated that wooden groynes supported greater numbers of species than rock groynes. Study 3 was a preliminary study that had certain limitations, including qualitative methods in locating tidal height in a microtidal environment (Poole, UK) and low replication and sampling effort. These data are valuable as preliminary results, but future studies using equipment for measuring exact tidal height should be employed in specific locations prior to planning coastal construction.

2.4.1 Concluding remarks

This study provided an inventory of intertidal NNS in harbours along the south coast of England, complementing previous Rapid Assessment Surveys conducted along the same geographic region in subtidal habitats (Arenas et al., 2006a; Bishop et al., 2015a; Bishop et al., 2015b). As such, this and previous reports provide a comprehensive summary of the suite of NNS present in harbours along the south coast of England.

Our results highlight the importance of global shipping and transportation for the primary introduction of NNS and the role of artificial structures and smaller vessels in facilitating secondary spread to neighbouring harbours and bays. Our surveys also suggest that most hard substrates along the coast will host some NNS, but the suite of species will vary between topographically complex natural, and less complex artificial habitats.

Ocean sprawl is accelerating the rate of NNS introduction and spread, contributing to biotic homogenisation and the growing biodiversity crisis. Understanding the ecological role of artificial structures in the marine and coastal environments is critical for preserving native biodiversity and building resilience to establishment of NNS. Factors affecting the degree of invasibility need urgent investigation so that ecologists might develop the predictive capability to identify harbours at high risk of invasion, which can aid in effective horizon scanning.

3. CHAPTER THREE

Impacts of coastal urbanisation on species diversity are scale and metric dependent

Abstract

Burgeoning human population and habitat modification is driving a global biodiversity crisis. Population growth is focussed on coastlines worldwide leading to accelerated habitat transformation to accommodate industry, commerce, transport and residential development. Furthermore, coastlines are being squeezed by rising and stormier seas as a consequence of climate change. Subsequently, artificial structures (e.g., seawalls, groynes, breakwaters) have replaced natural habitats, placing extraordinary stress on coastal and marine biodiversity and ecosystem functioning, with knock-on effects for ecosystem services. The need for reliable measures to obtain baseline diversity data, detect changes in biological communities in response to human drivers and inform and measure success of restoration efforts is becoming increasingly important. In this study, sites were surveyed within an urbanised harbour to assess species diversity in natural and artificial habitats at two spatial scales: within-site (centimetres - metres) and among-site (metres - kilometres) using different diversity measures (taxon and functional richness, taxon and functional abundance and β-diversity). Regional species diversity (γ-diversity) did not differ between natural and artificial habitats, while mean taxon (α-diversity) and functional richness were greater in natural compared to artificial habitats at both spatial scales. Within-site β-diversity was greater in natural compared to artificial habitats, while among-site β-diversity was greater in artificial compared to natural habitats. Taxon richness and abundance of mobile organisms were greater in natural habitats, while taxon richness but not abundance of sessile organisms was greater in natural habitats. Differences in taxon and functional abundance depended on specific taxonomic and functional groups. Different results obtained under various

measures and scales of analyses highlight the importance of looking beyond simple conventional methods of measuring diversity (i.e., taxon richness) to reduce the risk of overlooking valuable ecological information. Understanding the ecological role of artificial structures is critical for preserving biodiversity in the face of continued coastal development and is the first step in informing management decisions for eco-engineering interventions for restoring urban coastlines.

3.1 Introduction

The global human population continues to grow (Bloom, 2011; Gerland et al., 2014), with markedly higher population growth in coastal areas (Hugo, 2011; Barragán and de Andrés, 2015; Neumann et al., 2015; Firth et al., 2016b); all while the world is facing the certainty of sea level rise and stormier seas (Church and White, 2006; Nicholls and Cazenave, 2010; Bader et al., 2011; Field et al., 2012). The majority of mega-cities are located within the coastal zone (Timmerman and White, 1997; Firth et al., 2016b), hence ways in which to protect human lives and infrastructure from rising sea levels are becoming increasingly necessary, giving rise to coastlines dominated by engineered artificial structures (e.g. seawalls, groynes, breakwaters; Vitousek et al., 1997; Duarte, 2014; Firth et al., 2016b). One of the many consequences of hard engineered coastlines is the degradation or loss of coastal and marine habitats (i.e., salt marshes, rocky shores, coral reefs, seagrass beds; Bulleri and Chapman, 2010; Firth et al., 2016b; Morris et al., 2019). Subsequently, the biodiversity (Bulleri and Chapman, 2004; Bulleri et al., 2005; Moschella et al., 2005), ecological structure (Airoldi and Beck, 2007; Jackson et al., 2008b; Aguilera et al., 2014), functioning (Airoldi and Beck, 2007; Mayer-Pinto et al., 2018a) and connectivity (Firth et al., 2016b; Bishop et al., 2017) of coastal and marine ecosystems has become compromised. Furthermore, the movement of climate migrants (Mieszkowska et al., 2006) and opportunistic and non-native species (Dafforn et al., 2009; Dafforn et al., 2012; Sammarco, 2015; Bishop et al., 2017), as well as biotic homogenization (McKinney and Lockwood, 1999; McKinney, 2006) is aided in some instances by artificial structures themselves (Mineur et al., 2012; Airoldi et al., 2015a). Thus, there is a growing need to measure anthropogenic impacts on biodiversity so that risks can be evaluated and management strategies, such as mitigation and compensation, can be implemented (Bas et al., 2016).

Biodiversity is composed of three components: genetic diversity, species diversity and ecosystem diversity (Convention on Biological Diversity, 2006; Colwell, 2009). Species diversity is comprised of both species richness (number of different species present in a given area regardless of identity) and relative abundance (number of individuals of each species; Colwell, 2009; Tuomisto, 2010a). Ecologists and conservationists frequently focus only on the ‘species’ part of biodiversity, often mislabelling “species diversity” as “biodiversity” (Colwell, 2009). Furthermore, mean species richness is commonly used in ecological-based studies as the sole measurement of biodiversity (e.g., Chapman, 2003; Firth et al., 2013b; Firth et al., 2014a). Using species richness as a proxy for biodiversity is an imperfect measure (Costanza et al., 2007), but it is often the only way to assess diversity with limited resources. It is becoming evident, however, that assessments should consider more than number of species alone, as this measure ignores other aspects of biodiversity, such as identity and abundance of species, functional roles and spatial scales (Chapman et al., 2009; Winfree et al., 2015), as well as habitat patch diversity (Hawkins, 2003; Giller et al., 2004). Moreover, mean species richness may not be sensitive enough to detect important differences between levels of factors in a study or experiment, and therefore may overlook ecological information necessary for conservation and management decisions (Warwick and Clarke, 1998; Winfree et al., 2015; Hillebrand et al., 2018). For example, when examining differences in species richness between artificial rock pools in the lower and upper intertidal zone, Firth et al. (2016a) found no significant difference in mean species richness between treatments, despite there being nearly double the total number of species found in lower (63) compared to upper (37) pools; in addition to significant differences in β-diversity and community composition between shore heights. Whilst the relative difference in average species richness was ecologically relevant, this was not detected through a statistical comparison of means. This same study examined species richness from two different time points (12 mos. and 24 mos.), with nearly four times the number of species observed at month 24 compared to the first sampling event. These differential results emerging from one experiment highlight the importance of looking beyond simple diversity measures (mean α-diversity) and considering different spatial and temporal scales where possible. Ecologists must therefore be aware that diversity values may be perceived differently based on how they are quantified.

At the smallest scale, alpha (α) diversity is a measure of local species diversity (number of species) within a particular patch or sampling unit. At the broadest scale, gamma (γ) diversity is a measure of regional species diversity and represents the total pool of species in a defined area (Tuomisto, 2010b; Anderson et al., 2011). In between, beta (β) diversity is a measure of the variation in identities of species among sampling units in a given area (Anderson et al., 2011). β-diversity was originally defined by Whittaker (1960) as $\beta_w = \gamma/\alpha$, and has since been debated at length and it has subsequently been modified to describe diversity in different ways (e.g., relative abundnace, Shannon Index; Gering et al., 2003; Anderson et al., 2006; Anderson et al., 2011). β-diversity is commonly used to examine the scale at which community composition differs among groups, shedding light on factors and processes driving differences among communities (Bevilacqua et al., 2012; Barros et al., 2014; Porter et al., 2018).

Coastal artificial structures are generally considered poor substitutes for their natural rocky shore counterparts (Thompson et al., 2002; Chapman, 2003; Lai et al., 2018) and can at best be described as “ersatz” rocky shores (poor substitutes for rocky shores; Moschella et al., 2005; Geist and Hawkins, 2016). Numerous studies have investigated differences in species diversity between natural and artificial habitats, but interestingly, the direction of results does not always agree. Many of these studies have found that natural habitats support greater numbers (Chapman, 2003; Moschella et al., 2005) and abundances (Chapman and Bulleri, 2003; Lai et al., 2018) of species compared to artificial habitats. However, other studies detected no differences between habitats (Bulleri et al., 2005), although results were dependent on a variety of factors such as tidal height (Chapman and Bulleri, 2003; Bulleri et al., 2005), orientation of substrate (Knott et al., 2004) and spatial scale of assessment (Bulleri et al., 2004; Firth et al., 2016a). Deficits in species diversity compared to natural shores have repeatedly been attributed to reduced topographic complexity (Moschella et al., 2005; Firth et al., 2013b), increased incline and reduced spatial extent of structures (Chapman and Underwood, 2011), as well as scouring as they often abut coarse sand, gravel or shingle shores (Dugan et al., 2011).

Interest among ecologists, governments and stakeholders in preserving and enhancing biodiversity and ecosystem functioning in heavily urbanised areas is increasing, and the shift towards ecologically-sensitive coastal engineering is gaining momentum (Evans et al., 2017, 2019; Morris et al., 2018a; Morris et al., 2019; Strain et al., 2019b). Ecologically-sensitive coastal development is a relatively new concept; the field is still very much in the “experimental phase”, with the majority of tested designs focussing on enhancement of species diversity through addition of topographic complexity on artificial structures (e.g., Moschella et al., 2005; Borsje et al., 2011; Chapman and Underwood, 2011; Firth et al., 2014b; Loke and Todd, 2016). Baseline survey data can help understand the biodiversity and ecological functioning of artificial structures compared to natural habitat, and is the first step in informing conservation and management decisions, as well as assessing the suitability of the habitats for eco-engineering interventions (Mayer-Pinto et al., 2017). As baseline survey data is often lacking or not adequate for informing management decisions (Legg and Nagy, 2006; Chee et al., 2017), species diversity surveys are urgently needed to support the development of eco-engineering designs that address site- and species-specific targets.

Whilst there is a general consensus that local mean species richness (α-diversity) is lower on artificial structures compared to natural rocky shores (e.g., Chapman, 2003; Gacia et al., 2007; Firth et al., 2013b), it is imperative to move beyond this simple biodiversity measure and consider a broader suite of response variables at a range of spatial scales. Using Plymouth Sound as a model system, in this study, we employed multiple different species diversity measures (taxon and functional richness, abundance and composition, as well as β-diversity) to assess species diversity differences between natural and artificial habitats. We used “taxon richness” rather than “species richness” because many organisms could not be identified down to species level. We predicted that all diversity measures would exhibit some difference among natural and artificial habitats, but that mean taxon richness alone would fail to capture the full scope of differences. We surveyed biological communities at 54 sites within natural and artificial habitats at two spatial scales – within-site (i.e., comparing quadrats (cm-m); α- and β-diversity) and among-site (i.e., comparing sites (m-km); α- and β-diversity) – to specifically test the following hypotheses: (1) natural habitats would support greater mean taxon and functional richness, taxon and functional abundance (number of individuals or percent cover per taxa or functional group) and different taxon and functional composition compared to artificial habitats at both spatial scales; and (2) natural habitats would support greater β-diversity compared to artificial habitats at both spatial scales. As Plymouth Sound receives freshwater input from multiple sources (see sec 3.2.1), we addressed salinity as a potential driver of differences in species diversity between habitats. Finally, maps of continuous α-diversity values were generated to visualise diversity patterns across Plymouth Sound.

3.2 Materials and methods

3.2.1 Model system: Plymouth Sound

Plymouth Sound (50.352222, -4.135556; Figure 3-1) is an outer estuarine inlet comprising a range of habitat types, including rocky reef, sandy beaches and mudflats, with a long history of reclamation and human modification of the land-sea interface; a third of the Sound is classified as artificial (Knights et al., 2016). Many areas in the Sound are designated as Sites of Special Scientific Interest (SSSI) and Special Areas of Conservation (SAC), with the area as a whole listed as a European Marine Site (Langston et al., 2003). Moreover, Plymouth Sound is soon to be the first National Marine Park in the UK, placing it at the same status as the UK's 15 National Parks. There is freshwater input from several rivers, the largest including the Rivers Tamar, Tavy, Plym and Lynher (Langston et al., 2003; Knights et al., 2016). The Sound is flanked by sloping natural rocky shores composed of Palaeozoic shale and limestone, which extend along the west and east coasts (Knights et al., 2016). Artificial structures to support human activity (i.e., piers, discharge pipes, breakwaters, seawalls) are interspersed among the natural habitats.

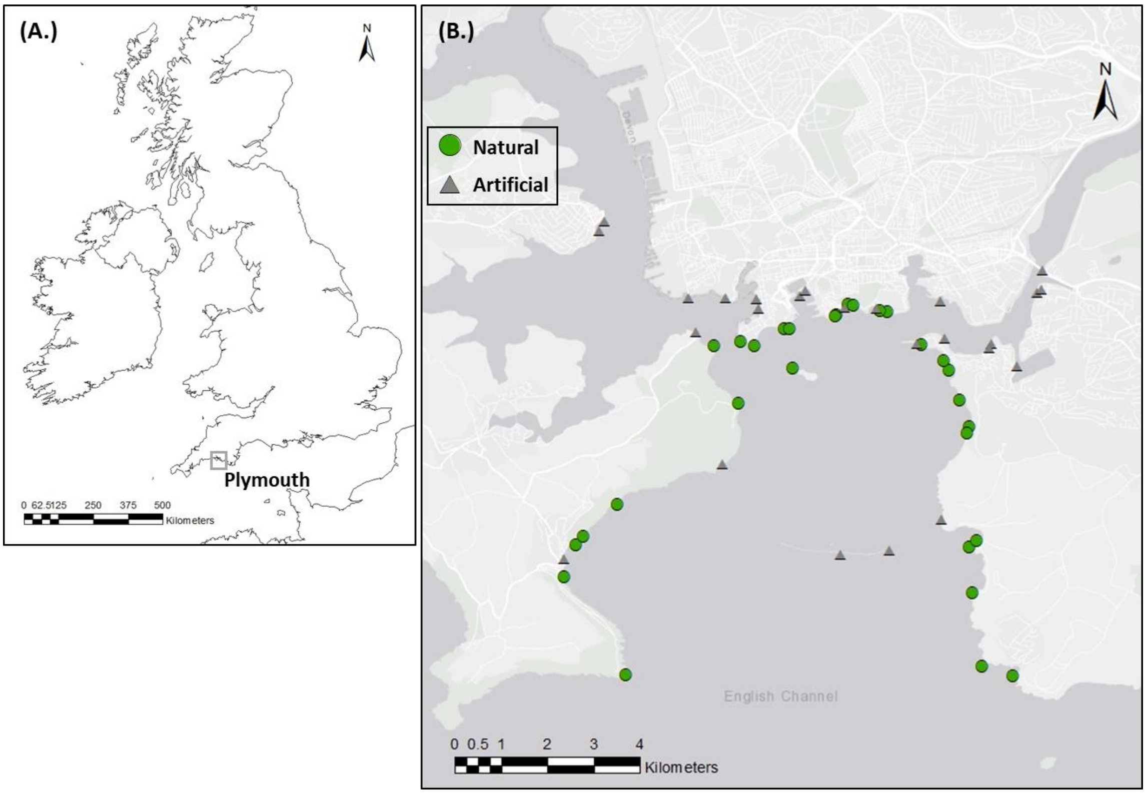


Figure 3-1. Surveys were conducted in (A.) the UK within (B.) Plymouth Sound. In (B.) green circles represent sites within natural habitats and grey triangles show sites within artificial habitats.

3.2.2 Survey design

Fifty-four sites were surveyed around Plymouth Sound, stretching from Penlee Point in the west to Wembury in the east; 29 surveys were conducted on natural rocky shores and 25 surveys were conducted on seawalls created from naturally sourced stone (Figure 3-1; see Appendix 2, Table 1 for site details). There were no natural sites surveyed up the mouths of both rivers, as natural sites are absent from these areas, and similarly, very few artificial sites were sampled in the south east and south west regions of the Sound due to the limited presence of artificial structures. Surveys were made in the mid-intertidal zone (1.5-2.5 m above CD) during low tide, within a 5 x 5 m “site”; although this area was slightly condensed in artificial habitats because the steeper slope of artificial structures results in reduced area available to survey and avoided problems of surveying a greater spread of tidal elevations. Surveys were made during summer and autumn of 2017 and 2018. At each site, 15 quadrats (25 x 25 cm) were haphazardly placed and all space-occupying biota within were identified and quantified. Recorded biota were > 1 mm and excluded epiphytes and species dwelling in trapped material such as silt and mud. Mobile organisms were counted, and sessile organisms were quantified using percentage cover. Organisms were positively identified down to species level whenever possible. When species-level identification was not possible, however, consistent morphotaxa were used (e.g., “Corallinaceae crust” for all calcareous encrusting red algal species). To standardise for slope and topographic complexity, only vertical or sloping (≥ 45° angle) substrata were sampled and ensuring quadrats were placed on freely draining smooth surfaces, rejecting those with pools or deep crevices. At each site, salinity (psu) and temperature (°C) were measured during the time of sampling (low water). Salinity was opportunistically measured at a subset of sites at high water under normal weather conditions, as well as following a severe rainfall event (December 2018) to obtain an estimate of low salinity extremes. To attain a more comprehensive picture of salinity in the area, field measurements were supplemented with historical observations from around Plymouth Sound (Milne, 1938; Butler and Tibbitts, 1972; Uncles et al., 1986; Uncles and Stephens, 1990; Siddorn et al., 2003). These sources included observations and modelled data from high and low water, spring and neap tides and year-round measurements.

3.2.3 Response variables

This study investigated the effects of habitat (natural, artificial) on the following response variables: (1) mean taxon richness (number of taxa); (2) mean functional richness (number of functional groups); (3) taxon abundance (number of individuals or percent cover per taxa); (4) functional abundance (number of individuals or percent cover per functional group); (5) taxon composition (number of taxa and their relative abundance); (6) functional composition (number of functional groups and their relative abundance); (7) β-diversity within sites (comparing quadrats) and (8) β-diversity among sites (comparing sites).

3.2.4 Statistical analyses

Taxon and functional richness (α-diversity; presence/absence data) and abundance were analysed at the quadrat and site scales separately. Taxa were categorised into major taxonomic (patellids, littorinids, trochids, Cirripedia, Porifera, Chlorophyta, Ochrophyta and Rhodophyta) and functional groups (grazer, omnivore, predator, lichen, thin filamentous, foliose, corticated macrophyte, leathery macrophyte, articulated calcareous, crustose, other algae and cyanobacteria; Littler and Arnold, 1982; Phillips, 1996; Arenas et al., 2006b). For mean richness, only taxonomic and functional groups with ≥ 5 individuals per group were used for analyses and shown in figures. Similarly, for mean abundance comparisons, only taxonomic and functional groups with ≥ 1 individual or 1% mean abundance were used for analyses and shown in figures. Prior to analyses, abundance data were square root-transformed to reduce the influence of very abundant species (Anderson et al., 2008). Data were “zero-adjusted” by adding a dummy species to every sample when necessary, and then Bray-Curtis similarity matrices were computed. Permutational multivariate analysis of variance tests (PERMANOVA; Anderson, 2001) were used to test for community composition differences between natural and artificial habitats, and were based on 9999 permutations of residuals under a reduced model. A two-way nested design was used for each test, with random factor Site nested in fixed factor Habitat (2 levels: natural and artificial).

To address the hypothesis regarding β-diversity, both classic (Whittaker, 1960) and multivariate (Anderson et al., 2006; Anderson et al., 2011) measures were employed to analyse differences in species assemblages at the quadrat (within-site) and site (among-site) scales (Figure 3-2). In terms of classic measures, additive β_w ($\beta = \gamma - \overline{\alpha}$) was used because $\overline{\alpha}$ and γ are expressed in the same units, allowing for easy interpretation and direct comparisons of α- and β-diversities across multiple studies (Gering et al., 2003; Crist and Veech, 2006; Anderson et al., 2011). Within-site $\overline{\alpha}$ was obtained from the mean taxon richness of all quadrats by site; while within-site γ was the total number of taxa recorded for each site. Among-site $\overline{\alpha}$ was calculated from mean taxon richness of all sites by habitat; while among-site γ was the total number of taxa recorded for each habitat. Multivariate measures were also used because Whittaker's β-diversity measures diversity for a given area, but cannot statistically test for differences among different areas (Anderson et al., 2006). Distance-based permutational tests for homogeneity of multivariate dispersions (PERMDISP) based on Sørensen distance matrices (presence/absence data) among *a-priori* groups were performed on the full communities (i.e., both sessile and mobile organisms; Anderson, 2006; Anderson et al., 2006). To statistically analyse β-diversity using abundance information, PERMDISP tests based on Bray-Curtis similarity matrices were run on mobile and sessile data separately after data were square-root transformed. PERMDISP tests were based on distances to centroids with 9999 permutations.

Ordination of samples was visualised using non-metric multi-dimensional scaling (nMDS) plots. β-diversity among sites within natural and artificial habitats were visualised separately using correlation plots created in R Studio (version 1.1.423) using the 'corrplot' package (R Core Team, 2017) and based on Sørensen distance matrices. To test for percentage contributions of individual taxa to dissimilarities between natural and artificial habitats, a similarity percentage (SIMPER) test was run. Tests for differences were conducted in PRIMER v6 with the PERMANOVA+ add-on (PRIMER-E Ltd, Plymouth, UK; Anderson et al., 2008) using the PERMANOVA and PERMDISP routines, and visualised using the nMDS routine. Taxon accumulation curves were generated using the 'species observed' ('Sobs') routine in PRIMER v.7 from 9999 random permutations. To create a map of predicted α-diversity values within

Plymouth Sound from the current dataset, the kriging technique in ArcMap (v.10.4) was employed. Kriging is a type of interpolation that understands the underlying spatial behaviour of a limited number of data points, and from it predicts values for areas without data points. Salinity was measured at low water at every site during biological data collection, and then a representative subsample of sites was measured again at high water during an extreme rainfall event to capture extremes in salinity. The difference in salinity measured at high water between natural and artificial habitats was statistically tested. Salinity at high water was used for analysis because these data would thus give us the most extreme scenario in salinity variation. Salinity data were square-root transformed and then normalised. Euclidean dissimilarity matrices were then computed and a one-way PERMANOVA test was run based on 9999 permutations of unrestricted permutation of raw data.

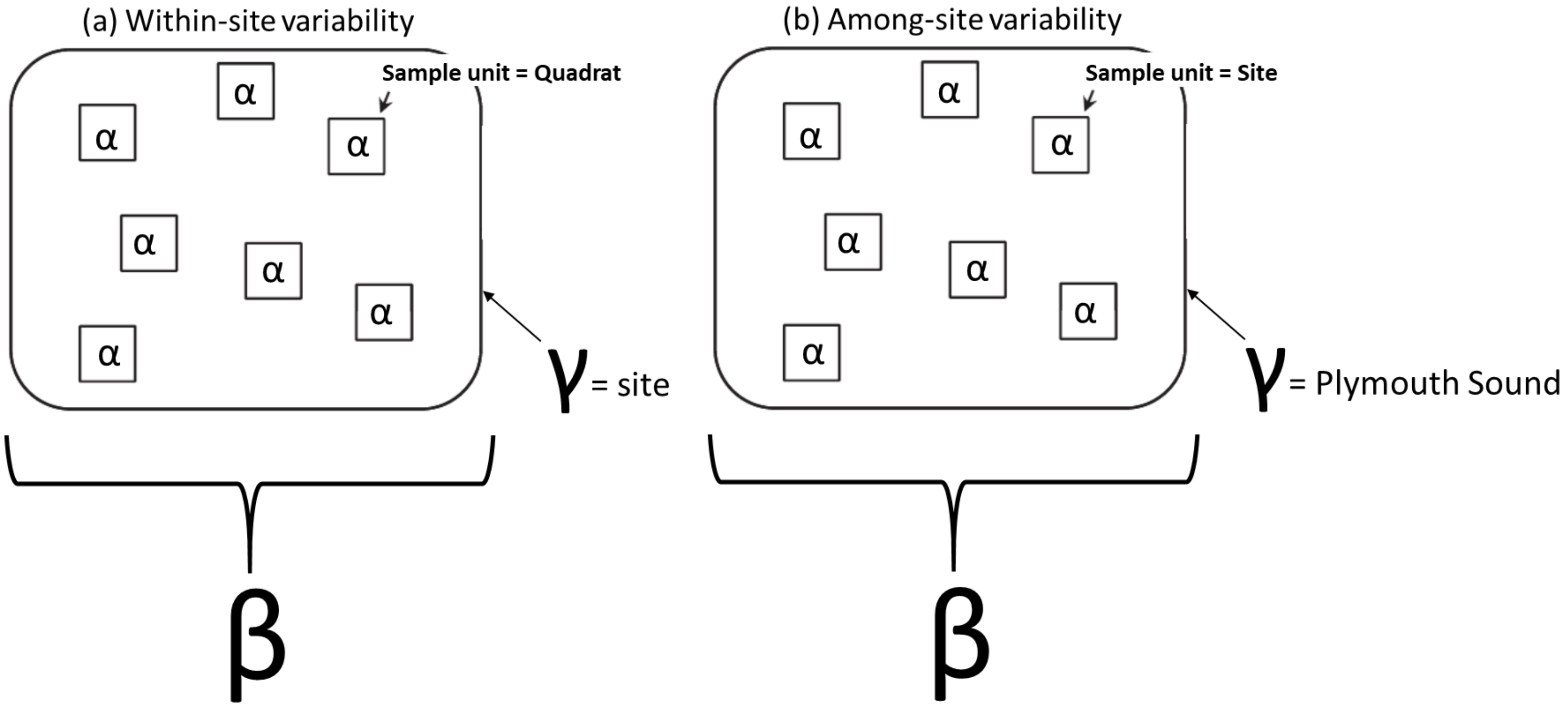


Figure 3-2. Schematic diagram of (a) within-site and (b) among-site β-diversity. β-diversity is the variation in identities of species among sampling units in a given area. $\beta = \gamma - \bar{\alpha}$, where α is the average taxon richness in quadrats and γ is the site for within-site β-diversity; and α is the average taxon richness per site and γ is Plymouth Sound for among-site β-diversity.

3.3 Results

3.3.1 Environmental context and general results

Water temperatures ranged from 9.7 °C in December to 21.3 °C in September reflecting seasonal differences at time of sampling. Salinity ranged from 30-35 psu at low water across all sites showing these sites are generally fully marine in character. Values of 13-32 psu were measured at high water following a severe rainfall event, and 32-35 psu at high water under normal weather conditions. This demonstrates that, although fully marine conditions at high water are typical, short-term reductions in salinity can occur when immersed. The lowest salinity values were all recorded in artificial habitats: Admirals Hard in Stonehouse (2 sites) at the mouth of the River Tamar, under Laira Bridge (1 site) and at Oreston (2 sites) at the mouth of the River Plym (Figure 3-3). Historical records and modelled estimates of salinity in Plymouth Sound and the mouth of the River Tamar measured at all states of the tide ranged from 19.5-34.5 psu. Mean salinity values (measured at high water after an extreme event) were significantly greater in natural compared to artificial habitats ($p < 0.001$).

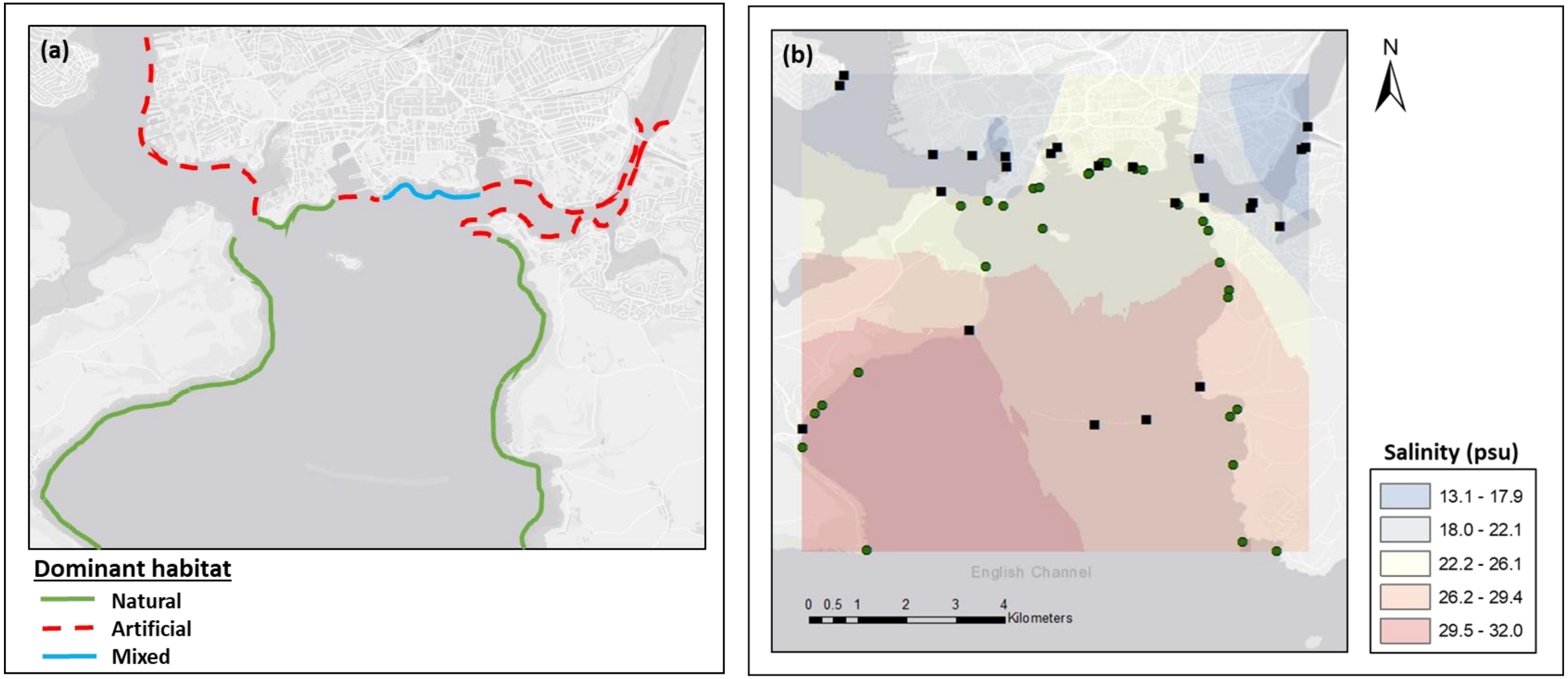


Figure 3-3. (a) Habitats in Plymouth Sound that were surveyed in this study. The majority of the urbanised areas of Plymouth are either artificial or a mix of artificial and patchy natural reefs. Habitats that flank the Sound on the east and west sides are dominated by natural substrate. (b) Continuous values of salinity (psu) across Plymouth Sound were generated from salinity measurements from a subset of the study sites using the kriging method in ArcGIS. Natural sites are represented by green circles and artificial sites are represented by black squares. The English Channel is to the south, and the Rivers Tamar and Plym are to the northwest and northeast, respectively. Measurements of salinity used here were taken at high water immediately following an extreme rainfall event (December 2019) to demonstrate salinity range in the Sound. Salinity values following the extreme rainfall between natural and artificial sites were significantly different ($p < 0.001$). Salinity measurements under normal conditions were not different between natural and artificial sites (not shown here).

Mean taxon richness (α-diversity) was significantly greater in natural compared to artificial habitats at the within-site scale (Figure 3-4a), as well as at the among-site scale (Table 3-1a; Figure 3-4b). Within-site β-diversity was significantly greater in natural compared to artificial habitats (Figure 3-4c), whereas, among-site β-diversity was significantly greater in artifical compared to natural habitats (Figure 3-4d),

A total of 59 taxa were recorded across the 54 sites (Appendix 2, Table 2). γ-diversity was similar in natural (50) and artificial (49) habitats. Ten taxa were unique to natural habitats, whilst nine taxa were unique to artificial habitats (Table 3-1a). Overall, Rhodophyta was the dominant taxonomic group (18 taxa), with the next most speciose groups the Cirripedia and Ochrophyta (6 taxa; Table 3-1b). A total of 13 functional groups were recorded across all surveys, with functional richness greater in artificial (12 taxa) compared to natural (10 taxa; Table 3-1b). The functional group with the greatest number of taxa was the filter feeders (17 taxa); with the next most speciose group being the grazers (11 taxa).

Four non-native species were found in both natural and artificial habitats: Darwin's barnacle, *Austrominius modestus* (Darwin, 1854) was found in 79% of natural and 84% of artificial sites; the red alga, *Caulacanthus okamurae* Yamada, 1933 was found in 17% of natural and 12% of artificial sites; the Pacific oyster, *Magallana gigas* (Thunberg, 1793) was found in 14% of natural and 32% of artificial sites; and the red ripple bryozoan, *Watersipora subatra* (Ortmann, 1890) was found in 10% of natural and 8% of artificial sites. One additional non-native species – the orange-striped anemone, *Diadumene lineata* (Verrill, 1869) – was found in 4% of natural sites (Appendix 2, Table 2).

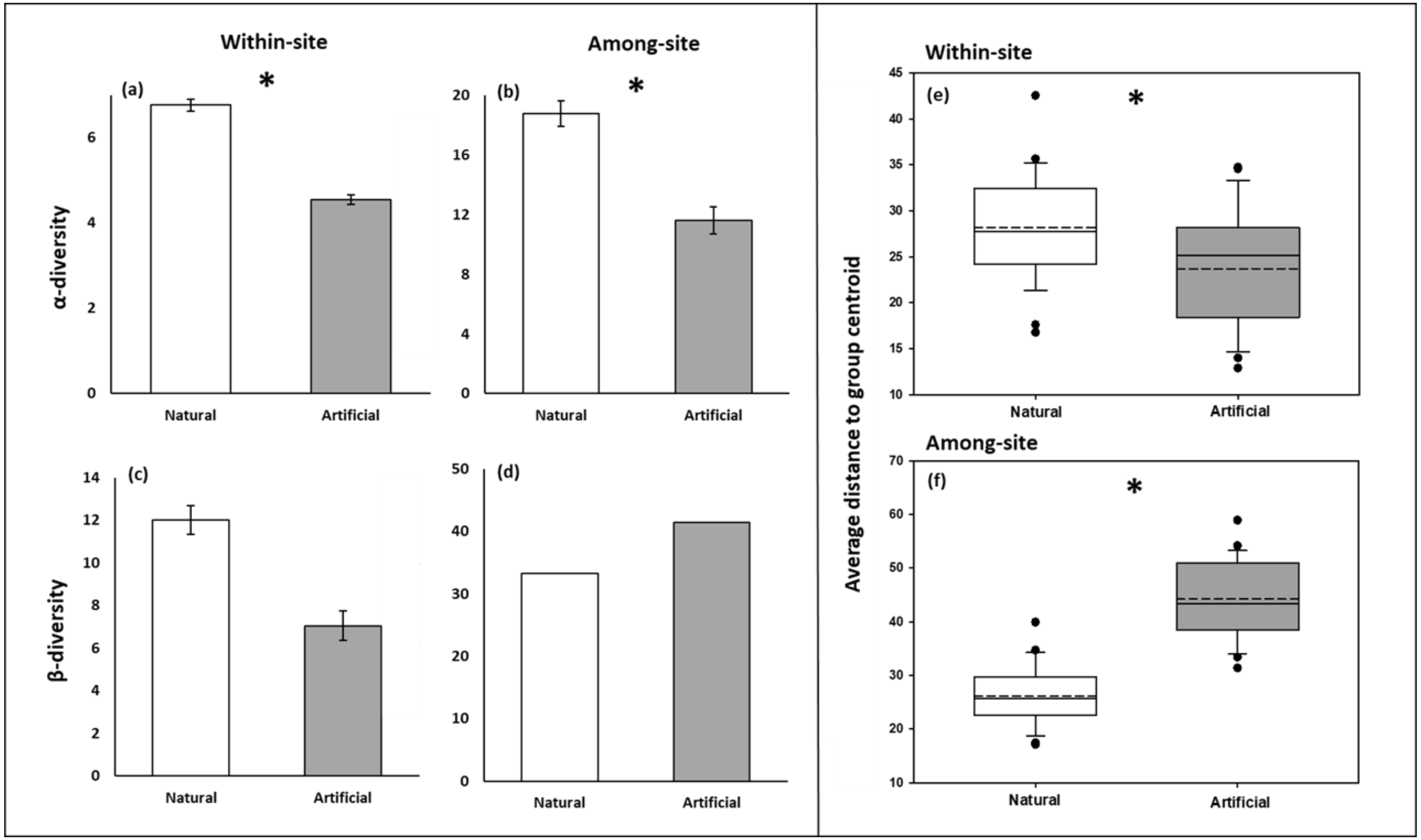


Figure 3-4. Mean α-diversity (taxon richness) of community composition was significantly greater in natural compared to artificial habitats both (a) within-site and (b) among-sites. Mean β-diversity using Whittaker's β was significantly greater in natural compared to artificial habitats at the (c) within-site level, but was significantly lower in natural compared to artificial habitat at the (d) among-site level. Because Whittaker's β-diversity measures diversity for a given area and cannot statistically test for differences among areas, multivariate measures were employed (e, f). (e) Within sites (α = quadrat), variation in species composition was greater in natural compared to artificial habitats. (f) Among sites (α = site), variation in species composition was greater in artificial compared to natural habitats. Box plots were based on mean distances from group centroids calculated from distance-based permutational tests for homogeneity of multivariate dispersions (PERMDISP). The dashed and solid lines represent the mean and median, respectively. The box itself contains the middle range of the data, with the upper boundary representing the 75th percentile, and the lower boundary representing the 25th percentile. Black dots represent outliers. Asterisk (*) indicates significant differences between natural and artificial habitats.

Table 3-1. (a) General summary of taxon and functional richness recorded in natural and artificial habitats, and (b) summary of total richness, mean richness and abundance of taxa in each major taxonomic and functional group. Mean abundance in (b) is by quadrat. '>/<' indicates the direction of significance. 'c' and '%' indicate counts of mobile and percent cover of sessile organisms, respectively. If differences are significant, there is '*' or '**' in the significance column ('sig.'), indicating a p-value of < 0.05 or < 0.01, respectively. 'no test' in the significance column indicates that no statistical test was run due to number of taxa per group being < 5 taxa for mean richness and < 1 individual or 1% coverage for mean abundance. A '†' in the 'dif' column indicates where tests for mean richness and abundance disagreed.

(a)	**Total**	Natural	>/<	Artificial	sig.
Total taxon richness (γ)	**59**	50	>	49	-
Taxon richness - quadrat (α)	**-**	6.5 ± 0.1	>	4.5 ± 0.1	**
Taxon richness - site (α)	**-**	18.1 ± 0.9	>	11.1± 0.9	**
Functional richness	**13**	10	<	12	-
Non-native species richness	**5**	5	>	4	-
Unique taxa	**-**	10	>	9	-

(b)		Total richness			Mean (± 1 SE) richness				Mean (± 1 SE) abundance				
	Total	Natural	>/<	Artificial	Natural	>/<	Artificial	sig.	Natural	>/<	Artificial	sig.	dif.
Mobility													
mobile	**13**	8	<	12	6.1 ± 0.3	>	3.7 ± 0.4	**	19.6 ± 0.7	>	11.5 ± 0.8	**	
sessile	**46**	42	>	37	12.7 ± 0.8	>	7.9 ± 0.8	*	93.3 ± 2.2	>	88.5 ± 3.4	no	†
Major taxonomic group													
Patellids (c)	**2**	2	=	2	1.8 ± 0.1	>	1.1 ± 0.1	no test	15.5 ± 0.5	>	7.7 ± 0.5	**	
Littorinids (c)	**4**	2	<	4	0.4 ± 0.1	<	0.6 ± 0.2	no test	1.9 ± 0.4	<	2.3 ± 0.6	no	
Trochids (c)	**3**	2	<	3	1.5 ± 0.1	>	1.0 ± 0.2	no test	2.3 ± 0.2	>	0.6 ± 0.1	no test	
Cirripedia (%)	**5**	5	=	5	4.2 ± 0.2	>	2.5 ± 0.2	**	48.1 ± 1.7	>	39.0 ± 1.8	**	
Porifera (%)	**2**	2	=	2	1.1 ± 0.2	>	1.0 ± 0.2	no test	1.6 ± 0.3	>	0.8 ± 0.1	no test	
Chlorophyta (%)	**2**	2	=	2	1.0 ± 0.1	>	0.8 ± 0.1	no test	2.3 ± 0.5	<	5.7 ± 0.9	**	
Ochrophyta (%)	**5**	5	=	5	1.6 ± 0.2	=	1.6 ± 0.3	no	8.2 ± 1.1	<	29.3 ± 2.4	**	†
Rhodophyta (%)	**18**	16	>	15	5.5 ± 0.4	>	2.3 ± 0.4	**	31.6 ± 2.0	>	16.1 ± 1.6	**	
Functional group													
Grazer (c)	**11**	7	<	10	3.8 ± 0.2	>	2.7 ± 0.3	**	13.9 ± 0.4	>	9.0 ± 0.7	**	
Omnivore (c)	**1**	0	<	1	0.0 ± 0.0	<	0.1 ± 0.1	no test	0.0 ± 0.0	=	0.0 ± 0.0	no test	
Predator (c)	**1**	1	=	1	0.8 ± 0.1	>	0.1 ± 0.1	no test	0.2 ± 0.0	>	0.1 ± 0.3	no test	
Filter feeder (%)	**17**	17	>	14	4.1 ± 0.4	>	3.0 ± 0.3	no	49.5 ± 1.7	>	38.7 ± 1.7	**	†
Lichen (%)	**2**	2	>	0	0.1 ± 0.0	>	0.0 ± 0.0	no test	0.1 ± 0.1	>	0.0 ± 0.0	no test	
Thin filamentous (%)	**6**	5	=	5	0.8 ± 0.2	>	0.7 ± 0.2	no	0.8 ± 0.2	<	8.1 ± 1.2	*	†
Foliose (%)	**3**	3	=	3	1.4 ± 0.1	>	1.0 ± 0.2	no test	4.3 ± 0.7	<	8.4 ± 1.2	no	
Corticated macrophyte (%)	**8**	8	>	6	3.0 ± 0.2	>	1.0 ± 0.2	**	22.1 ± 1.5	>	4.5 ± 0.8	**	
Leathery macrophyte (%)	**6**	5	>	4	1.4 ± 0.2	>	1.2 ± 0.3	no	9.0 ± 1.1	<	24.5 ± 2.2	**	†
Articulated calcareous (%)	**1**	1	=	1	0.3 ± 0.1	>	0.1 ± 0.1	no test	0.2 ± 0.1	>	0.1 ± 0.1	no test	
Crustose (%)	**1**	1	=	1	0.9 ± 0.0	>	0.3 ± 0.1	no test	8.7 ± 0.9	>	3.2 ± 0.6	**	
Other algae (%)	**1**	0	<	2	0.0 ± 0.0	<	0.1 ± 0.1	no test	0.0 ± 0.0	<	0.2 ± 0.1	no test	
Cyanobacteria (%)	**1**	0	<	1	0.0 ± 0.0	<	0.1 ± 0.0	no test	0.0 ± 0.0	<	0.7 ± 0.3	no test	

3.3.2 Taxon and functional richness

Mean taxon richness was significantly greater at both the quadrat and the site scales (Figure 3-4a, b). The mean number of taxa accumulated over quadrats in natural habitats increased quicker and was consistently greater than in artificial habitats (Figure 3-5a), while over sites, the rate of taxon accumulation, and ultimately γ-diversity, was similar between natural and artificial habitats (Figure 3-5b). Numbers of mobile and sessile organisms were significantly greater in natural than artificial habitats. Amongst the major taxonomic groups with ≥ 5 taxa per group, mean taxon richness of the Cirripedia and Rhodophyta was greater in natural compared to artificial habitats, while no significant difference was detected in the Ochrophyta between habitats (Table 3-1b).

Mean functional richness was significantly greater in natural compared to artificial habitats at both spatial scales. Of the functional groups that were statistically compared between habitats, the grazers and corticated macrophytes had significantly greater numbers of taxa in natural than artificial habitats, while there were no significant differences in filter feeders, thin filamentous, and leathery macrophytes between habitats (Table 3-1b).

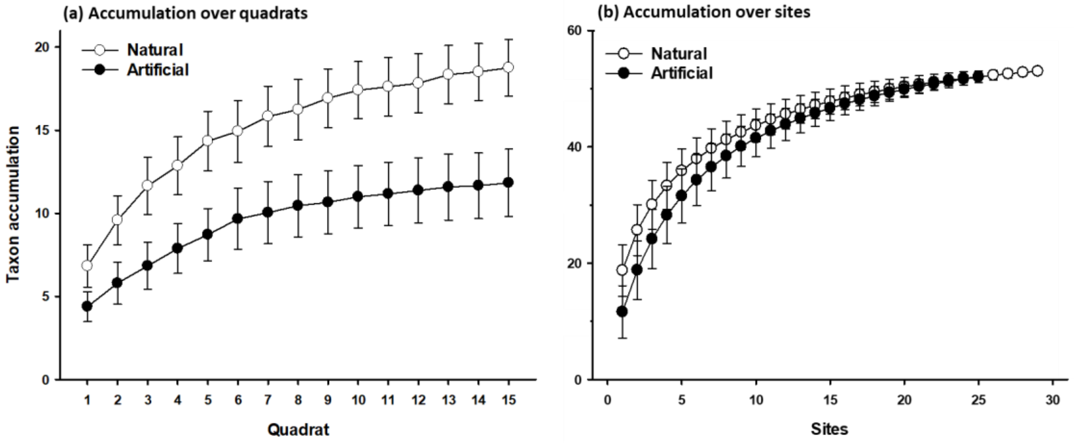


Figure 3-5. Mean cumulative number of taxa (± 95% confidence intervals) over (a) quadrats (n = 15) and (b) sites (natural, n = 29; artificial, n = 25). Natural habitat supported 50 taxa, while artificial habitat supported 49 taxa.

3.3.3 β-diversity

β-diversity was dependent on the scale at which species assemblages were examined. Results from the classic (β_W) and the multivariate (PERMDISP) measures supported each other at both spatial scales (Table 3-2). Within-site β-diversity was significantly greater in natural compared to artificial habitats (Figure 3-4c), meaning that taxon richness of quadrats per site in natural habitats varied more compared to taxon richness of quadrats in sites within artificial habitats. Among-site β-diversity was however, significantly greater in artifical compared to natural habitats (Figure 3-4d, Figure 3-6), meaning that the number of taxa among sites in artificial habitats varied more than the number of taxa among sites in natural habitats. Tests for homogeneity of multivariate dispersion (PERMDISP) of mobile and sessile taxa using abundance data supported presence/absence results (Table 3-3), with greater within-site β-diversity in natural compared to artificial habitats (Figure 3-4e), but greater among-site β-diversity in artificial compared to natural habitats (Figure 3-4f; Table 3-2). These analyses showed that there was a similar variation around the mean between habitats for within-site β-diversity, but that there was more variation around the mean in artifical compared to natural habtiats for among-site β-diversity.

Table 3-2. Summary of classic and multivariate β-diversity results in natural and artificial habitats at two spatial scales: (a) within-site and (b) among-site. Mean d_{cen} values are average distances from group centroids, which is a measure of dispersion among groups. All calculation methods found that β-diversity was lower in artificial compared to natural habitats when measured within sites, but was higher in artificial compared to natural habitats when measured among sites.

	(a) Within sites		**(b) Among sites**	
	Natural	Artificial	Natural	Artificial
Classic β-diversity measures				
βw†	12.00 ± 0.66	7.05 ± 0.70	33.24	41.4
Multivariate dispersion (mean d_{cen})				
Sørensen†	28.16 ± 1.07	23.69 ± 1.25	26.11 ± 1.01	44.25 ± 1.40
Bray-Curtis mobile‡	21.99 ± 0.77	17.96 ± 1.72	18.38 ± 1.40	38.41 ± 2.07
Bray-Curtis sessile ‡	33.33 ± 1.50	24.79 ± 2.03	29.98 ± 1.47	41.76 ± 1.74

†Calculations carried out using presence/absence data.

‡Calculations carried out using abundance data.

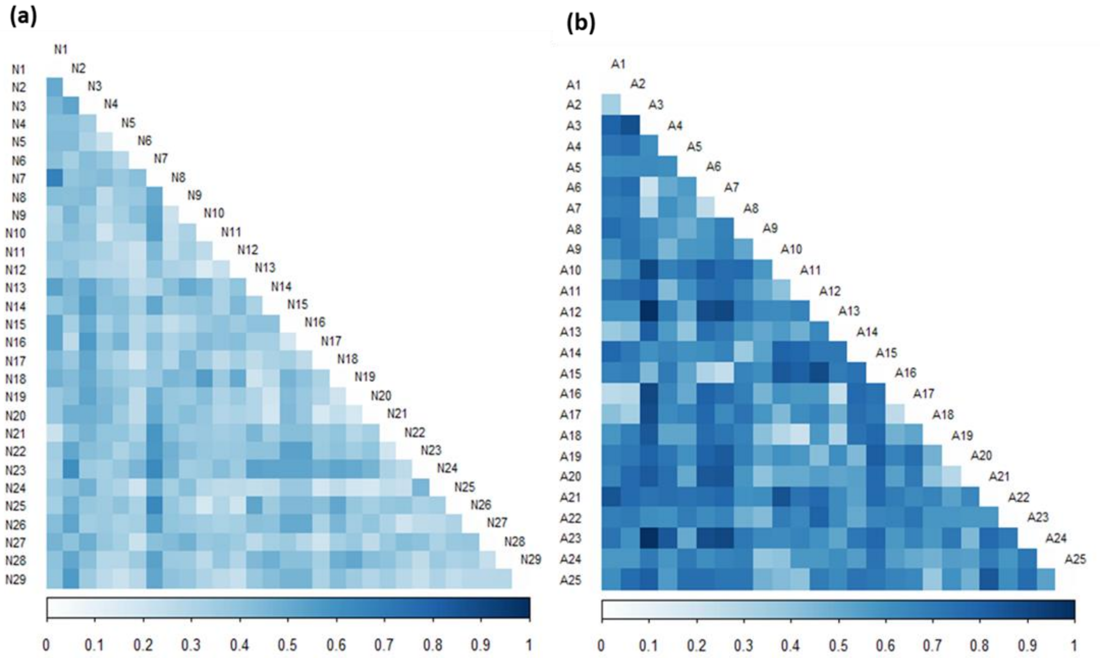


Figure 3-6. Correlation plots of β-diversity of sites in (a) natural and (b) artificial habitats. Plots were based on Sørensen resemblance matrices. β-diversity was greater in artificial than natural habitats. The coloured bar indicates the degree of dissimilarity between sites, with the darkest colour (values closest to 1) representing the most dissimilar assemblages.

Table 3-3. PERMANOVA tests comparing within-site and among-site β-diversity between natural and artificial habitats for (a) taxon richness (full community), (b) mobile taxa and (c) sessile taxa. PERMANOVAs were based on tests for homogeneity of multivariate dispersion (PERMDISP). Significant P-values are bolded.

(a) PERMANOVA comparing average distance to centroids from taxon richness data (full community) between natural and artificial habitats.

Within-site

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	2.774	2.774	7.6691	**0.0072**
Residual	52	18.809	0.36172		
Total	53	21.583			
Transformation:	pres/abs				

Among-site

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	4419.9	4419.9	114.97	**0.0001**
Residual	52	1999.1	38.443		
Total	53	6418.9			
Transformation:	pres/abs				

(b) PERMANOVA comparing average distance to centroids from community composition abundance data of mobile taxa between natural and artificial habitats.

Within-site

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	218.23	218.23	4.9955	**0.0305**
Residual	52	2271.6	43.684		
Total	53	2489.8			
Transformation:	SQRT + zero-adjusted				

Among-site

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	5384.2	5384.2	67.324	**0.0001**
Residual	52	4158.7	79.975		
Total	53	9542.9			
Transformation:	SQRT + zero-adjusted				

(c) PERMANOVA comparing average distance to centroids from community composition abundance data of sessile taxa between natural and artificial habitats.

Within-site

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	978.84	978.84	11.848	**0.0016**
Residual	52	4295.9	82.614		
Total	53	5274.8			

Transformation: SQRT + zero-adjusted

Among-site

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	1861.7	1861.7	27.202	**0.0001**
Residual	52	3559	68.442		
Total	53	5420.7			

Transformation: SQRT + zero- adjusted

3.3.4 Taxon and functional abundance

Mean abundance of mobile organisms was significantly greater in natural compared to artificial habitats, while mean abundance of sessile organisms did not differ (Table 3-1b). Of the major taxonomic groups tested for differences between habitats (mean abundance ≥ 1 individual or 1%), the patellids, Cirripedia and Rhodophyta were significantly more abundant in natural compared to artificial habitats, while the Chlorophyta and Ochrophyta were significantly more abundant in artificial habitats, and the littorinids did not differ between habitats (Table 3-1b, Figure 3-7a, b). Of the functional groups that significantly differed between habitats, the grazers, filter feeders, corticated macrophytes and crustose algae were significantly more abundant in natural compared to artificial habitats. Conversely, the thin filamentous and leathery macrophytes were significantly greater in artificial compared to natural habitats. There were no significant differences detected between habitats for the foliose functional group (Table 3-1b, Figure 3-8a, b).

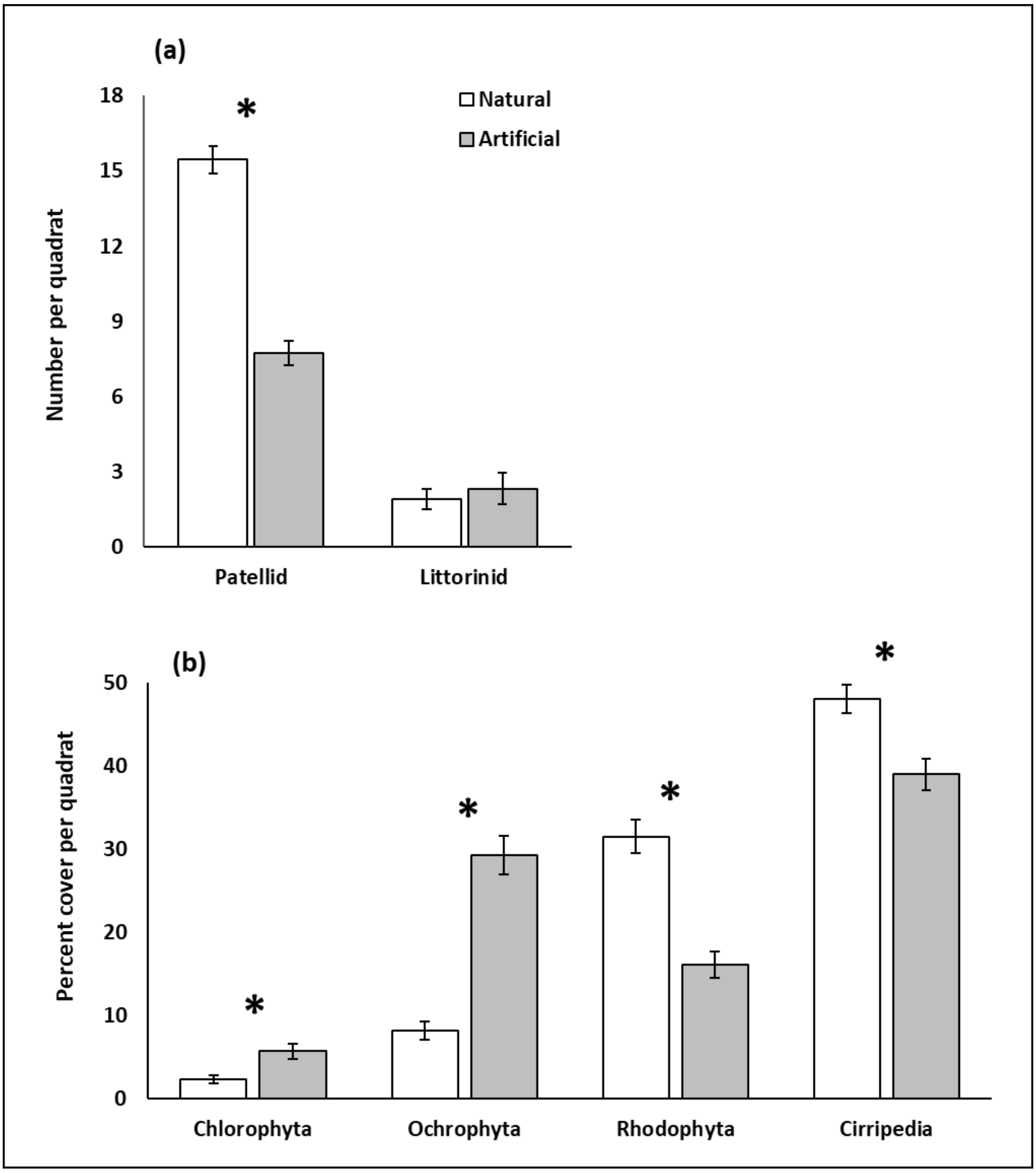


Figure 3-7. Mean abundance of major taxonomic groups of (a) mobile taxa in counts and (b) sessile taxa in percentage cover per quadrat in natural and artificial habitats. Asterisk (*) above bars indicates a significant difference in abundance between natural and artificial habitats. All p-values were < 0.01. Taxonomic groups with < 1 individual or 1% mean abundance were omitted from analysis and figures.

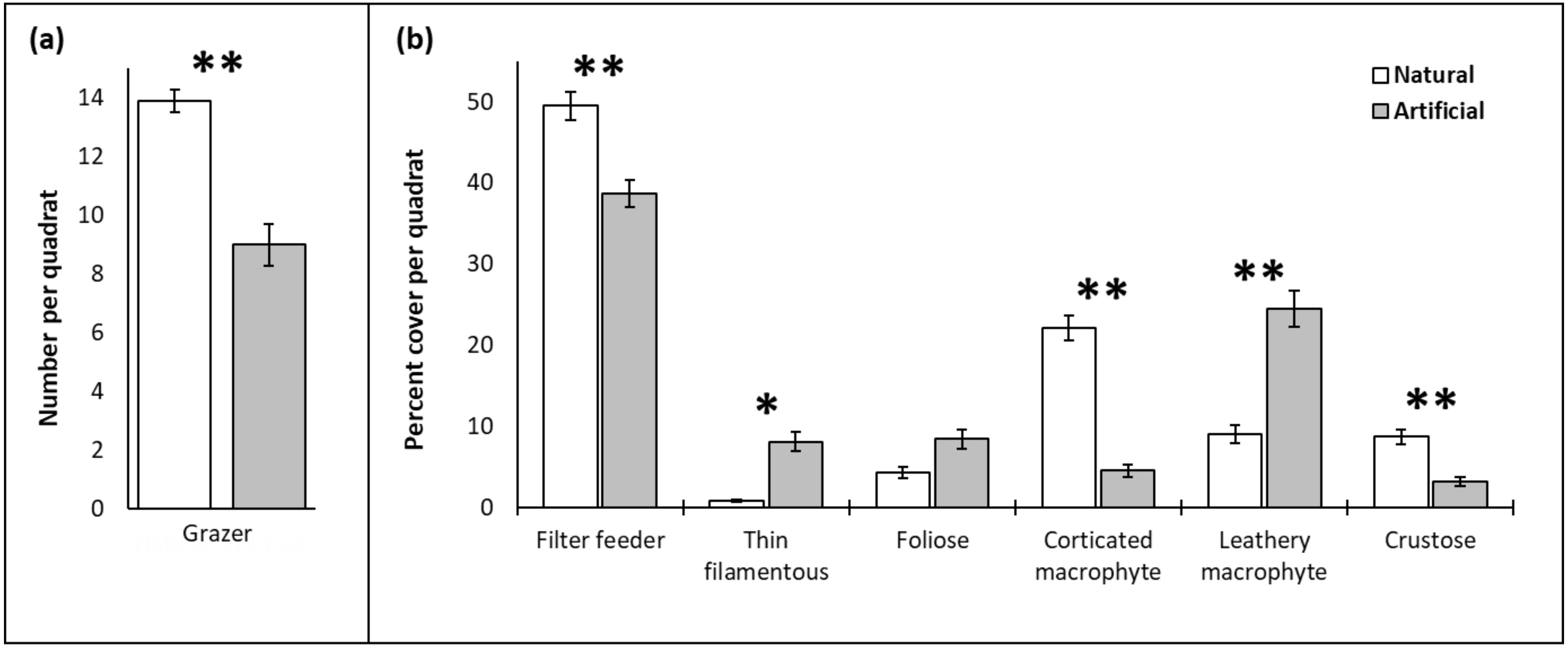


Figure 3-8. Mean abundance of functional groups of (a) mobile and (b) sessile taxa in natural and artificial habitats. Asterisks indicate significant difference between habitats (‘*’, $p < 0.05$; ‘**’, $p < 0.01$). Functional groups with < 1 individual or 1% mean abundance were omitted from analysis and figures.

3.3.5 Taxonomic and functional composition

Taxonomic and functional composition were both significantly different between natural and artificial habitats (Table 3-4a, b, Figure 3-9). An analysis of the contribution from individual taxa (SIMPER) showed that, in terms of mobile taxa, the common limpet, *Patella vulgata*, contributed the most to the dissimilarity between artificial and natural habitats, with *P. vulgata* more abundant in natural compared to artificial habitats (Table 3-5a). Approximately 50% of the dissimilarity observed in sessile communities between natural and artificial habitats was attributed to Cirripedia, *Osmundea* spp., Corallinaceae and *Catenella caespitosa*, with all taxa being more abundant in natural compared to artificial habitats (Table 3-5b).

Table 3-4. PERMANOVAs comparing (a) taxonomic and (b) functional composition between natural and artificial habitats. Significant P-values are bolded.

(a) PERMANOVA comparing taxonomic composition between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	98542	98542	6.4704	**0.0001**
Site(Habitat)	52	792000	15230	15.574	**0.0001**
Res	756	739310	977.92		
Total	809	1629800			
Transform:	sqrt + zero adjusted				

(b) PERMANOVA comparing functional composition between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	76778	76778	8.1827	**0.0003**
Site(Habitat)	52	488000	9382.9	18.703	**0.0001**
Res	756	379000	501.67		
Total	809	944000			
Transform:	SQRT + zero adjusted				

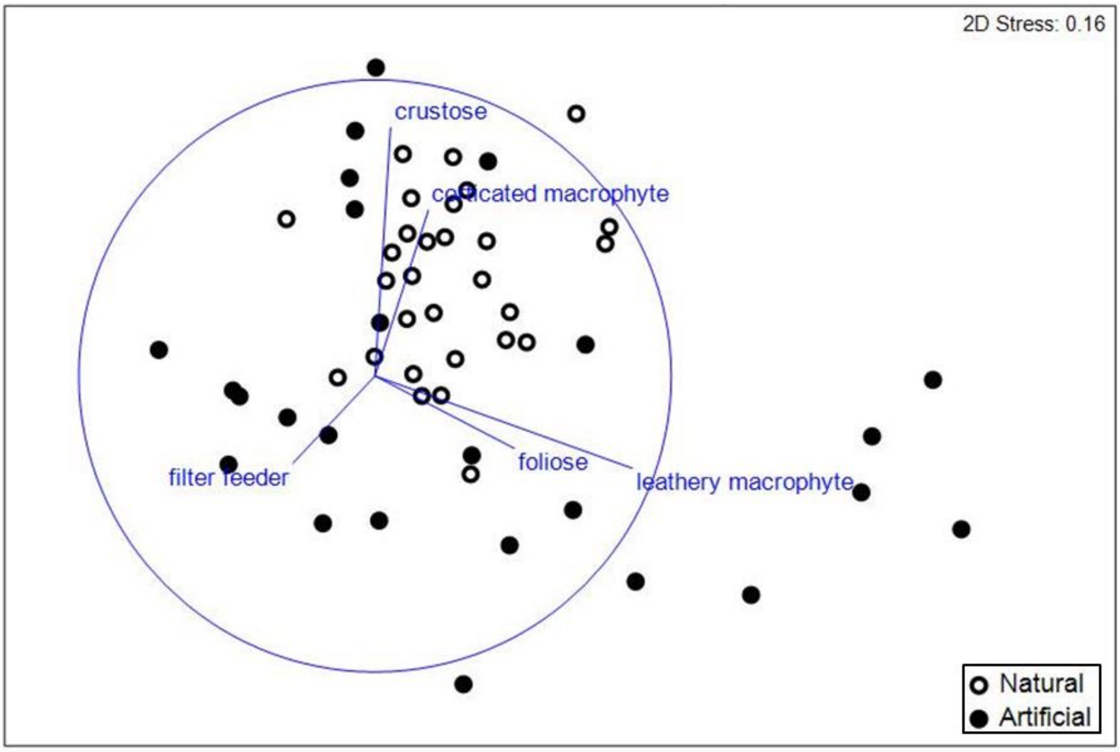


Figure 3-9. Non-metric MDS ordination plot of community composition comparing sites within natural and artificial habitats with functional groups overlaid. Sites in artificial habitats were more different from each other compared to sites in natural habitats. Vector lines indicate the directions in which functional group numbers increase, and the lengths of the lines represent the strength of pattern in those group counts along that direction.

Table 3-5. SIMPER table showing differences in average abundances (square root transformed; indicated by > or <) and contributions of individual species to assemblage composition dissimilarities between natural and artificial habitats for (a) mobile and (b) sessile taxa. Consistency of contribution is shown by ‘Diss/SD’, which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(a) Mobile:	**Average dissimilarity = 61.9%**	**Natural**	**>/<**	**Artificial**	**% Contr**	**Diss/SD**
	Patella vulgata (%)	3.1	>	1.9	50.1	1.1
	Steromphala umbilicalis (c)	0.9	>	0.2	18.1	0.8
	Patella depressa (%)	0.3	>	0.2	7.7	0.6

(b) Sessile:	**Average dissimilarity = 66.8%**	**Natural**	**>/<**	**Artificial**	**% Contr**	**Diss/SD**
	Cirripedia (%)	5.9	>	5.1	23.6	1.1
	Osmundea sp. (%)	2.1	>	0.2	10.5	0.8
	Corallinaceae (%)	1.6	>	0.6	9.2	0.7
	Catenella caespitosa (%)	1.2	>	0.2	7.0	0.6
	Ulva spp. (%)	0.5	<	1.2	6.9	0.5
	Fucus spiralis (%)	0.8	>	0.7	6.3	0.5

Ascophyllum nodosum (%)	0.1	<	1.4	5.5	0.5
Fucus vesiculosus (%)	0.2	<	0.9	4.3	0.4

SIMPER analysis showed that five functional groups contributed 78% towards the overall dissimilarity between habitats: corticated macrophyte (21.1%), leathery macrophyte (18.5%), filter feeder (13.7%), crustose algae (13.0%) and foliose algae (11.3%). The corticated macrophyte, filter feeder and crustose algae groups were significantly more abundant in natural habitats, while the leathery macrophyte group was significantly more abundant in artificial habitats, with no significant differences between habitats in foliose algae (Figure 3-8).

3.3.6 Kriging analysis

Continuous values of α-diversity by site around Plymouth Sound generated by the kriging method generally showed that diversity increases with increasing distance from the central urbanised and lower salinity areas of the Sound (Figure 3-10). Species diversity "hot spots" were located on the east and west sides of the Sound in both natural and artificial habitats. These areas of the Sound are dominated by natural rocky shores. Lower α-diversity was noticable at sites in natural and artificial habitats at the mouth of the River Tamar, while diversity at sites in artifical habitats were relatively high at the mouth of the River Plym (natural habitats are absent in the River Plym). Both rivers are dominated by hard artificial structures.

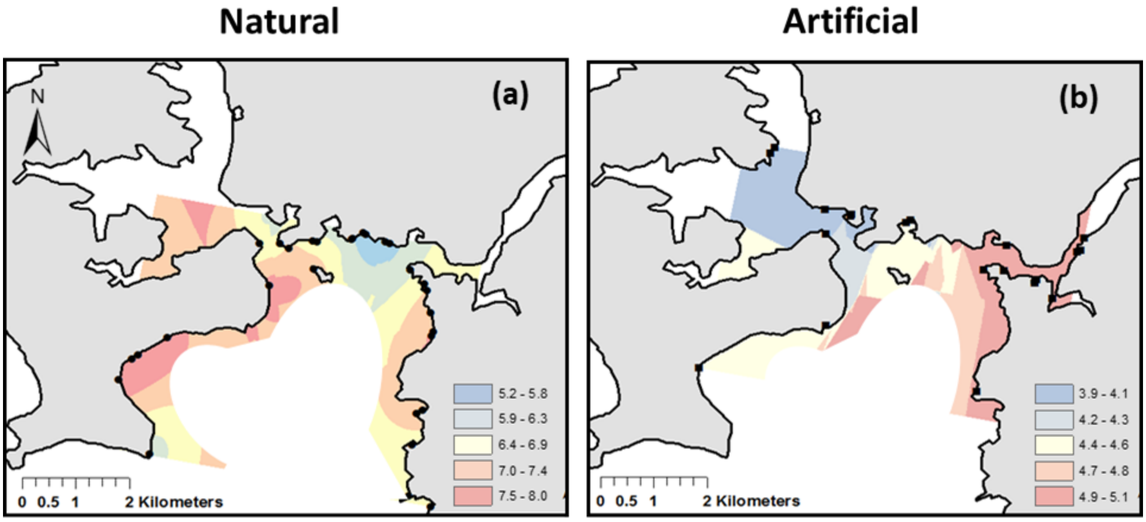


Figure 3-10. Kriging analysis maps showing α-diversity in (a) natural and (b) artificial habitats per site. Points on the map represent total taxon richness of each site, with red indicating higher taxon richness and blue representing lower taxon richness. Sites in natural habitats are positioned further south towards the English Channel, while sites in artificial habitats are positioned further up the rivers. Note the different scales between (a) natural and (b) artificial habitat maps.

3.4 Discussion

This study aimed to quantify the differences in biological communities between natural and artificial habitats using a number of different response variables at two spatial scales. Surveys found that species diversity was different in natural compared to artificial habitats, but the direction and magnitude of differences were dependent on the scale of assessment and diversity measure used. As expected, mean taxon (α-diversity) and functional richness were greater on natural rocky shores compared to artificial structures at both the within- and among-site scales, while mean abundance of taxon and functional groups depended on the groups analysed. β-diversity was greater in natural compared to artificial habitats at the within-site scale, but counter to our prediction, at the among-site scale, β-diversity was greater in artificial than natural habitats.

If this study were to have only analysed mean taxon richness – one of the most common response variables used in ecological studies – there would have been a simple conclusion that natural habitats supported greater numbers of taxa compared to artificial habitats. The differences in biotic communities between the habitats were, however, much more complex. Although mean taxon richness was greater in natural compared to artificial habitats at both spatial scales, the total number of taxa (γ-diversity) was nearly equal between natural and artificial habitats, and moreover, diversity among sites (β-diversity) in artificial habitat varied much more than expected. The fact that differential results were obtained using different diversity measures at two spatial scales highlights the importance of employing the most appropriate analyses for the question being asked or for the specific management goals, with the understanding that consideration of multiple diversity measures and scales may be necessary.

β-diversity was predicted to be greater in natural compared to artificial habitats at both the within- and among-site levels, as natural rocky shores are topographically more complex than artificial structures at a range of spatial scales (mm-km; Knott et al., 2004; Moschella et al., 2005). Variation in the identities of species among sites, however, was greater in artificial compared to natural habitats, indicating that biological communities can differ based on the scale in which they are analysed.

There were limitations with the experimental design of the current study, as 80% (20 of 25) of the sites in artificial habitat were located in sheltered estuarine conditions; these locations were slightly up the Rivers Plym and Tamar or at the mouths of these rivers. This was in contrast to natural sites being more evenly distributed across Plymouth Sound (Figure 3-1). In general, artificial structures tend to be built in heavily urbanised and polluted areas and are often located in sheltered estuaries, which by nature, experience fluxes in environmental variables such as nutrients (Statham, 2012), salinity and water temperature (Whitehead et al., 2009). In Plymouth Sound, almost the entire seafront, as well as up the Rivers Plym and Tamar, are armoured; whereas habitats further from the urbanised areas of Plymouth are natural (Figure 3-3a). Sites surveyed, therefore, experienced differences in salinity and exposure gradients (see Appendix 2, Table 1 for rankings of exposure by site), which may confound the results. Thus, salinity and exposure gradients cannot be eliminated as potential factors in influencing biological community composition between natural and artificial habitats. This is important to acknowledge because environmental and physical factors have been shown to affect the assemblage of local biological communities (Coates, 1998; McQuaid and Lindsay, 2000; Przeslawski, 2004). For example, Gomes-Filho et al. (2010) found that the non-native barnacle, *Austrominius modestus*, was present further up estuaries compared to native barnacles, and native species showed clear patterns of distribution throughout the entire profile of estuaries in Plymouth Sound, likely due to salinity gradient. Photosynthetic micro-organisms that are important for the functioning of rocky shores were found in greater abundances on exposed compared to sheltered shores (Thompson et al., 2005), biomass of intertidal organisms has been shown to be influenced by exposure gradient (McQuaid and Branch, 1984) and grazing activity in limpets is greater on exposed compared to sheltered intertidal rocky shores (Jenkins and Hartnoll, 2001). In the current study, salinity values taken at the time of surveys were measured at low water and did not vary greatly. However, measurements taken at high water following an extreme rainfall event showed that sites near the mouths of the Rivers Tamar and Plym experienced lower salinity conditions than sites closer to the English Channel. Salinity reports from historical records and past studies showed that in Plymouth Sound, including at the mouths of both rivers, salinity did not drop below 19.5 psu and fluctuated approximately 6-15 psu depending on the study (Milne, 1938; Butler and Tibbitts, 1972; Uncles et al., 1986; Uncles and Stephens, 1990; Siddorn et al., 2003). These lower salinity sites are likely exposed to such conditions only during heavy rainfall, with effects being exacerbated during spring tides. To ensure unbiased sampling effort, future studies should consider surveying sites with uniform exposure and salinity gradients, as well as any other relevant physical factors, such as temperature, light availability and pollution load.

Processes driving variation in community composition among sites in artificial habitats are probably localised, as artificial structures in Plymouth Sound can be considered fragmented landscapes, with little physical connectivity amongst them (they are not contiguous in design). This is in comparison to natural rocky shores in Plymouth Sound. In the northern section, around the City of Plymouth, natural rocky shores are non-contiguous and fragmented, while natural rocky shores on the east and west sides of Plymouth Sound are contiguous, only occasionally being interspersed by natural beaches and artificial structures. Artificial structures can change the physical environment immediately surrounding the structure, modifying normal coastal processes both in the immediate vicinity and downstream (Airoldi et al., 2005a; Dugan et al., 2011), such as hydrodynamics, sediment accumulation and deposition, wave impact and sand scour (Miles et al., 2001; Govarets and Lauwaert, 2009; Dugan et al., 2011). Moreover, artificial structures are more vulnerable to short-term disturbances through trampling from humans, regular maintenance (Govarets and Lauwaert, 2009; Airoldi and Bulleri, 2011), locality to other maritime activities such as docking of boats (K. O’Shaughnessy, pers. obs.) and use of antifouling paints (Weis and Weis, 1996). Effects from short-term disturbances can be exacerbated by the altered hydrodynamics around a structure; in particular, waves reflected off vertical seawalls can create turbulence and may actually interact with incoming waves, causing increased sand scour along the structure (French, 2002; Bush et al., 2004). Disturbances may dislodge or crush mobile invertebrates (e.g., limpets and snails) and sessile species (e.g., mussels and algae), creating bare space for colonisation by non-native or opportunistic species (Govarets and Lauwaert, 2009; Airoldi and Bulleri, 2011; Bracewell et al., 2012). Thus, depending on when artificial structures were constructed or last disturbed, they may be in different stages of ecological succession (Benedetti-Cecchi et al., 2000; Chiantore et al., 2018), resulting in different emergent community composition among structures (Airoldi, 2000; Reed et al., 2000). In this study, the majority of artificial structures surveyed were concentrated in the urbanised areas of Plymouth Sound, in particular, at the mouths of the Rivers Tamar and Plym. Two surveys were conducted on seawalls at the mouth of the River Plym, where a local engineering company operates on a regular basis. Additionally, one survey was conducted on a seawall immediately beneath a major bridge connecting Plymouth city centre to the neighbouring suburbs. Immediately adjacent to the bridge is an associated cycle and pedestrian bridge. Construction work was recently undertaken on this bridge to transform it from a rail to a pedestrian bridge, probably causing disturbance to flora and fauna on the seawall. At the mouth of the River Tamar, two surveys were conducted on seawalls adjacent to a vehicle ferry terminal, while one survey was done on a seawall adjacent to a smaller pedestrian ferry dock. It is likely that these ferries cause intermittent disturbance to the local biotic communities in the form of docking/tying-up or resuspending sediment from the sea floor (i.e., increasing turbidity; Rhoads and Boyer, 1982; Ellis et al., 2002; Airoldi and Hawkins, 2007). Moreover, many of the sites in artificial habitat were located in the urbanised areas of Plymouth Sound, meaning they likely received elevated levels of runoff from terrestrial sources compared to less urbanised areas of the Sound. O’Connor (2013) found that, although differences in species diversity were not detected, there was greater spatial variability of rocky shore communities near sewage discharge points compared to communities without a sewage outfall present. It is possible that these human activities act in concert with environmental disturbances (e.g., waves, sand scour, sedimentation) to arrest artificial structures in early successional stages, affecting their ability to support fully stabilised communities (Dean and Connell, 1987).

Biological processes likely act in synergy with physical disturbances to determine colonising communities in natural and artificial habitats. Morphologically simple and fast growing filamentous and foliose algae were more abundant in artificial compared to natural habitats in these surveys. These groups included highly productive and ephemeral species such as *Ulva* spp., *Polysiphonia* spp., *Porphyra* spp. and *Ceramium* spp. (Littler and Arnold, 1982; Steneck and Dethier, 1994; Phillips, 1996). They are characteristic of early successional stages (Murray and Littler, 1978; Sousa, 1980) that are known to rapidly colonise new or cleared substrata (Sousa, 1979; Noël et al., 2009). In conditions where these opportunist taxa persist (e.g., lack of grazers, presence of physical disturbances), their presence can restrict the settlement of longer-lived algal species (Sousa, 1979; Sousa, 1980). Where, however, conditions are not favourable for opportunistic algae, settlement of perennial algae and barnacles occurs (Sousa, 1979; Sousa, 1980), allowing for diverse and stabilised communities. Similarly, grazers are known to be facilitators of succession, as they graze down algae and create space for spores and larvae of other species (Benedetti-Cecchi, 2000; Benedetti-Cecchi et al., 2000). As abundances of grazing invertebrates on artificial structures in this study were low, succession of biotic communities to a stabilized state might not occur, preserving communities in early successional stages.

Among-site β-diversity may be considered a surrogate measure for ecological connectivity because it describes the relationship between the regional species pool (γ-diversity) and species richness of sites (α-diversity; Whittaker, 1960; Witman et al., 2004; Chiantore et al., 2018). Among-site β-diversity is negatively related to biological homogeneity, meaning that sites with similar community composition are likely to be highly connected to the regional species pool (Chiantore et al., 2018). In this study, among-site β-diversity was lower among natural sites, thus, sites in natural habitats may have been more connected to the regional species pool compared to sites in artificial habitats. Our study was conducted at the meso- (1-100 km) and local (1 m-1 km) scales (greatest distance between sites was 9 km). It is therefore possible that all sites in this study had equal access to the regional species pool, but local physical (e.g., desiccation stress, wave exposure) and biological (e.g., competition, predation) conditions were likely to have influenced larval recruitment, survival to adulthood and reproductive success (Sousa, 1984; Reed et al., 2000).

Community composition of functional groups differed between natural and artificial habitats, suggesting that the ecological functioning of artificial structures is different to natural rocky shores. Greater abundances of grazers and filter feeders were found in natural compared to artificial habitats, while greater abundances of leathery macrophytes (mostly fucoids) were recorded in artificial compared to natural habitats. Gastropod and other marine invertebrate larvae have been shown to be positively affected by red algae; they are known to settle on encrusting reds, being induced by chemical cues on the algal substrate (Morse et al., 1984; Morse and Morse, 1984; Johnson et al., 1991). Moreover, encrusting red algal species have been found in gut contents of grazing invertebrates (Lai et al., 2018). In the current study, crustose algae were limited on artificial structures, suggesting that the lack of these algae may explain the low abundances of grazing invertebrates in artificial habitats. On the other hand, grazer abundance may be negatively influenced by dense patches of mature algae, which have been shown to limit the grazing ability of gastropods as they are unable to adhere to the slippery algae or penetrate to the substrate below (Underwood and Jernakoff, 1981). Alternatively, leathery macrophytes may not have been able to establish on natural rocky shores due to the regulating effect of limpets on the growth of larger canopy algae (Hawkins, 1983b; Hawkins, 1983a; Jenkins et al., 2005; Coleman et al., 2006). Limpets are voracious predators of the spores of fucoid algae in temperate intertidal rocky shores (Hawkins, 1983b; Hawkins, 1983a; Jenkins et al., 2001; Jenkins et al., 2005). Two common mid-shore limpet species on natural rocky shores in the southwest of England, *Patella vulgata* and *P. depressa*, are known to experience reduced feeding activity during their respective reproductive seasons *(*i.e., winter for *P. vulgata* and spring/summer for *P. depressa*; Jenkins et al., 2001; Moore et al., 2007). Although *P. vulgata* was more abundant than its conspecific in both habitats, even during the season when *P. vulgata* reduced its feeding, *P. depressa* was actively foraging on fucoid species, thereby creating a year-round limiting effect on settlement and growth of leathery macrophytes (Moore et al., 2007), with this effect more pronounced in natural compared to artificial habitats. The ability of grazers to limit the growth of large canopy algae allows barnacles to persist (Hawkins, 1981; Hawkins, 1983b; Moore et al., 2007). In the current study, there were significantly lower abundances of Cirripedia in artificial habitats, demonstrating that artificial structures in Plymouth Sound may lack the biological interactions that allow for barnacle settlement and survival. Therefore, artificial habitats potentially support lower rates of water filtration compared to natural rocky shores, which can have clear negative effects on water quality for the wider ecosystem, especially in heavily urbanised harbours.

Past studies have assessed diversity differences between artificial and natural habitats, finding lower species richness (Moschella et al., 2005; Gacia et al., 2007; Firth et al., 2013b), different community composition (Bulleri et al., 2005; Lai et al., 2018), fewer mobile species (Chapman, 2003; Pister, 2009) and greater numbers of non-native species (Glasby et al., 2007; Dafforn et al., 2009; Dafforn et al., 2012) on artificial structures. However, other studies have found either the opposite pattern or no pattern in response variables depending on taxa examined (Lam et al., 2009; Marzinelli et al., 2009), tidal height (Chapman and Bulleri, 2003; Bulleri et al., 2005), structure type (Bulleri and Chapman, 2004; Chapman, 2006) and time of sampling (Bulleri and Chapman, 2004; Bulleri et al., 2004; Chapman, 2012; Firth et al., 2016a), as well as chosen diversity measures and analyses (Martin et al., 2005; Firth et al., 2016a). Our surveys concurred to some extent with previous studies, in that artificial structures supported lower mean taxon richness, and biotic communities in natural and artificial habitats supported similar assemblages of common taxa, but significant differences between groups were attributed to abundance and frequency of occurrence of individual species (Chapman and Bulleri, 2003; Lai et al., 2018). However, our study also raises the argument that assessing species diversity is more complicated than simply quantifying the number of species between two habitats; assessment should depend on overall conservation and management goals.

Capturing the full species diversity picture can reveal essential information on dominance and rarity of species (Chapman, 2003; Matias et al., 2012; Firth et al., 2016a), as well as provision of ecosystem services for future management strategies (Chapman, 1999; O'Connor and Crowe, 2005; Hillebrand et al., 2018). The current study measured species diversity, which by definition, considers the number of species and the relative abundance of species in a given community (Hawksworth, 1995; Tuomisto, 2010a; Hillebrand et al., 2018). Interpreting the productivity of a population relies on knowing the number of individuals in the community (Yee and Juliano, 2007), as this provides information on the viability of a population and the probability of its extinction in that ecosystem (Storch et al., 2018). The numbers (and indeed sizes) of individuals within a community can also influence the provision of ecosystem services (Winfree et al., 2015), such as water filtration and primary production (Wilkinson et al., 1996). For example, in this study, analyses of abundance data revealed greater abundance of filter feeders in natural compared to artificial habitats, while analysis of numbers of taxa within the filter feeders showed no difference between habitats. When abundance data is considered here, results suggest that natural habitats provide better substrate and conditions for settlement and growth of filter feeding species, which subsequently affects rates of water filtration and quality. Similarly, no difference was detected in taxon richness of the leathery macrophytes, but there was a significant difference in abundance of this group between habitats. There are clear benefits in knowing abundance information for macroalgae, as they are considered important carbon fixators (Gao and McKinley, 1994; Muraoka, 2004; Chung et al., 2011). Although the Ochrophyta (i.e., leathery macrophytes) are the least photosynthetically active of the macroalgae (Steneck and Dethier, 1994; Phillips, 1996; Chung et al., 2011), in large abundances like found on artificial structures in Plymouth Sound, they have the potential to draw out substantial amounts of carbon from the atmosphere (Chung et al., 2011). It is therefore imperative to consider abundance of individuals as well as the number of species present when conducting species diversity surveys, as this will provide information on the ecological functioning and emergent services of habitats.

Trait-based and functional approaches are becoming more common in the field of community ecology (Litchman and Klausmeier, 2008; Schleuning et al., 2015; Santini et al., 2016). Hawksworth (1995) argued that ecologists should no longer rely on numbers of species present as an adequate measure of species diversity, as using a single number to measure diversity assumes that all species within a given area contribute equally to a community. This is because species richness measures do not detect the loss and replacement of specific species and their functioning within the ecosystem. For example, if one species is replaced by another species of different morphology and functioning, changes in the genetic and ecological roles of that system may change without the number of species actually changing (Hillebrand et al., 2018). In the southwest of England, it is predicted that climate change will cause “northern” cold water species, such as *P. vulgata*, and “southern” warm water species such as the top shells, *Phorcus lineatus* and *Steromphala umbilicalis,* to move north (Mieszkowska et al., 2006; Hawkins et al., 2009). On temperate intertidal rocky shores, all three species are important grazers of microalgae (Hawkins et al., 1989) and *P. vulgata* is an important consumer of macroalgal spores (Hawkins, 1983b; Hawkins, 1983a). Southern species may move in to replace these species (Mieszkowska et al., 2006; Firth et al., 2009; Hawkins et al., 2009), and if the new species fill a different ecological role than their predecessors (i.e., grazers), micro- and macroalgae may grow unchecked with subsequent effects on barnacles and other filter feeders (Hawkins, 1983b). Therefore, community structure may be reorganised, with consequences for the ecological functioning of ecosystems. The surveys in this study showed that grazing invertebrates, and in particular, patellids, were more abundant on natural rocky shores compared to artificial structures, suggesting that climate change may restructure natural habitat to function more like artificial habitats in Plymouth Sound (i.e., low abundance of grazers and high abundance of leathery macroalgae). Regardless of the effects and to which habitats, if continuous monitoring efforts do not collect species abundance data, vital information predicting effects of climate change could be overlooked.

3.4.1. Ecological engineering of urban coastlines

Continued coastal development to protect human lives and infrastructure is inevitable. Fortunately, the impetus to consider ecologically sensitive designs of coastal infrastructure to preserve biodiversity is gaining momentum (Evans et al., 2017; Strain et al., 2017a; Strain et al., 2019a). Ecological engineering – the design of sustainable ecosystems for the benefit of human society and the natural environment (Odum, 1962; Odum and Odum, 2003) – is an emerging field in coastal and marine environments. Over about the last decade, a wide range of designs have been trialled globally that have included addition of topographic complexity on hard built structures to create desirable habitats (Martins et al., 2010; Chapman and Underwood, 2011; Browne and Chapman, 2014; Firth et al., 2014b; Evans et al., 2016a; Perkol-Finkel et al., 2017; Strain et al., 2017b; Hall et al., 2018), incorporating precast habitat enhancement units into pre-existing structures (Firth et al., 2014b; Sella and Perkol-Finkel, 2015) and hybrid designs, which involve constructing a hard stabilising structure on the seaward side of planted vegetation (Kamali et al., 2010; Bilkovic and Mitchell, 2013). More recently, there has been a push to trial designs on larger spatial scales (Sella and Perkol-Finkel, 2015; Cordell et al., 2017; Living Seawalls, 2019). The ability to forecast the identities and numbers of species that may recruit to, and survive on, artificial structures with some level of confidence will be imperative in informing ecological engineering designs (Airoldi et al., 2005a). One of the first steps in employing ecologically sensitive designs in coastal development is to conduct ecological surveys in the location of interest (Mayer-Pinto et al., 2017). Baseline ecological surveys can help determine the secondary (ecological) management objectives and identify the drivers of diversity differences between natural and artificial habitats, which can then inform small-scale trials in the location of interest before implemented on a larger scale. For example, in this study, abundance of mobile grazing organisms was significantly lower on artificial structures compared to natural rocky shores. A potential driver of this pattern might be the lack of complex microhabitats, which grazers have been shown to inhabit on natural rocky shores (Chapman and Bulleri, 2003; Bulleri and Chapman, 2004; Lam et al., 2009; Aguilera et al., 2014). Additionally, specific plant material such as turf algae and microbial film has been found in the gut contents of grazing invertebrates (Hawkins et al., 1989; Burgos-Rubio et al., 2015; Lai et al., 2018). Therefore, interventions to encourage mobile grazers should also aim to encourage settlement of turf algae and growth of biofilm. Thus, potential ecological engineering experiments could involve installing small (cm) pits or grooves on artificial structures to provide complexity for algal spore settlement and habitat for mobile grazers (Martins et al., 2010; Chapman and Underwood, 2011; Firth et al., 2014b).

The kriging method was employed to visualise species diversity at a landscape scale (i.e., Plymouth Sound). In this way, managers can target heavily urbanised areas that might have potential to support eco-engineering interventions with an aim to boost species diversity. Artificial structures of interest might be those adjacent to natural rocky shores, where the species pool will be larger in terms of abundance of species, and that suite of species will be more characteristic of natural rocky shore assemblages. This technique can help maximise the ecological gains while minimising cost to stakeholders.

3.4.2. Concluding remarks

This study showed that, although natural and artificial habitats supported similar total taxon richness (γ-diversity), at both spatial scales on average, artificial structures supported different species assemblages and fewer numbers of species compared to natural rocky shores. Interestingly, variation in community composition (β-diversity) was greater in artificial habitat compared to natural habitat at the site scale. If total number of taxa at one spatial scale would have been the only response variable measured, conclusions drawn concerning species diversity in natural and artificial habitats would have been much less informative.

The world is experiencing a biodiversity crisis (Wheeler et al., 2004; Monastersky, 2014). The way ecologists interpret biodiversity can have major implications for conservation management of threatened species or entire ecosystems (Rogers et al., 1999). Thus, despite the increasing urgency to monitor diversity in a timely and inexpensive manner, the future of species diversity monitoring must consider more than the conventional measures alone (i.e., species richness) so that we do not overlook valuable ecological information. This may seem like a challenging task, but the consequences of continuing with the status quo may include living in a world that contains many fewer species, with severe implications for the structure and functioning of ecosystems and their emergent services.

4. CHAPTER FOUR

Effects of habitat complexity and mussel seeding in intertidal habitats across two geographic locations

Abstract

Urbanisation along coastlines and estuaries has driven humans to build defences to protect infrastructure from rising sea levels, erosion and stormier seas worldwide. Artificial structures are proliferating in the coastal and marine environments (“ocean sprawl”), resulting in a loss of natural habitat, species diversity and ecosystem functioning. To mitigate the impacts of natural habitat loss, the practice of ecological engineering – or “eco-engineering” – of coastal infrastructure has been developed and tested over the past decade. Eco-engineering techniques are designed to achieve sustainable ecosystems that integrate human society with its natural environment for the benefit of both. This study tested the effects of habitat complexity and mussel seeding on intertidal seawalls in two geographic locations (Plymouth, British Isles and Tel Aviv, Israel). Although no formal comparisons were made between the geographic regions, the results are presented together here to emphasize that eco-engineering experiments should involve comparisons across geographic localities to understand generalities of patterns of effects at larger scales. Taxon and functional richness and community composition were compared among flat tiles, 2.5 cm tiles, 5 cm tiles, seawall plots and control tiles (control tiles were only used in Tel Aviv) and between seeded and unseeded tiles (seeding was only used in Plymouth). Results differed between the locations. In general, in Plymouth, habitat complexity had no effect on taxon richness; differences were between seawall and tiles only. Habitat complexity did, however effect community composition, with differences between flat and complex tiles, as well as seawall plots and all other tiles. In Tel Aviv, complex tiles supported greater taxon

richness and different community composition compared to flat tiles and seawall plots. The differential results obtained from these experiments demonstrates the need for continued testing of eco-engineering interventions in a variety of different geographic locations under different environmental conditions.

4.1 Introduction

Urbanisation of coastal areas is rapidly increasing, with reports estimating as much as 40% of the global population living within 100 km of the coastline (Cohen et al., 1997; Small and Nicholls, 2003; UNEP, 2006; Firth et al., 2016b). Driven by climate change, rising sea levels and stormier seas are leading to greater erosion of coastlines, with severity predicted to increase over the coming decades (Rodwell et al., 1999; Grevemeyer et al., 2000; Thompson et al., 2002; Brown et al., 2013; Neumann et al., 2015; Vitousek et al., 2017). Human response has traditionally been to build artificial structures to protect valuable coastal infrastructure and allow for continued development of the coast (Airoldi and Beck, 2007; Govarets and Lauwaert, 2009; Dugan et al., 2011; Firth et al., 2013a). Artificial structures are now so ubiquitous that in some regions, they cover more than half the coastline (Davis et al., 2002; Dafforn et al., 2015b; Firth et al., 2016b). These structures contribute to “ocean sprawl” – a term that has recently been coined (Duarte et al., 2012) to describe the proliferation of artificial structures (i.e., seawalls, breakwaters, jetties) in marine and coastal environments (also see Firth et al., 2016b; Bishop et al., 2017; Heery et al., 2017).

The rapid development of coastlines worldwide has led to the damage or loss of natural habitats (Airoldi et al., 2005a; Dugan et al., 2011; Firth et al., 2016b), placing extraordinary stress on coastal environments, with knock-on effects on ecosystem services, such as habitat provision (Sugden et al., 2009; Barbier et al., 2011; Engle, 2011; Grabowski et al., 2012), carbon sequestration (Barbier et al., 2011; Engle, 2011), water filtration and nutrient cycling (Coen et al., 2007; Sugden et al., 2009; Barbier et al., 2011; Engle, 2011). Ocean sprawl has facilitated the spread of non-native species (Bax et al., 2002; Airoldi et al., 2015a; see Firth et al., 2016b; Dafforn, 2017 for reviews) and species spreading in response to climate change (Mieszkowska et al., 2006; Hawkins et al., 2008; Hawkins et al., 2009; Firth et al., 2015). Increasing occurrence of non-native species has resulted in biotic homogenization (McKinney and Lockwood, 1999; McKinney, 2006; Bishop et al., 2017), threatening global biodiversity (Bax et al., 2003) and altering the ecological functioning of coastal environments (Griffiths et al., 1992; Stachowicz et al., 2002; Mayer-Pinto et al., 2018a).

Artificial structures in coastal and marine environments provide hard substrate for biological colonisation (Pratt, 1994; Chapman and Bulleri, 2003; Chapman, 2006; Qvarfordt et al., 2006). Past studies have found that artificial structures support lower biodiversity and different community composition compared to their natural counterparts (i.e., rocky shore; Thompson et al., 2002; Chapman, 2003; Chapman and Bulleri, 2003; Martin et al., 2005; Moschella et al., 2005; Lai et al., 2018). However, some studies detected no differences between habitats, but differences were dependent on a variety of factors such as tidal height (Chapman and Bulleri, 2003; Bulleri et al., 2005), orientation of substrate (Knott et al., 2004) and spatial scale of assessment (Bulleri et al., 2004; Firth et al., 2016a). Differences in species diversity between natural and artificial habitats have been attributed to the lack of topographic (or habitat) complexity on artificial structures (Chapman, 2003; Moschella et al., 2005; Bulleri and Chapman, 2010; Aguilera et al., 2014). Habitat complexity includes microtexture (< 1 cm) such as grooves and pits, and small (centimetres) and larger scale (centimetres - metres) habitats such as crevices, rock pools and gaps between boulders (Moschella et al., 2005; Firth et al., 2013b; Coombes et al., 2015; Liversage et al., 2017). Artificial structures are typically built with a steep or vertical inclination (Knott et al., 2004;

Chapman and Underwood, 2011; Firth et al., 2016c) and are smaller in areal extent compared to natural rocky shores, effectively condensing the area where species can occupy (Chapman, 2003; Chapman and Bulleri, 2003; Knott et al., 2004; Bulleri and Chapman, 2010; Chapman and Underwood, 2011). The materials used for construction of artificial structures are typically hard in nature and featureless in design (lack of microhabitats), which influences the composition of the colonising community (Davis et al., 2002; Burcharth and Lamberti, 2007; Iveša et al., 2010; Chapman and Underwood, 2011; Green et al., 2012). Artificial structures, therefore, are by no means complete surrogates for the natural habitats they replace (Chapman, 2003; Moschella et al., 2005).

Ecological studies across multiple ecosystems have traditionally found that greater habitat complexity supports greater biodiversity (Kohn, 1967; Kohn and Leviten, 1976; Heck Jr and Wetstone, 1977; Kostylev et al., 2005; Smith et al., 2014; Lavender et al., 2017). Colonisation of substrate depends on available space (Johnson et al., 2003; Bulleri, 2005a; Chapman and Underwood, 2011; Chapman, 2017) and can change over time (Smith et al., 2014). Smith et al. (2014) showed that sessile invertebrate recruitment to bare substrate was high initially, but over time, slowed as substrate became colonised, as there was naturally less space for recruitment. Once the basal substrate is completely colonised, secondary biological complexity dominates (Smith et al., 2014). Although studies have suggested that the increased surface area of complex habitats is responsible for greater diversity (i.e., the ‘species-area relationship’; Preston, 1960; Connor and McCoy, 1979; Kostylev et al., 2005; Chapman, 2017; Gatti et al., 2017), Loke and Todd (2016) found greater species diversity with greater complexity independent of surface area, and that species diversity was influenced by the type of structural complexity provided. This finding highlights the importance of available resources for species coexistence in a particular habitat (Schoener, 1974; Finke and Snyder, 2008).

There is now a growing awareness that traditional hard engineering is no longer ecologically and economically sustainable (Airoldi et al., 2005a; Airoldi et al., 2009; Dugan et al., 2011), especially under future climate change scenarios (Fankhauser and Tol, 2005; Koch, 2010; Narayan et al., 2016). As a response, ecologists have been developing techniques in ecological engineering (or "eco-engineering"; Odum, 1962) in coastal and marine environments. Eco-engineering is the combination of engineering with ecological knowledge to create a sustainable ecosystem for the benefit of both nature and human society (Odum, 1962; Mitsch, 1996; Mitsch and Jørgensen, 2003; Odum and Odum, 2003). The field of eco-engineering acknowledges that artificial structures have potential beyond their primary function to mitigate ecological impacts of urbanisation by secondarily functioning to enhance ecosystem services (Chapman and Underwood, 2011; Firth et al., 2014b; Toft et al., 2014; Dafforn et al., 2015b; Cordell et al., 2017; Evans et al., 2017; Mayer-Pinto et al., 2017).

Eco-engineering of artificial structures typically involves adding topographic complexity (on the scale of millimetres - metres) to hard built structures to enhance species diversity (Moschella et al., 2005; Borsje et al., 2011; Firth et al., 2014b; Perkol-Finkel and Sella, 2015; Perkol-Finkel et al., 2017; Hall et al., 2018) and discourage the spread of non-native species (Stachowicz et al., 1999; Dafforn, 2017; Morris et al., 2017b). Eco-engineering can also involve transplanting (Perkol-Finkel et al., 2012; Campbell et al., 2014; Ferrario et al., 2016) or seeding (Strain et al., 2017b) threatened species for conservation purposes or providing nursery habitat for commercial species (Martins et al., 2010). Also, larval settlement of target species to enhance associated assemblages can be encouraged (O'Connor and Crowe, 2007; Neo et al., 2009; Ng et al., 2015; Strain et al., 2017b). Previous designs have added topographic complexity to structures through a variety of techniques ranging from small (millimetres - centimetres) to large (metres) scale, and have included creating pits, grooves and crevices (Moschella et al., 2005; Martins et al., 2010; Chapman and Underwood, 2011; Firth et al., 2014b; Jackson, 2015), adding rock pools (Chapman and Blockley, 2009; Browne and Chapman, 2011; Firth et al., 2013b; Browne and Chapman, 2014; Firth et al., 2014b; Perkol-Finkel and Sella, 2015; Evans et al., 2016a), retrofitting complex tiles or panels (Goff, 2010; Perkol-Finkel and Sella, 2013; Loke and Todd, 2016; Cordell et al., 2017) and placing pre-cast habitat enhancement units within a rock armour breakwater to function as boulders (Firth et al., 2014b; Sella and Perkol-Finkel, 2015).

Eco-engineering of artificial structures along the coast can have a myriad of positive secondary functional effects. The primary goal of most eco-engineering designs is to enhance biodiversity and ecosystem functioning by adding complex habitats (Chapman and Underwood, 2011; Firth et al., 2014b; Perkol-Finkel and Sella, 2015; Sella and Perkol-Finkel, 2015; Evans et al., 2016a; Firth et al., 2016a; Morris et al., 2017a; Perkol-Finkel et al., 2017; Hall et al., 2018; Morris et al., 2018b), which can also help to reduce the establishment of non-native species and create a more resilient ecosystem (Stachowicz et al., 1999; Dafforn, 2017). Eco-engineering can also provide habitat to support fisheries and aquaculture (Hawkins et al., 1992b; Whitmarsh et al., 2008), improve water quality through biofiltration (Allen and Hawkins, 1993; Wilkinson et al., 1996) and promote education (Hall et al., 2019) and general aesthetic appeal of biodiversity in urban areas which can contribute to human well-being (Millennium Ecosystem Assessment, 2005; Sugden et al., 2009; Faith et al., 2010).

Eco-engineering can target certain colonising organisms such as barnacles, mussels, oysters and algae can have a “bioprotective effect” through physical strengthening of the materials, protection from salt-water ingress, temperature extremes and wave action (Coombes et al., 2013; Naylor et al., 2017). These initial colonising organisms also create biological complexity, which has been shown to be important for the subsequent colonising community (Bros, 1987; Pinn et al., 2008; Coombes et al., 2015). For example, Bros (1987) found that the removal of barnacles from settlement tiles reduced further colonisation by other organisms compared to tiles with barnacles remaining. Ecosystem engineers, such as mussels and oysters, create biologically-induced habitat that enhances the three-dimensional structure of a reef, which increases surface area, subsequently providing more space for more organisms (Borthagaray and Carranza, 2007; Jackson et al., 2008a; Pinn et al., 2008; Romero et al., 2015). Chemical cues from adult bivalves encourage intraspecies settlement (Tamburri et al., 2008; Smee et al., 2013), thereby enhancing the three-dimensional structure of the habitat. Moreover, naturally occurring biofilm known to develop on bivalves has been shown to increase bivalve larval recruitment (Bao et al., 2007; Ganesan et al., 2010; Wang et al., 2012), which in turn, encourages colonisation of other organisms (Bros, 1987; Pinn et al., 2008). Furthermore, many restoration projects have used ecosystem engineers to enhance and restore degraded habitat and preserve valuable ecosystem services (Grabowski and Peterson, 2007, Klinger, 2007, Borsje et al., 2010).

4.1.1 The World Harbour Project

The World Harbour Project is a global initiative directed by the Sydney Institute of Marine Science, and is aimed at building ecologically stable and resilient harbours in urbanised port cities around the world (World Harbour Project, 2018). The project was initiated as a response to climate change and sea level rise affecting the economy and ecology of major harbour cities across the globe. This project has developed objectives for better understanding ecosystem functioning and developing and implementing best-management practices for heavily urbanised harbours. This has been achieved through workshops, collaboration of researchers and specific research projects. University of Plymouth was invited to participate in the “Green Engineering” workgroup, of which there were 15 partner cities that conducted the same experiment in intertidal habitats in a range of different climates worldwide. The goal was for all partners to follow standard protocol and use the same materials to obtain results that can be comparable across geographic regions. Results obtained in Plymouth contributed to the overall global analysis but were also retained for individual analysis for this thesis.

The overarching aim of this study was to test the efficacy of enhancing topographic complexity on species diversity in intertidal habitats in Plymouth, British Isles and Tel Aviv, Israel. Both locations used the protocol designed by the World Harbour Project, thus results can be more comparable than results from experiments using different protocols. Although there were no formal statistical comparisons conducted between the two geographic locations, both were included to make the point that eco-engineering experiments need to go beyond testing in one location under similar conditions, so that we can investigate the generalities of effects of enhancements. The effects of an additional factor on species diversity in Plymouth was investigated: The effects of bivalve seeding using mussels (*Mytilus* spp. Linnaeus, 1758), as mussels are ecosystem engineers (Borthagaray and Carranza, 2007; Pinn et al., 2008). Mussels enhance the three-dimensional structure of a habitat by adding biological complexity. In particular, bivalves have been shown to provide habitat and refuge for colonising species such as algae, micro- and macroinvertebrates (O'Connor and Crowe, 2007; O'Connor and Crowe, 2008), as well as promote intraspecific settlement of larvae (Tamburri et al., 2008; Smee et al., 2013). Species diversity was measured using taxon and functional richness and community composition. Complex (two different levels), flat and control tiles, as well as cleared seawall plots were employed to test the following hypotheses:

1. Taxon and functional richness will be greater on, and community composition will differ between, complex tiles compared to control tiles/cleared seawall plots.

2. Taxon and functional richness will be greater on, and community composition will differ between, seeded compared to unseeded tiles (British Isles only).

4.2 Materials and methods

4.2.1 Study Sites

Experiments were run in Plymouth, British Isles and Tel Aviv, Israel (Figure 4-1). Experiments were undertaken at two sites in Plymouth and one site in Tel Aviv. The study sites in Plymouth were located at Mayflower Marina (50.364558, -4.172333) and Turnchapel Wharf (50.3593, -4.117736) in Plymouth Sound, which is located along the southwest coast of England. Both sites contained vertical and featureless intertidal seawalls with naturally occurring populations of the mussel, *Mytilus* spp. The seawall at Mayflower Marina faces southeast, while the seawall at Turnchapel Wharf faces west. Both seawalls are located on the landward side of Plymouth Breakwater, and are thus sheltered from wave action. Plymouth Sound is a heavily urbanised harbour with a long history of human modification. The Sound is flanked by sloping natural rocky shores composed of Palaeozoic shale and limestone, which extend along the west and east coasts (Knights et al., 2016). Along these areas, artificial structures to support human activity (i.e., fishing piers, discharge pipes, breakwaters, seawalls) are interspersed among the natural rocky shores. A recent publication estimated that up to a third of Plymouth’s coastline is armoured, with most of the artificial structures being constructed from naturally-sourced rock (Knights et al., 2016).

Experiments in Israel were conducted in a single marina in Tel Aviv (Herzliya Marina; 32.162333, 34.794083), which is positioned along the most densely populated area on the Israeli Mediterranean coast. The experimental seawall at Herzliya Marina faces west and is located in a sheltered environment. Herzliya Marina is the largest marina in the eastern Mediterranean Sea, and provides docking for tens of thousands of global visitors annually (ECOncrete Inc., 2019). Arid climate conditions coupled with its geological position in the Mediterranean Sea, results in species-poor waters off the Tel Aviv coast (Azov, 1991).

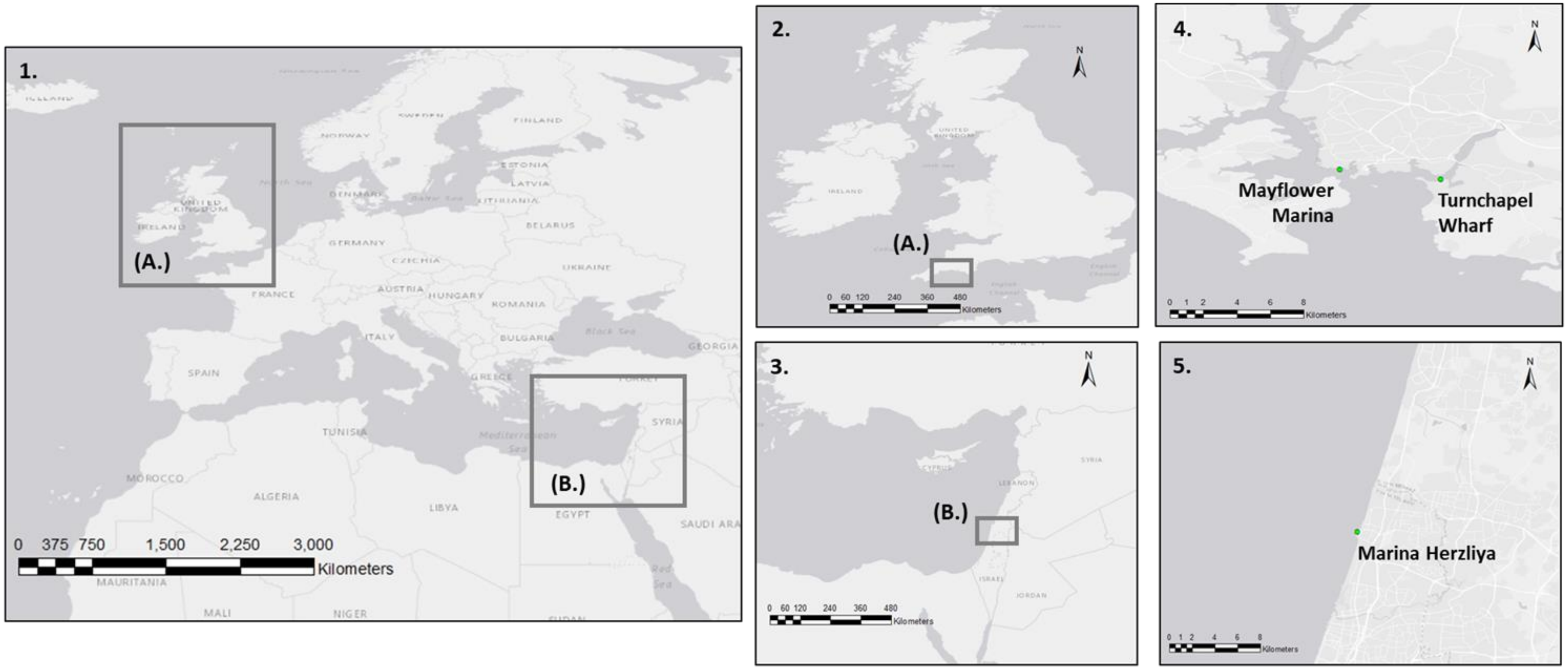


Figure 4-1. Study sites in (A.) Plymouth Sound, British Isles included Mayflower Marina and Turnchapel Wharf, while the study site in (B.) Tel Aviv, Israel was Marina Herzliya in the eastern Mediterranean Sea.

4.2.2 Description of experimental tiles and plots

Concrete tiles were created from moulds using 3-D printing, and were composed of sand, cement and glass fibres (Reef Design Lab, Melbourne, Australia; Figure 4-2). Sand and glass fibres were used in the mix to offset the negative effects of cement in the marine environment (see section 1.5.1 for more information on effects of concrete). The design of tiles was determined by the World Harbour Project, and all study locations were required to use these specific tiles. Tile treatments included: (1) flat tiles without crevices or ridges; (2) complex tiles, with 2.5 cm high and 1.7-6.5 cm wide ridges, each separated by 1.5-5 cm wide crevices (‘2.5 cm’ treatment); and (3) complex tiles, with ridges and crevices as described for the 2.5 cm treatment, except ridges were 5 cm high (‘5 cm’ treatment). All tiles were created with fine-scale microtexture (< 1 mm grooves) on the ridges. The three levels of tile complexity were chosen to test the effects of high elevation complexity compared to no complexity, with an intermediate complexity also included to determine how much complexity is enough to cause a biological effect. Microtexture was added to tiles because small scale texture has been shown to enhance recruitment and survival of larvae (Coombes et al., 2015). Furthermore, increasing the number of microhabitats and space available for colonisation will likely increase the number of individuals utilising the space (Kostylev et al., 2005). For experiments in Tel Aviv, two additional treatments were used: flat control tiles without microtexture (made of 80% sand and 20% Portland cement) and cleared seawall plots. For experiments in Plymouth, an additional cleared seawall plot treatment was used.

Figure 4-2. Eco-friendly experimental tiles (a) showing the flat, 2.5 cm and 5 cm complexity treatments (from left to right), with tiles seeded with mussels shown above, and (b) attached to the seawall at Turnchapel Wharf, Plymouth, British Isles.

4.2.3 Seeded mussels

The mussel, *Mytilus* spp., was chosen to be seeded on British tiles because it is a habitat-forming species common on some areas of rocky intertidal habitats in Plymouth Sound (Hilbish et al., 2002). Plymouth is located within the range of the more cold-water blue mussel, *Mytilus edulis* Linnaeus, 1758, and the warm-water *Mytilus galloprovincialis* Lamarck 1819; the latter is expanding in response to climate change but has always been present in the British Isles (Seed, 1971; Ahmad and Beardmore, 1976). It is likely that that *M. galloprovincialis*, *M. edulis* and hybrids (Skibinski et al., 1978) of these two species were used in this experiment, therefore all mussel species will be referred to here as 'mussels' or '*Mytilus* spp.'

4.2.4 Experimental design

Experiments from the two countries were treated separately for the following reasons: (1) Mussel seeding was added as a factor to the British experiments but not the Israeli experiments; (2) The control treatments differed between the countries; and (3) In Plymouth Sound, mean high water spring tides are 5.5 m (Natural Environment Research Council), while tides in the Mediterranean are on the order of centimetres (McElderry, 1963). Regardless of the differences in experimental designs between countries, we maintain it is useful to informally compare localities to observe generalities in patterns of effects.

4.2.4.1 Plymouth, British Isles

At both sites, ten tiles of each of the three complexity treatments were affixed to intertidal seawalls in a randomised order at mean low water neap (2.5 m above CD) in a single horizontal row. Five of the ten tiles from each treatment were seeded with 65 individuals of *Mytilus* spp. (20-25 mm shell length; 22.5 ± 0.1, mean ± 1 SE) in clusters of five individuals (seven clusters in crevices; six clusters on ridges) using non-toxic Gorilla® superglue (Cincinnati, OH, USA). The number and size of mussels was chosen based on World Harbour Project protocol, which stated that 30-35% of each tile needed to be covered in bivalves. Individuals of *Mytilus* spp. were sourced from Whitsand Bay (50.346086, -4.255325). An additional five cleared plots (0.25 x 0.25 m) served as seawall controls and were arranged amongst tile treatments in a randomised order. Prior to tile attachment, a 0.30 x 0.30 m area on the seawall where each tile was to be affixed was cleared of all flora and fauna using chisels and wire brushes. Each tile was attached in the same orientation with ridges running vertically so that water would not be retained at low tide, and tiles were spaced a minimum of 0.5 m from each other. Experiments commenced at both sites in August 2016, and were left in place for 12 months. All the above methods followed World Harbour Project protocol.

4.2.4.2 Tel Aviv, Israel

Five tiles of each of the three complexity treatments were affixed to an intertidal seawall in a single horizontal row in a randomised order in the intertidal. All experimental tiles were oriented with ridges running vertically so that water would completely drain from the tiles at low tide. An additional five concrete tiles composed from the same material as the seawall without crevices, ridges and microtexture, and five cleared plots were included amongst the experimental tiles to serve as controls. No tiles were seeded with bivalves. Experiments commenced in August 2016 and were left in place for 12 months. All the above methods followed World Harbour Project protocol.

4.2.5 Sampling procedure

4.2.5.1 Plymouth, British Isles

Experimental tiles and seawall control plots were monitored at months 1, 3, 6, 9 and 12 for counts of mobile taxa and percentage cover of sessile taxa in case tiles were lost before the conclusion of the experiment. Photographs were taken of each tile and seawall plot in the field, and then percentage cover of sessile organisms was estimated by digitally overlaying a grid of 10 x 10 boxes on each photograph using freely available grid-drawing software (ArtTudor; Liverpool, UK). After 12 months, experimental tiles were removed from seawalls and placed into sealable bags to retain all organisms. Percentage cover of sessile taxa and counts of mobile taxa within control seawall plots were obtained in the field (in case scraping action damaged organisms for downstream identification) before all visible flora and fauna were scraped from the plots and placed in sealable bags. All experimental tiles and scrapings were transported back to the laboratory for analysis. In the laboratory, all organisms were removed from tiles and identified, and counts of mobile taxa and percentage cover of sessile taxa were obtained separately for crevices and ridges on 2.5 cm and 5 cm complexity tiles (flat tiles did not contain crevices and ridges). Organisms were identified down to the lowest taxonomic resolution possible. Salinity (psu) and water temperature (°C) were measured with a refractometer and a Testo 206 instrument (Testo SE & Co., UK), respectively, at months 1, 3, 6, 9 and 12 (Appendix 3, Table 1).

4.2.5.2 Tel Aviv, Israel

Experimental tiles and seawall control plots were monitored at months 1, 3, 6, 9 and 12 for counts of mobile taxa and percentage cover of sessile taxa in case tiles were lost before the conclusion of the experiment. After 12 months, final data were collected by taking photographs of each tiles and seawall plot in the field, and analysis of percentage cover (no mobile organisms were present) was estimated using CoralNet software (Beijbom et al., 2012). Organisms were identified down to the lowest taxonomic resolution possible. Salinity (specific gravity, Sg) and temperature (°C) were measured using a hydrometer (Sera, D 52518, Heinsberg, Germany) and a temperature probe, respectively, at months 1, 3, 6, 9 and 12 (Appendix 3, Table 1).

4.2.6 Statistical analyses

4.2.6.1 Plymouth, British Isles

Species diversity was quantified using final taxon and functional richness and community composition data from the conclusion of the experiment. To investigate differences among treatments in functional groups, taxa were classified into three functional groups: grazers, filter feeders and primary producers. Mean taxon and functional richness were quantified using univariate analysis of variance tests (ANOVA) on untransformed presence/absence data on Bray-Curtis similarity matrices. Community composition was analysed using permutational multivariate analysis of variance tests (PERMANOVA) using fourth root transformed abundance data to reduce the influence of very abundant species (Anderson, Gorley, & Clarke, 2008) after Bray-Curtis similarity matrices were computed.

The hypothesis that tiles seeded with mussels will support greater taxon and functional richness, and different community composition, compared to unseeded tiles was not tested, as mussels were lost to predation within one month of experiment commencement. There were initially, however, remaining mussel shell fragments and glue on tiles from the seeded mussels. Thus, to test the effects of shell fragments and glue, we ran a 3-way PERMANOVA on Site (random; 2 levels: Mayflower Marina, Turnchapel Wharf), Treatment (fixed; 4 levels: seawall, flat, 2.5 cm, 5 cm) and Mussel Seeding (fixed; 2 levels: seeded and unseeded). There were no effects of remaining shell fragments and glue on taxon richness and composition; therefore, “seeded” and “unseeded” tile treatments were pooled for analysis.

To test the hypothesis about differences in taxon and functional richness and community composition among tile treatments, a two-way PERMANOVA was used with factors: Site (random; 2 levels: Mayflower Marina, Turnchapel Wharf) and Treatment (fixed; 4 levels: seawall plot, flat, 2.5 cm, 5 cm). PERMANOVAs were based on 9999 permutations of residuals under a reduced model and post-hoc pairwise tests were run where applicable. Where there were not enough possible permutations to perform a reasonable test, Monte Carlo tests were run to obtain more meaningful *P*-values (Anderson et al., 2008)

4.2.6.2 Tel Aviv, Israel

Species diversity was quantified using final taxon and functional diversity and community composition data collected at the conclusion of the experiment. To investigate differences among treatments in functional groups, taxa were classified into three functional groups: filter feeders, primary producers and detritivore/scavengers.

Mean taxon and functional richness were quantified using univariate analysis of variance tests (ANOVA) on untransformed presence/absence data after Bray-Curtis similarity matrices were computed. Community composition was analysed using one-way permutational multivariate analysis of variance tests (PERMANOVA) using square root transformed abundance data to reduce the influence of abundant species (Anderson, Gorley, & Clarke, 2008) after Bray-Curtis similarity matrices were computed.

To test the hypothesis about differences in taxon and functional richness and community composition among tile treatments, a one-way PERMANOVA was used with factor Treatment (fixed; 5 levels: seawall plot, control, flat, 2.5 cm, 5 cm) and was based on 9999 permutations of residuals under a reduced model. Post-hoc pairwise tests were run where applicable. Where there were not enough possible permutations to perform a reasonable test, Monte Carlo tests were run to obtain more meaningful *P*-values (Anderson et al., 2008).

4.2.6.3 Plymouth, British Isles and Tel Aviv, Israel

All multivariate data sets were visualised using non-metric multi-dimensional scaling (nMDS) plots. In cases where stress on the two-dimensional nMDS plot was high (~0.2), the three-dimensional solutions (lower stress) were visualised to confirm observed patterns, and the two-dimensional plots were retained. All statistical tests were run in PRIMER v6 with the PERMANOVA+ add-on (PRIMER-E Ltd, Plymouth, UK; Anderson et al., 2008) using the PERMANOVA routine, and data visualised using the nMDS routine. Where significant differences in community composition were detected among treatments, percentage contributions of individual taxa to dissimilarities between treatments were analysed using the similarity percentage (SIMPER) routine in PRIMER v6.

4.3 Results

4.3.1 Plymouth, British Isles: General overview

Overall, 13 taxa were observed on tiles, with one species unique to complex tiles (the Pacific oyster, *Magallana gigas* [Thunberg, 1793]) and two species unique to 2.5 cm complexity tiles (an encrusting bryozoan, *Cryptosula pallasiana* [Moll, 1803] and a lichen, *Verrucaria maura* Wahlenberg, 1803). There were seven mobile taxa and six sessile taxa. Overall, two non-native species were observed in treatments at Turnchapel Wharf (a barnacle, *Austrominius modestus* [Darwin, 1854] and *M. gigas*), while only *A. modestus* was recorded at Mayflower Marina (Table 4-1); *M. gigas* was present on the surrounding seawall but did not settle on the experimental plots.

At the conclusion of the experimental period, total taxon richness of tile treatments was greatest on 2.5 cm tiles at Turnchapel Wharf (10 taxa) and lowest on 5 cm tiles at Mayflower Marina (3 taxa). Total functional richness was greatest on flat and 2.5 cm tiles at both sites (3 taxa) and lowest on 5 cm tiles at both sites (2 taxa). Cleared seawall plots at Mayflower Marina and Turnchapel Wharf supported taxon richness of 1 and 4, respectively, and functional richness of 1 and 2, respectively (Figure 4-3). Salinity ranged from 25-35 psu, while temperature ranged from 7.7-19.2 °C (Appendix 3, Table 1). Taxon richness of treatments varied over the 12-month experimental period at both sites (Figure 4-4).

Table 4-1. Summary table for taxa recorded by functional group on experimental tiles and cleared seawall plots in Plymouth, British Isles recorded throughout the 12-month experiment. Non-native species are indicated by ‘NNS’ superscript.

	Tile Treatment				**Site**	
Taxa	**seawall**	**flat**	**2.5 cm**	**5 cm**	**Mayflower Marina**	**Turnchapel Wharf**
Grazers						
Patella vulgata (Linnaeus, 1758)	✓	✓	✓	✓	✓	✓
Patella depressa (Pennant, 1777)	✓	✓	✓	✓	✓	✓
Gibbula umbilicalis (da Costa, 1778)	✓	✓	✓	✓		✓
Phorcus lineatus (da Costa, 1778)	✓	✓	✓	✓		✓
Littorina littorea (Linnaeus, 1758)	✓	✓	✓	✓		✓
Littorina saxatilis (Olivi, 1792)	✓	✓	✓	✓		✓
Littorina spp.*		✓	✓			✓
Filter Feeders						
Austrominius modestus (Darwin, 1854)$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓
Magallana gigas (Thunberg, 1793)$^{\text{NNS}}$			✓	✓		✓
Cryptosula pallasiana (Moll, 1803)			✓			✓
Primary Producers						
Ulva spp.	✓	✓	✓	✓	✓	✓
Fucus spp.**		✓	✓	✓	✓	✓
Verrucaria maura (Wahlenberg, 1803)			✓			✓
Total taxon richness	**8**	**10**	**13**	**10**	**5**	**13**

**Littorina obtusata* or *L. fabalis*

***Fucus vesiculosus or F. spiralis*

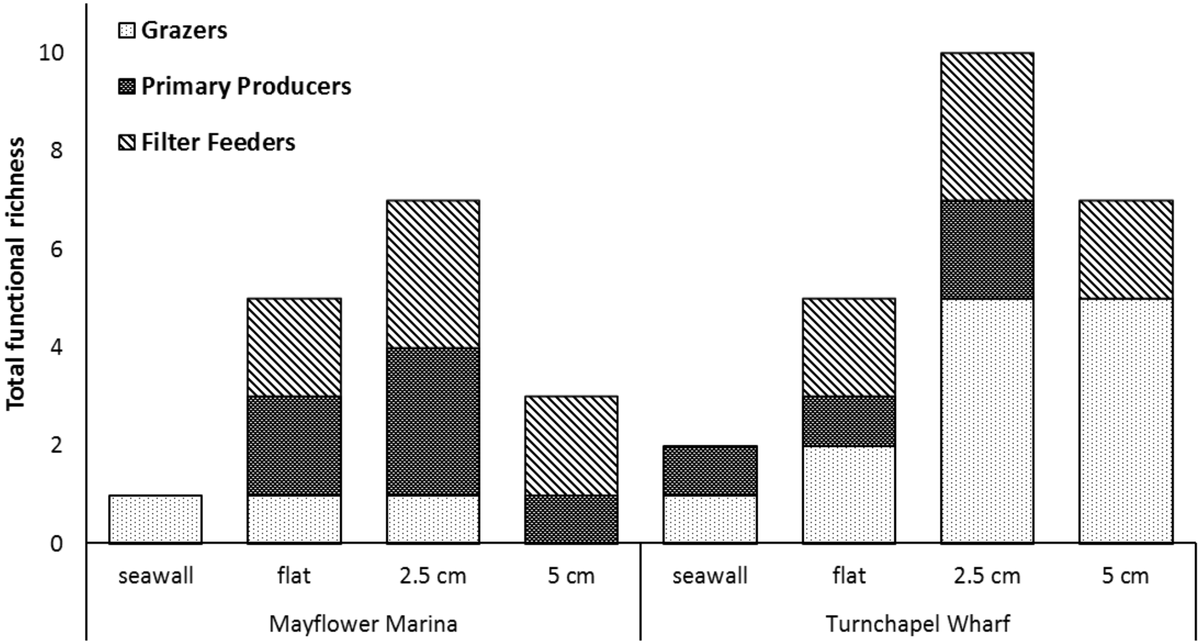


Figure 4-3. Number of taxa within each functional group by tile treatment at Mayflower Marina and Turnchapel Wharf in Plymouth, British Isles recorded at the conclusion of the 12-month experimental period.

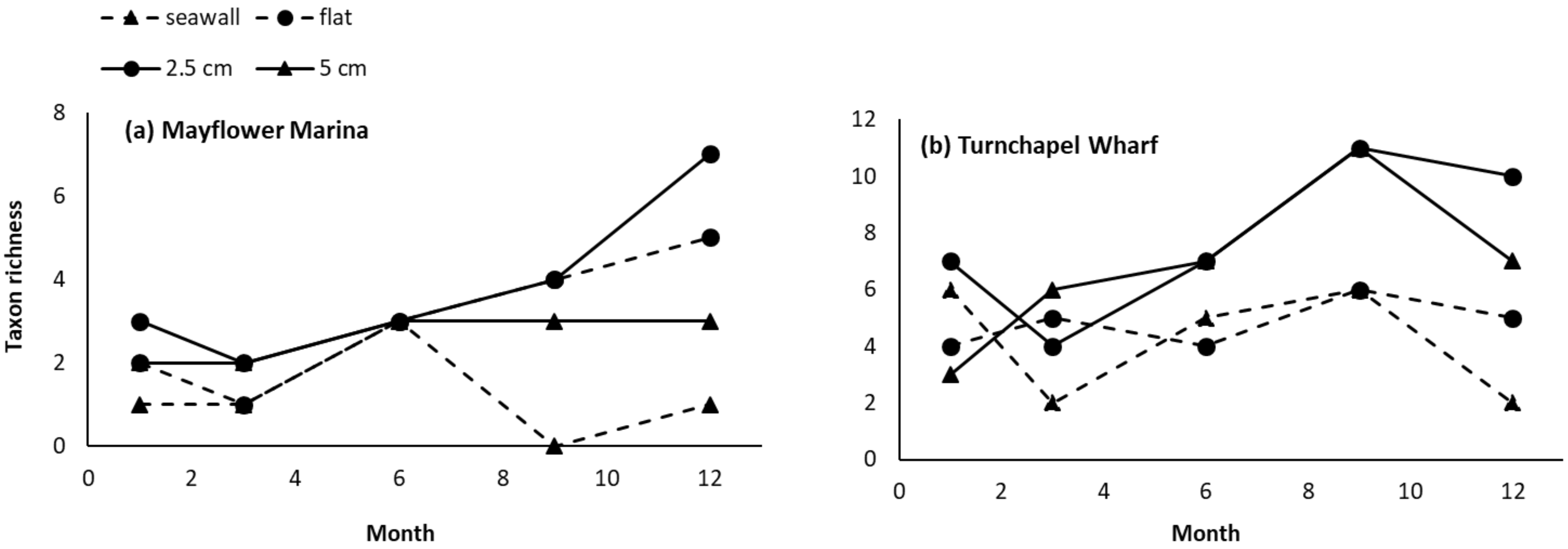


Figure 4-4. Temporal changes in taxon richness by tile treatment at (a) Mayflower Marina and (b) Turnchapel Wharf over the course of the 12-month experiment. Taxon richness was recorded at months 1, 3, 6, 9 and 12. Note the different scales for taxon richness.

4.3.2 Plymouth, British Isles: Comparison of taxon and functional richness among tile treatments

There was a significant main effect of treatment on both taxon and functional richness (Table 4-2; Figure 4-5) with all three tile types supporting significantly greater taxon and functional richness compared to the seawall. The average number of taxa recorded in the seawall plots was 0.8 ± 0.1, while flat tiles supported 2.1 ± 0.1, 2.5 cm tiles supported 2.6 ± 0.1 and 5 cm tiles supported 2.5 ± 01.

Table 4-2. Two-way ANOVAs comparing mean (a) taxon and (b) functional richness among tile treatments in Plymouth, British Isles recorded at the conclusion of the 12-month experimental period. Where unique permutations were < 100, Monte Carlo tests were run and P(MC) values were used to determine significance. Significant p-values are bolded.

(a) Taxon

Source	df	SS	MS	Pseudo-F	P(perm)
Site	1	2.89	2.89	4.8038	**0.0343**
Treatment	3	23.693	7.8976	19.173	**0.0474**
Si x Tr	3	1.2357	0.4119	0.68467	0.5729
Residual	62	37.3	0.60161		
Total	69	65.443			

Transform: no transformation

(b) Functional

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Site	1	0.04	0.04	0.496	0.5131	351	0.4824
Treatment	3	13.89	4.63	97.2	0.1181	140	**0.0021**
Si x Tr	3	0.14	0.05	0.59048	0.6236	1809	0.6200
Residual	62	5.00	0.08				
Total	69	19.09					

Transform: no transformation

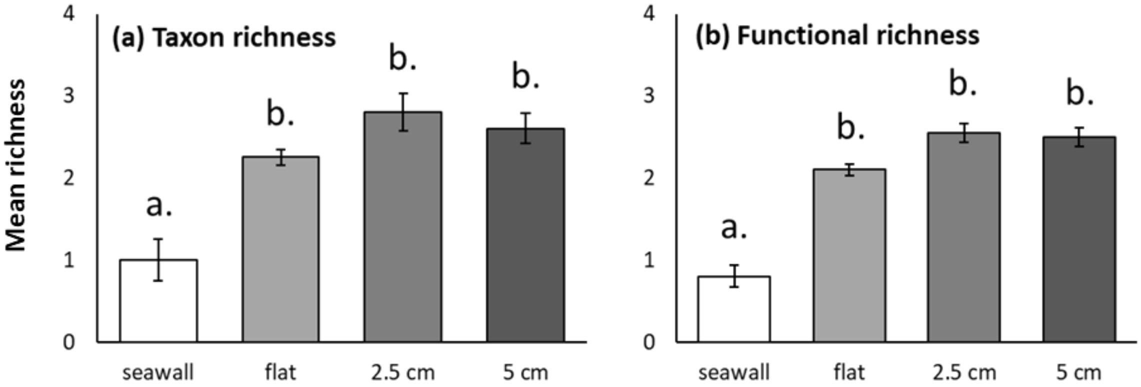


Figure 4-5. Comparison of mean (a) taxon and (b) functional richness among tile treatments in Plymouth, British Isles recorded at the conclusion of the 12-month experimental period. Error bars represent standard error. Letters show where there are significant differences between treatments determined by post-hoc pairwise comparisons (both (a) and (b): seawall, n = 5; flat, n = 10; 2.5 cm, n = 10; 5 cm, n = 10; (a): p = 0.0474; (b): p = 0.0021). Significant differences were seen between the seawall and all experimental tile treatments for (a) taxon richness and (b) functional richness.

4.3.3 Plymouth, British Isles: Comparison of taxon and functional composition among tile treatments

There was a significant interaction between treatment and site for both taxon and function composition (Figure 4-6; Table 4-3a, b). Post-hoc pairwise comparisons revealed significant differences in taxon composition between seawall plots and all other treatments, as well as flat tiles and all other treatments at both sites. Post-hoc pairwise comparisons for functional composition showed that there were significant differences between seawall plots and all other treatments at both sites, but at Mayflower, there were also significant differences between flat tiles and 2.5 cm and 5 cm tiles.

SIMPER analyses from Mayflower Marina showed that differences between seawall plots and tiles were driven by *Ulva* spp. and *A. modestus*, with both being more abundant on tiles than seawall plots. Over 60% of dissimilarity between flat tiles and complex tiles (2.5 cm and 5 cm) were attributed to *Ulva* spp. and *A. modestus*, with both being more abundant on complex tiles than flat tiles. Over 75% of dissimilarity between 2.5 cm and 5 cm tiles were attributed to *M. gigas*, *Ulva* spp., *A. modestus* and *Patella vulgata*, with *M. gigas* more abundant on 5 cm tiles, and *Ulva* sp., *A. modestus* and *P. vulgata* more abundant on 2.5 cm tiles. SIMPER analysis from Turnchapel Wharf revealed that dissimilarities between seawall plots and tiles were attributed to *A. modestus* and *Ulva* spp., with both being more abundant on tiles compared to seawall plots. Over 20% of the dissimilarity between flat and complex tiles (2.5 cm and 5 cm) was attributed to *A. modestus*, with abundances greater on complex tiles compared to flat tiles. Greater than 60% of the dissimilarity between 2.5 cm and 5 cm tiles was attributed to *M. gigas*, *Littorina littorea*, *P. vulgata*, *Littorina* spp. and *Steromphala umbilicalis*, with all taxa more abundant on 5 cm tiles except *L. littorea* (Table 4-4).

Table 4-3. Two-way PERMANOVAs comparing (a) taxon and (b) functional composition among tile treatments in Plymouth, British Isles recorded at the conclusion of the 12-month experimental period. Significant p-values are bolded.

(a) Taxon

Source	df	SS	MS	Pseudo-F	P(perm)
Site	1	7567	7567	26.271	**0.0001**
Treatment	3	30448	10149	4.6888	0.074
Si x Tr	3	6493.9	2164.6	7.5151	**0.0001**
Residual	62	17858	288.03		
Total	69	68764			
Transform:	fourth root				

(b) Functional

Source	df	SS	MS	Pseudo-F	P(perm)
Site	1	5356.8	5356.8	44.161	**0.0001**
Treatment	3	26447	8815.6	4.8656	0.1036
Si x Tr	3	5435.5	1811.8	14.937	**0.0001**
Residual	102	12373	121.3		
Total	109	62585			
Transform:	fourth root				

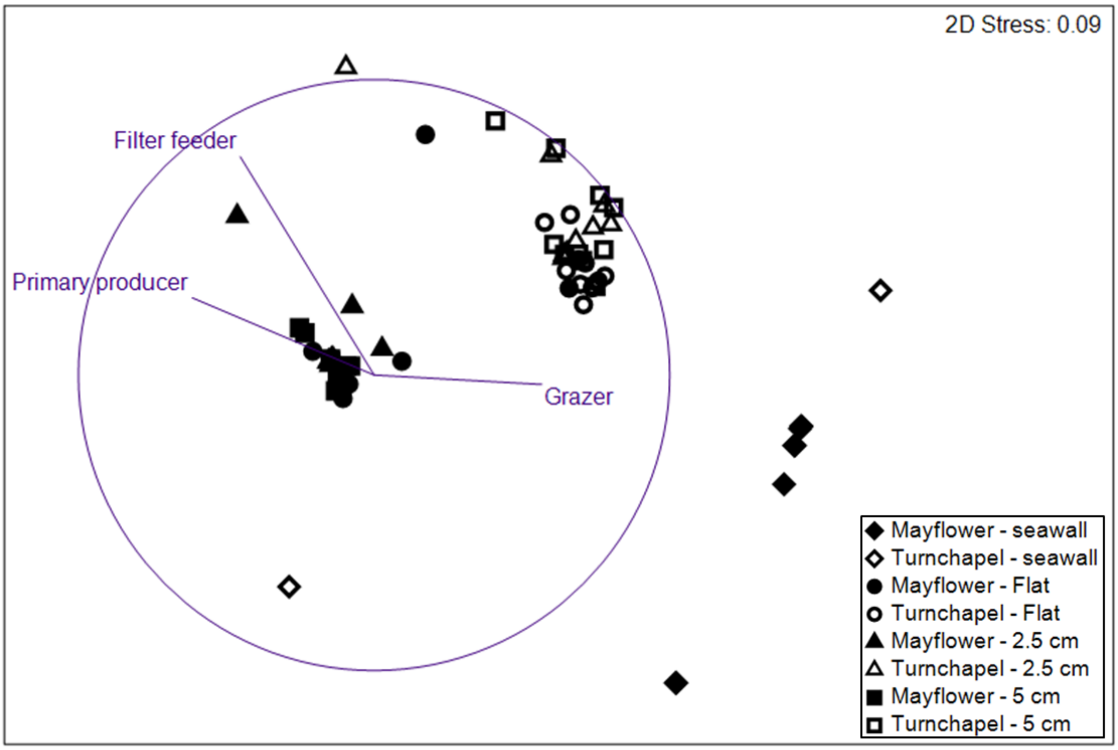


Figure 4-6. nMDS ordination plot comparing community composition among tile treatments in Plymouth, British Isles recorded at the conclusion of the 12-month experimental period, with functional groups overlaid. There was a significant site by treatment effect (p = 0.0001).

Table 4-4. Differences in average abundances (fourth-root transformed; indicated by > or <) and contributions ('%' for percentage or 'c' for counts) of individual species to community composition dissimilarities between treatments at (i) Mayflower Marina and (ii) Turnchapel Wharf in Plymouth, British Isles recorded at the conclusion of the 12-month experimental period for (a) seawall and flat tiles, (b) seawall and 2.5 cm tiles, (c) seawall and 5 cm tiles (d) flat and 2.5 cm tiles, (e) flat and 5 cm tiles and (f) 2.5 cm and 5 cm tiles. Consistency of contribution is shown by ‘Diss/SD’, which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(i) Mayflower Marina

(a)	**Average dissimilarity = 91.5%**	**seawall**	**>/<**	**flat**	**% Contr**	**Diss/SD**
	Austrominius modestus (%)	0.0	<	2.8	47.7	4.5
	Ulva spp. (%)	0.0	<	2.2	33.2	1.5

(b)	**Average dissimilarity = 96.7%**	**seawall**	**>/<**	**2.5 cm**	**% Contr**	**Diss/SD**
	Ulva spp. (%)	0.0	<	3.6	42.7	5.5
	Austrominius modestus (%)	0.0	<	3.4	40.3	6.1

(c)	**Average dissimilarity = 100.0%**	**seawall**	**>/<**	**5 cm**	**% Contr**	**Diss/SD**
	Ulva spp. (%)	0.0	<	3.3	41.9	6.7
	Austrominius modestus (%)	0.0	<	3.3	40.8	8.4

(d)	**Average dissimilarity = 25.2%**	**flat**	**>/<**	**2.5 cm**	**% Contr**	**Diss/SD**
	Ulva spp. (%)	2.2	<	3.6	45.3	0.9
	Austrominius modestus (%)	2.8	<	3.4	16.9	2.8
	Patella vulgata (c)	0.4	>	0.2	13.7	0.8

(e)	**Average dissimilarity = 21.6%**	**flat**	**>/<**	**5 cm**	**% Contr**	**Diss/SD**
	Ulva spp. (%)	2.2	<	3.3	46.8	0.8
	Austrominius modestus (%)	2.8	<	3.3	16.6	1.8
	Magallana gigas (%)	0.1	<	0.4	16.3	0.6

(f)	**Average dissimilarity = 11.5%**	**2.5 cm**	**>/<**	**5 cm**	**% Contr**	**Diss/SD**
	Magallana gigas (%)	0.2	<	0.4	28.4	0.6
	Ulva spp. (%)	3.6	>	3.3	19.6	1.4
	Austrominius modestus (%)	3.4	>	3.3	15.3	1.1
	Patella vulgata (c)	0.2	>	0.0	11.9	0.5

(ii) Turnchapel Wharf

(a)	Average dissimilarity = 75.9%	seawall	>/<	flat	% Contr	Diss/SD
	Austrominius modestus (%)	0.0	<	2.8	60.2	4.3
	Patella vulgata (c)	0.9	<	1.4	15.7	1.0

(b)	Average dissimilarity = 80.1%	seawall	>/<	2.5 cm	% Contr	Diss/SD
	Austrominius modestus (%)	0.0	<	3.4	55.5	4.0
	Patella vulgata (c)	0.9	<	1.4	12.0	1.0
	Ulva spp. (%)	0.6	>	0.0	8.4	0.5

(c)	Average dissimilarity = 77.7%	seawall	>/<	5 cm	% Contr	Diss/SD
	Austrominius modestus (%)	0.0	<	3.3	55.5	4.3
	Patella vulgata (c)	0.9	<	1.5	14.2	1.1
	Ulva spp. (%)	0.6	>	0.0	8.9	0.5

(d)	Average dissimilarity = 23.3%	flat	>/<	2.5 cm	% Contr	Diss/SD
	Austrominius modestus (%)	2.8	<	3.4	23.5	2.5
	Littorina littorea (c)	0.0	<	0.4	15.5	0.8
	Patella vulgata (c)	1.4	=	1.4	13.7	1.1
	Fucus sp. (%)	0.2	=	0.2	10.7	0.5
	Magallana gigas (%)	0.1	<	0.2	10.6	0.5

(e)	Average dissimilarity = 20.6%	flat	>/<	5 cm	% Contr	Diss/SD
	Austrominius modestus (%)	2.8	<	3.3	21.0	1.8
	Magallana gigas (%)	0.1	<	0.4	20.1	0.6
	Patella vulgata (c)	1.4	<	1.5	16.2	1.6
	Littorina spp. (c)	0.1	<	0.3	15.4	0.7

(f)	Average dissimilarity = 23.5%	2.5 cm	>/<	5 cm	% Contr	Diss/SD
	Magallana gigas (%)	0.2	<	0.4	16.6	0.6
	Littorina littorea (c)	0.4	>	0.1	14.6	0.8
	Patella vulgata (c)	1.4	<	1.5	13.8	1.1
	Littorina spp. (c)	0.1	<	0.3	11.9	0.7
	Steromphala umbilicalis (c)	0.1	<	0.3	11.5	0.7
	Austrominius modestus (%)	3.4	>	3.3	9.5	1.0

4.3.4 Tel Aviv, Israel: General overview

A total of 13 taxa were recorded across all experimental and control tiles and plots, one of which was a non-native species: the fingerprint oyster, *Alectryonella plicatula* (Gmelin, 1791). The 2.5 cm and 5 cm tiles supported the greatest number of taxa (11 taxa) and functional groups (3 groups; Table 4-5; Figure 4-7). Taxon richness of treatments varied over the 12-month experimental period (Figure 4-8). Throughout the experiment, salinity ranged from 1.0248-1.0266 Sg (approx. 32.9-35.3 psu), pH ranged from 8.0-8.1 and temperature ranged from 15.7-30.4 °C (Appendix 3, Table 1).

Table 4-5. Summary table for taxa recorded by functional group on experimental tiles, control tiles and cleared seawall plots in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period. Non-native species are indicated by ‘NNS’ superscript.

Taxa	**Cleared seawall**	**Control tile**	**Flat**	**5 cm**	**2.5 cm**
Filter feeder					
Alectryonella plicatula (Gmelin, 1791)^{NNS}				✓	✓
Amphibalanus amphitrite (Darwin, 1854)	✓	✓	✓	✓	✓
Crambe crambe (Schmidt, 1862)				✓	✓
Encrusting bryozoan			✓	✓	✓
Ostrea edulis Linnaeus, 1758			✓	✓	✓
Schizoporella sp.		✓		✓	✓
Serpulidae	✓	✓		✓	✓
Spirorbidae	✓	✓	✓	✓	✓
Watersipora cucullata (Busk, 1854)			✓		
Primary producer					
Crustose coralline algae				✓	✓
Turf		✓	✓	✓	✓
Scavenger/detritivore					
Palaemon serratus (Pennant, 1777)		✓		✓	✓
Other					
Unidentified fouling organism		✓			
Total taxon richness	**3**	**7**	**6**	**11**	**11**

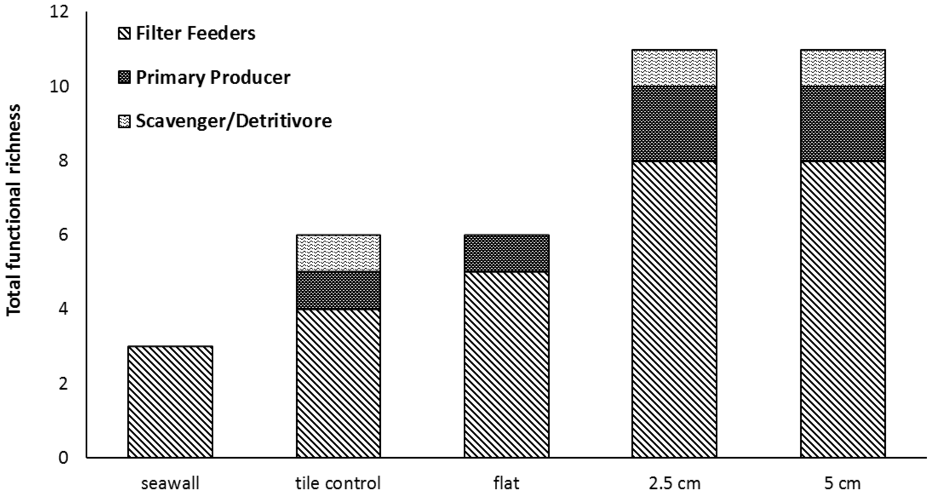


Figure 4-7. Number of taxa within each functional group by tile treatment in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period.

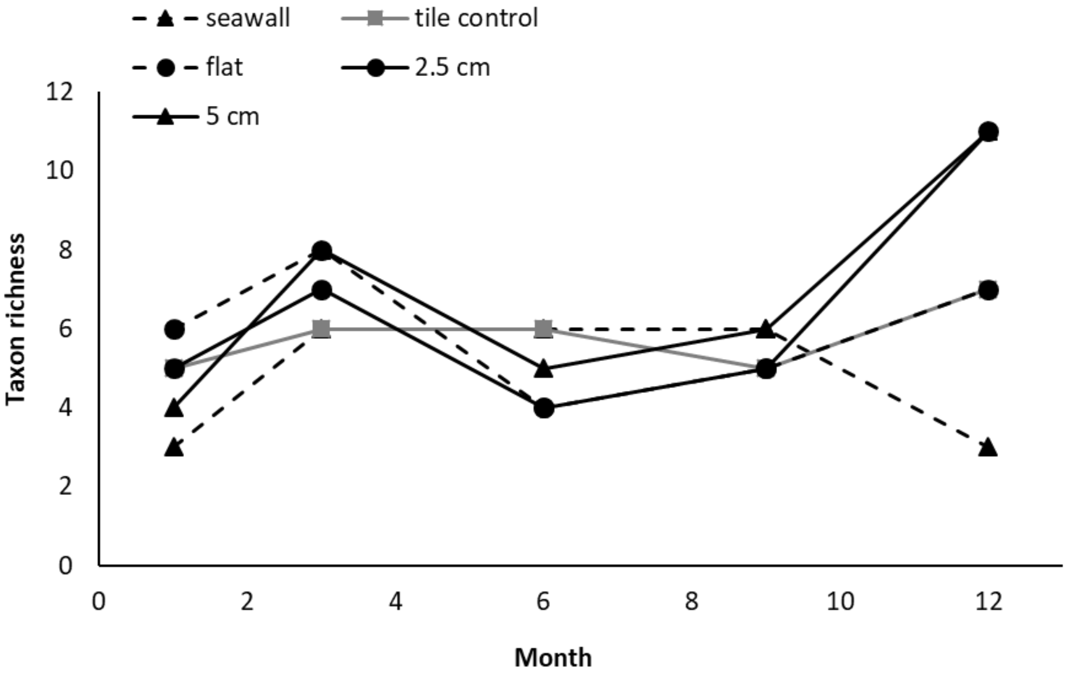


Figure 4-8. Temporal changes in taxon richness in Tel Aviv, Israel over the 12 month experimental period. Taxon richness was recorded at months 1, 3, 6, 9 and 12.

4.3.5 Tel Aviv, Israel: Comparison of taxon and functional richness among tile treatments

Mean taxon and functional richness was significantly different among tile treatments (Table 4-6a, b). Post-hoc pairwise tests showed there was significantly greater taxon richness on the 2.5 cm and 5 cm tiles compared to seawall plots; and significantly greater taxon richness on the 5cm tiles compared to the control and flat tiles (Figure 4-9a). Post-hoc pairwise comparisons revealed significantly greater functional richness on all tile treatments compared to seawall plots and 5 cm tiles compared to flat tiles (Figure 4-9b).

Table 4-6. One-way ANOVAs comparing mean (a) taxon and (b) functional richness among tile treatments in Tel Aviv, Israel. Significant p-values are bolded.

(a) Taxon

Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	4	11693	2923.3	3.0281	**0.0053**
Residual	20	19308	965.39		
Total	24	31001			
Transform:	no transformation				

(b) Functional

Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	4	3550.3	887.58	8.3731	**0.0002**
Residual	20	2120.1	106		
Total	24	5670.4			
Transform:	no transformation				

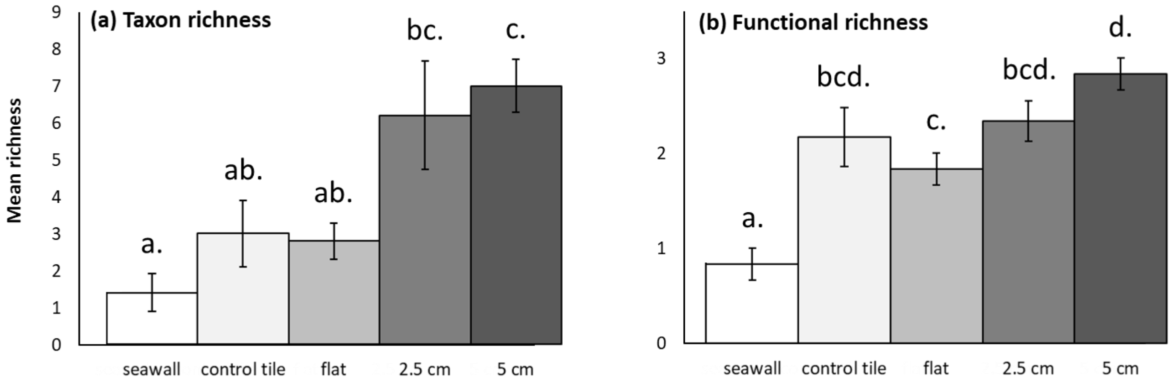


Figure 4-9. Comparison of mean (a) taxon and (b) functional richness among tile treatments in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period. Error bars represent standard error. Letters show where there are significant differences between treatments determined by post-hoc pairwise comparisons (both (a) and (b): seawall, n = 5; control, n = 5; flat, n = 5; 2.5 cm, n = 5; 5 cm, n = 5; (a): p = 0.0053; (b): p = 0.0002). There were significant differences between the seawall and the 2.5 cm and 5 cm tile treatments, as well as between the control and the 5 cm tiles, and the flat and 5 cm tiles for (a) taxon richness. Significant differences were observed between the seawall and all tile treatments, as well as between flat and 5 cm tiles for (b) functional richness.

4.3.6 Tel Aviv, Israel: Comparison of taxon and functional composition among tile treatments

There was a significant effect of tile treatment on both taxon and functional composition (Table 4-7a, b). Post-hoc pairwise comparison tests for taxon composition showed significant differences between seawall plots and flat and 5 cm tiles, control tiles and 2.5 cm and 5 cm tiles and flat tiles and 2.5 cm tiles (Figure 4-10). Post-hoc pairwise comparison tests for functional composition showed that there were significant differences between seawall plots and all other treatments, control tiles and 5 cm tiles and flat tiles and 5 cm tiles. SIMPER analysis revealed that turf-forming algae was the highest contributor to dissimilarities among all treatments (Table 4-8). Of the treatments that significantly differed in community composition abundance of turf algae was greater on: control tiles, flat tiles and 5 cm tiles compared to seawall plots; 2.5 cm and 5 cm tiles compared to control tiles; and 2.5 cm tiles compared to flat tiles.

Table 4-7. One-way PERMANOVA comparing mean (a) taxon and (b) functional composition among tile treatments in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period. Significant p-values are bolded.

(a) Taxon

Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	4	23626	5906.5	3.2363	**0.0001**
Residual	20	36501	1825.1		
Total	24	60127			
Transform:	square root				

(b) Functional

Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	4	21736	5434.1	3.9753	**0.0002**
Residual	20	27340	1367		
Total	24	49076			
Transform:	square root				

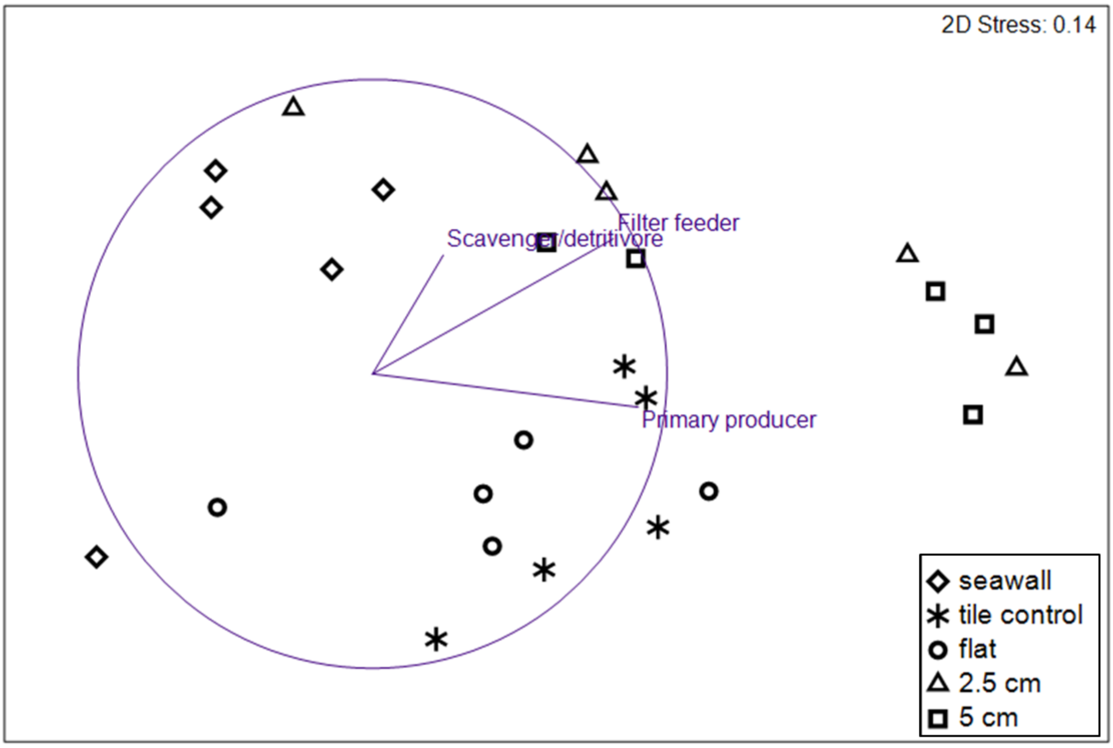


Figure 4-10. nMDS ordination plots comparing community composition among tile treatments in Tel Aviv, Israel (p = 0.0001) recorded at the conclusion of the 12-month experimental period, with functional groups overlaid.

Table 4-8. Differences in average abundances (square root transformed; indicated by > or <) and contributions ('%' for percentage) of individual species to assemblage composition dissimilarities between tile treatments in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period for (a) seawall compared to tile control, (b) seawall compared to flat tile, (c) seawall compared to 2.5 cm tile, (d) seawall compared to 5 cm tile, (e) tile control compared to flat tile, (f) tile control compared to 2.5 cm tile, (g) tile control compared to 5 cm tile, (h) flat tile compared to 2.5 cm tile, (i) flat tile compared to 5 cm tile and (j) 2.5 cm compared to 5 cm tile. Consistency of contribution is shown by ‘Diss/SD’, which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(a)	**Average dissimilarity = 85.7%**	**seawall**	**>/<**	**tile control**	**% Contr**	**Diss/SD**
	Turf algae (%)	0.0	<	3.1	47.5	2.5
	Amphibalanus amphitrite (%)	1.8	>	0.5	23.9	1.2

(b)	**Average dissimilarity = 80.0%**	**seawall**	**>/<**	**flat**	**% Contr**	**Diss/SD**
	Turf algae (%)	0.0	<	1.9	32.9	1.5
	Amphibalanus amphitrite (%)	1.8	>	0.6	28.5	1.3
	Spirorbidae (%)	0.6	<	1.0	22.0	0.8

(c)	**Average dissimilarity = 72.7%**	**seawall**	**>/<**	**2.5 cm**	**% Contr**	**Diss/SD**
	Turf algae (%)	0.0	<	3.3	19.9	1.5
	Encrusting bryozoan (%)	0.0	<	2.2	15.1	1.9
	Spirorbidae (%)	0.6	<	1.8	13.6	1.2
	Palaemon serratus (%)	0.0	<	0.9	13.2	0.8
	Amphibalanus amphitrite (%)	1.8	=	1.8	11.2	0.6

(d)	**Average dissimilarity = 83.4%**	**seawall**	**>/<**	**5 cm**	**% Contr**	**Diss/SD**
	Turf algae (%)	0.0	<	5.2	28.8	2.3
	Spirorbidae (%)	0.6	<	2.3	15.4	1.1
	Ostrea edulis (%)	0.0	<	2.3	12.4	1.8
	Encrusting bryozoan (%)	0.0	<	2.2	12.0	1.7
	Palaemon serratus (%)	0.0	<	1.1	8.2	1.6

(e)	**Average dissimilarity = 51.5%**	**tile control**	**>/<**	**flat**	**% Contr**	**Diss/SD**
	Turf algae (%)	3.1	>	1.9	34.4	1.0
	Spirorbidae (%)	1.5	>	1.0	25.0	1.2
	Amphibalanus amphitrite (%)	0.5	<	0.6	12.5	1.1

(f)	**Average dissimilarity = 69.9%**	**tile control**	**>/<**	**2.5 cm**	**% Contr**	**Diss/SD**
	Turf algae (%)	3.1	<	3.3	22.6	1.6
	Amphibalanus amphitrite (%)	0.5	<	1.8	15.9	1.1
	Encrusting bryozoan (%)	0.0	<	2.2	13.3	1.8

	Spirorbidae (%)	1.5	<	1.8	11.6	1.1
	Palaemon serratus (%)	0.3	<	0.9	10.0	0.8

(g)	**Average dissimilarity = 61.6%**	**tile control**	**>/<**	**5 cm**	**% Contr**	**Diss/SD**
	Turf algae (%)	3.1	<	5.2	23.6	2.3
	Ostrea edulis (%)	0.0	<	2.3	14.6	1.7
	Encrusting bryozoan (%)	0.0	<	2.2	14.2	1.6
	Spirorbidae (%)	1.5	<	2.3	12.8	0.9
	Palaemon serratus (%)	0.3	<	1.1	8.4	1.4

(h)	**Average dissimilarity = 71.6%**	**flat**	**>/<**	**2.5 cm**	**% Contr**	**Diss/SD**
	Turf algae (%)	1.9	<	3.3	20.4	1.6
	Amphibalanus amphitrite (%)	0.6	<	1.8	15.7	1.1
	Encrusting bryozoan (%)	0.2	<	2.2	13.4	1.9
	Spirorbidae (%)	1.0	<	1.8	12.4	1.1
	Palaemon serratus (%)	0.0	<	0.9	11.1	0.8

(i)	**Average dissimilarity = 67.7%**	**flat**	**>/<**	**5 cm**	**% Contr**	**Diss/SD**
	Turf algae (%)	1.9	<	5.2	25.0	1.8
	Spirorbidae (%)	1.0	<	2.3	14.7	1.1
	Encrusting bryozoan (%)	0.2	<	2.2	13.1	1.6
	Ostrea edulis (%)	0.4	<	2.3	12.8	1.7
	Palaemon serratus (c)	0.0	<	1.1	9.1	1.6

(j)	**Average dissimilarity = 50.8%**	**2.5 cm**	**>/<**	**5 cm**	**% Contr**	**Diss/SD**
	Turf algae (%)	3.3	<	5.2	25.0	1.2
	Ostrea edulis (%)	1.6	<	2.3	11.9	1.3
	Encrusting bryozoan (%)	2.2	=	2.2	11.8	1.3
	Spirorbidae (%)	1.8	<	2.3	11.3	0.8
	Amphibalanus amphitrite (%)	1.8	>	0.8	8.8	1.7
	Schizoporella sp. (%)	1.1	<	1.4	8.8	1.1

4.4 Discussion

This study tested the effects of enhanced complexity on species diversity on intertidal seawalls in Plymouth, British Isles and Tel Aviv, Israel. In Plymouth, we also tested the effects of mussel seeding on species diversity. We predicted that complex tiles and tiles seeded with mussels would support greater taxon and functional richness and different community composition than control tiles/cleared seawall plots and unseeded tiles.

In Plymouth, the addition of habitat complexity had an effect on community composition, with different communities observed on flat compared to complex tiles, as well as in seawall plots compared to all other experimental tiles. Contrary to our prediction, however, habitat complexity had no effect on number of taxa living on experimental tiles and seawall plots. This means that the presence of tiles had a greater influence than the complexity of tiles on the numbers of colonising taxa. Therefore, the addition of habitat complexity did not cause differences in number of taxa, but differences did emerge when identities of taxa and abundances of individuals were analysed. The hypothesis about seeded mussel effects on species diversity could not be tested because mussels were lost to predation within the first month of experiment commencement.

In Israel, as hypothesised, the complex tiles supported greater taxon richness and different community composition compared to flat tiles and seawall plots. For taxon richness, seawall plots differed from complex tiles, but did not differ from the control and flat tiles. This suggests that crevices, but not microtexture, were important in supporting greater numbers of taxa. However, for community composition, seawall plots did differ from control and flat tiles, as well as complex tiles, suggesting that the presence of tiles and crevices played a role in influencing the colonising community.

Previous studies examining effects of adding topographic complexity have found positive effects on mean taxon richness and community composition. In an experiment testing the effects of different structural complexities on species diversity, complex tiles were found to support greater numbers of taxa and different biological communities compared to granite control tiles after 13 months (Loke and Todd, 2016). This same experiment also tested these effects at two tidal heights (low and high), and found that effects were only detected at the lower tidal height. Similarly, Perkol-Finkel et al. (2017) found that panels made with topographic complexity, including holes (3 cm and 12 cm deep), supported greater mean taxon richness compared to seawall control plots in the intertidal after 22 months. This study was conducted in the Mediterranean Sea where the tidal range is approximately 30 cm (Einav et al., 1995), and so mid- and high-intertidal heights are virtually absent. During the current experiment, the lack of complexity effects in Plymouth could be attributed to the position of experimental tiles in the mid- rather than the lower intertidal. This is because placement of interventions in the lower intertidal usually results in greater species diversity, as this area is immersed on every tidal cycle and the potential pool of colonising species is greater (Moschella et al., 2005; Chapman and Underwood, 2011; Firth et al., 2016a; Loke and Todd, 2016).

A meta-analysis of eco-engineering interventions in estuarine and coastal environments found that the most effective interventions in intertidal habitats for enhancement of number of sessile species were water retaining features, crevices and seeding of habitat-forming taxa, while for number of mobile species, the addition of crevices and pits were the most effective (Strain et al., 2017a). The study also found that cover of barnacles and bivalves was most influenced by the addition of crevices and pits compared to other tested interventions. In the current experiment, in Plymouth, there was no effect of crevices on numbers of sessile and mobile organisms, while conversely, in Tel Aviv, there were clear effects of crevices on taxon richness. Differential results between the two locations might be explained by dissimilar climates and thus different temperature stress. Tel Aviv has a Mediterranean climate with an average yearly temperature of 20 °C and roughly 140 days of sunshine. Conversely, Plymouth is known for its wet and mild climate, with an average temperature of 11.4°C and about 70 days of sunshine per year (Met Office, 2019). The findings here highlight the importance of testing eco-engineering interventions across multiple locations to understand effects of interventions on different taxa under different environmental conditions.

The current experiments ran for 12 months, with an installation date in August. Taxa that colonised Plymouth tiles vary in their reproductive seasons (Fish, 1972; McCarthy et al., 2008; Bunker et al., 2017), but many reproduce in the spring and summer months (Orton and Southward, 1961; Underwood, 1972; Bunker et al., 2017). Therefore, initial colonisation was likely from opportunistic species and immigration of mobile species currently on the seawall (observation of larger animals) rather than settlement of new larvae and spores. An early recruiter was the invasive barnacle, *Austrominius modestus*, which has a year-round reproductive season (Muxagata et al., 2004), with a peak of well-developed gonads in September and October (O'Riordan and Murphy, 2000). The absence of other barnacle species on tiles and in seawall plots throughout the duration of the experiment suggests that *A. modestus* occupied space that might otherwise have been colonised by native barnacle competitors (Gallagher et al., 2015). Additionally, the estuarine nature of the location of experiments in Plymouth favoured settlement of *A. modestus* over native species, as *A. modestus* is typically found in brackish conditions, while *Semibalanus balanoides* (Linnaeus, 1767) and *Chthamalus montagui* Southward, 1976 (both native species) prefer marine conditions (Gomes-Filho et al., 2010). Moreover, it is also possible that *A. modestus* is now so ubiquitous in natural and artificial habitats in the British Isles (Crisp, 1958; Gallagher et al., 2015), that its larvae outcompete native barnacle larvae for settlement on bare space (Bracewell et al., 2013). It is certainly possible to facilitate settlement of desirable native species if the timing of eco-engineering intervention coincides with target taxa reproductive season. For example, Firth et al. (2014b) showed that placement of an engineering “BIOBLOCK” in a breakwater in February supported early settlement of the native *S. balanoides* rather than *A. modestus* (L. Firth, pers. comm.). Thus, the timing of installation is a vital consideration for targeting native species to offset colonisation by non-native and nuisance species where possible (Airoldi et al., 2005b; Airoldi and Bulleri, 2011; Evans, 2016).

To date, the duration of eco-engineering experiments is typically 12 months (reviewed in Strain et al., 2017a), after which, treatments are destructively sampled and success of the design is evaluated. Despite there being some evidence to suggest early successional stages in artificial and natural habitats differ (Bulleri, 2005b; Bulleri et al., 2005), succession of an intertidal community typically takes well beyond 12 months to stabilize (Hawkins et al., 1983; Bulleri, 2005b). For example, in a study investigating the effects of eco-engineering enhancements in energy dissipation units on a causeway, Firth et al. (2016a) found contrasting results between sampling conducted at 12 and 24 months, with nearly four times the number of species observed at month 24 compared to the first sampling event. New substrate placed in intertidal habitats will experience fluctuations in recruitment, growth and stabilization of algae, filter feeding invertebrates and grazing mobile species over timescales of years to decades (Hawkins, 1981; Hawkins et al., 1983). In a survey of sacrificial breakwater blocks of varying ages, Hawkins et al. (1983) found that barnacle cover took 20-25 years to stabilise, *Fucus* spp. took 15-20 years to stabilise and the *Patella vulgata* population structure stabilised at 18 years, with the youngest blocks (1-3 years) supporting very different community assemblages compared to older blocks (20-25 years). Grazing invertebrates are important facilitators of succession, as they graze down algae (Hawkins, 1981; Jenkins et al., 2005; Coleman et al., 2006) and create space for algal propagules and larvae of other species breaking inhibition by mid successional species (Sousa, 1979; Hawkins et al., 1983; Benedetti-Cecchi, 2000; Benedetti-Cecchi et al., 2000). In Tel Aviv, no grazers were observed on tiles at the end of the 12-month experiment, suggesting that these tiles might still be in early successional stages. Thus, there are clear limitations to the results obtained from the current experiments; we should only evaluate success from an early successional stage point of view with the understanding that recruitment and colonisation would likely increase over time, increasing the number of taxa and abundance of individuals, inevitably changing community composition and potentially resulting in divergent communities among treatments.

Physical factors can also affect the success of the eco-engineering intervention over the course of months to years. In an experiment testing the efficacy of a precast habitat enhancement unit (“BIOBLOCK”) on increasing biodiversity, Firth et al. (2014b) found that after 12 months, the “BIOBLOCK” supported greater species diversity compared to surrounding boulders, but 24 months post installation, the “BIOBLOCK” became inundated with sediment following extreme winter storms. In our experiments, no tiles were lost to environmental factors. There is, however, potential for storm events and regular wave action to dislodge tiles from the seawall (see Browne and Chapman, 2014), as materials used to attach tiles (i.e., anchor screws, bolts) age and rust over time. Loss of tiles would open up new patches of bare substrate and allow for secondary biological succession (Connell and Slatyer, 1977; Benedetti-Cecchi, 2000), which may positively affect the biodiversity of the seawall, as primary and secondary succession work naturally in tandem on diverse rocky shores. Bare space, however, can also facilitate colonisation by non-native and opportunistic species (Airoldi and Bulleri, 2011; Bracewell et al., 2013). The duration of the current experiments, therefore, may not have been long enough to ultimately determine long-term success (or indeed failure) of the interventions.

Variation in community assemblage and species richness among tile treatments may be due to differences in surface area of treatments. The 5 cm tile treatment had a surface area of 1,490 cm^2, the 2.5 cm tile treatment had a surface area of 1,023 cm^2 and the flat tile treatment had the lowest surface area of 625 cm^2. Surface area naturally increases with higher surface complexity (Kostylev et al., 2005), creating more space for organisms to occupy, relating to the ‘species-area relationship’ (Preston, 1960; Connor and McCoy, 1979; Losos and Schluter, 2000; Gatti et al., 2017). More available space allows for organisms to exploit habitat niches (Whittaker et al., 1973), which effectively reduces competition for resources (Schoener, 1989; Dudley and D'Antonio, 1991) and therefore allows for a more diverse assemblage of species to establish (MacArthur and MacArthur, 1961; Pocheville, 2015). In this light, future eco-engineering experiments that utilise topographic complexity as a factor should consider the additional surface area provided by the higher complexity treatments by standardising for this extra area. This can provide information on the effects of complexity independent of surface area (see Loke and Todd, 2016).

Ecological engineering designs should maximize the ecological and social benefits whilst minimizing the cost to stakeholders (Narayan et al., 2016; Morris et al., 2018a). It is therefore desirable to determine the most cost-effective design, which may be the smallest intervention possible to achieve the desired ecological goals. Previous eco-engineering experiments tested the efficacy of interventions at multiple scales on species diversity. In a study investigating the effects of drill-cored rock pools on biodiversity, Evans et al. (2016a) found that the 5 cm and 12 cm deep pools supported similar taxon richness and community composition. Similarly, an experiment examining the effects of 14 mm and 22 mm diameter drilled pits on a concrete wave breaker unit, found no significant difference in species richness between the two pit depths (Firth et al., 2014b; Jackson, 2015). In the current experiment, there were no differences in taxon richness and community composition between 2.5 cm and 5 cm tiles in both Plymouth and Tel Aviv, suggesting that the 2.5 cm ridge was a large enough enhancement to influence the colonising community. This result can inform future designs that incorporate ridges and crevices, so that the cost to stakeholders is minimised.

Secondary management goals of eco-engineering designs often include enhancing ecosystem services, such as habitat provision to support fisheries and aquaculture (Hawkins et al., 1992b; Bohnsack et al., 1994; Whitmarsh et al., 2008), water quality improvement through biofiltration (Allen et al., 1992) and education and general aesthetic appeal of biodiversity in urban areas contributing to human well-being (Airoldi et al., 2005a; Sugden et al., 2009; Mayer-Pinto et al., 2017). In both geographic locations, complex tiles supported greater functional richness compared to flat and control tiles and seawall plots. In particular, in Plymouth, experimental tiles supported three filter feeders and two primary producers, while seawall plots supported just one of each. Similarly, in Israel, complex tiles supported eight filter-feeding taxa, while flat tiles, control tiles and seawall plots supported only five, four and three, respectively. The number of primary producers in Israel was greater on complex tiles (2 taxa) compared to flat and control tiles (1 taxa) and seawall plots (0 taxa). Although on a small scale, these experiments clearly demonstrate the ability of complex tiles to enhance valuable ecosystem services such as carbon sequestration, primary productivity (i.e., through addition of macroalgae) and water filtration (i.e., through addition of filter feeders).

There are concerns that eco-engineering may facilitate the spread of non-native species (Dafforn et al., 2012; Evans et al., 2017; Naylor et al., 2017). Eco-engineering, however, aims to encourage diverse native biological communities, which can prevent the establishment of non-native species (Stachowicz et al., 1999; Stachowicz et al., 2002; Arenas et al., 2006b). In the current experiment, all tiles and seawall plots supported at least one non-native species in Plymouth. *Austrominius modestus* was found on all tiles and seawall plots, while *Magallana gigas* was only found on complex tiles. Both species were already present on the seawall prior to experiment implementation; the settlement of *M. gigas* on complex tiles only should therefore not be attributed to the design of the tiles, but rather regarded as chance. In Tel Aviv, complex tiles, but not flat tiles, control tiles and seawall plots, supported the one non-native species (*Alectryonella plicatula*). It is important to consider each non-native species on a case-by-case basis, as some non-natives are well established and ubiquitous throughout their expanded range (e.g., *Austrominius modestus*; Crisp, 1958; Gomes-Filho et al., 2010; Bracewell et al., 2012) and attempts at discouraging settlement will not be cost effective. Other non-native species, such as the Pacific oyster (*Magallana gigas*), pose a threat to native biodiversity through competition and displacement (Humphreys et al., 2014; Herbert et al., 2016). There have been attempts to eradicate populations around the British Isles (Guy and Roberts, 2010), although there remains support for use of *M. gigas* in aquaculture practices (Herbert et al., 2016). The current experiments demonstrate the difficulty in discouraging non-native species recruitment to eco-engineering interventions, and highlight the importance of future research to address methods of offsetting colonisation of specific non-native species.

4.4.1 Concluding remarks

There is increasing awareness that traditional hard built coastal defence structures are not ecologically sustainable (Airoldi et al., 2005a; Airoldi et al., 2009; Dugan et al., 2011), and under future climate change scenarios, they may not be economically viable (Fankhauser and Tol, 2005; Koch, 2010; Narayan et al., 2016). The impetus among scientists, coastal managers, government and the public to build multifunctional structures with built-in secondary ecological benefits is growing (Naylor et al., 2012; Evans et al., 2017; Evans et al., 2019; Strain et al., 2019a; Strain et al., 2019b). The field of eco-engineering of coastal structures, however, is still largely in the experimental phase; the evidence upon which to base large-scale installations in a variety of locations and conditions is lacking (Strain et al., 2017a). To inform sound eco-engineering practice, there is a need for wider testing of existing designs in different environmental settings, and to develop the predictive capability to forecast ecological outcomes (Airoldi et al., 2005a; Hulme, 2014; Evans, 2016). Our experiments addressed these concerns, as we tested equivalent designs in two different locations with different environmental conditions. Not surprising, we found that results varied between locations, reinforcing the idea that eco-engineering designs should consider site-specific conditions and taxa (Strain et al., 2017a). Here we found that: (1) In Plymouth, crevices influenced the colonising community but had no effect on taxon richness; (2) In Tel Aviv, crevices had a positive effect on both community composition and taxon richness, with complex tiles supporting greater numbers of taxa. Thus, depending on the secondary management goals (e.g., increase number of taxa, increase abundance of specific taxa, increase specific functional groups), further testing of eco-engineering interventions in Plymouth is necessary before interventions at the scale of entire structures can be undertaken. In Tel Aviv, however, future research can build on these effective interventions to develop site-specific approaches and more targeted secondary management goals that match the local taxa and address local conditions.

In order to move from small-scale trials to large-scale implementation at the entire structure level, a sound evidence base must underpin future eco-engineering designs. This means that reporting of failed designs and interventions with no effects is imperative. With careful planning, setting, and monitoring of secondary management goals, even heavily stressed coastal and marine ecosystems can support greater species diversity and provide valuable ecosystem services for humans and nature.

5. CHAPTER FIVE

Effects of habitat complexity, mussel seeding and shade on species diversity in subtidal habitats across two geographic locations

Abstract

The burgeoning human population has caused an increase in coastal development to accommodate industry, shipping, energy extraction, travel and aquaculture, as well as residential development and recreational activities. Climate change and sea level rise have exacerbated the effects of these human activities, resulting in a loss of natural habitat and irreversible damage to coastal ecosystems worldwide. As a response, ecologists are testing ecological engineering (or “eco-engineering”) techniques to enhance biodiversity, and ultimately resiliency, of coastal ecosystems. Eco-engineering is the practice of combining ecological with engineering design to achieve sustainable ecosystems for the benefit of humans and nature. This study tested the effects of habitat complexity, mussel seeding and shade in subtidal habitats in two geographic locations (Plymouth, British Isles and Tel Aviv, Israel). Although no formal comparisons were made between the geographic regions, the results are presented together here to emphasize that eco-engineering experiments should involve comparisons across geographic localities to understand generalities of patterns of effects at larger scales. Taxon and functional richness and community composition were compared among flat tiles, 2.5 cm tiles, 5 cm tiles, seawall plots (seawall plots were used in Tel Aviv only) and control tiles. In Plymouth only, taxon and functional richness and community composition were compared between tiles seeded with mussels and unseeded tiles, as well as shaded and unshaded tiles. Results differed between the locations. In general, in Plymouth, there was no effect of habitat complexity; however, the seeding of mussels did have an effect, with unseeded tiles supporting greater taxon richness than seeded

tiles. Community composition, but not taxon richness, were significantly different between shaded and unshaded tiles. In Israel, habitat complexity had no effect on taxon richness but did effect community composition. The differential results obtained from these experiments highlight the importance of testing multiple interventions in more than one geographic location. The majority of eco-engineering studies have been conducted in intertidal habitats, with only a few examples from subtidal habitats. There are clear challenges to implementing eco-engineering interventions in subtidal habitats, yet continued experimentation is urgently needed in all habitats to contribute to an evidence base that will inform future large-scale eco-engineering designs.

5.1 Introduction

The human population continues to grow, with the majority of the world's megacities located along the coastal zone (Brown et al., 2013; Neumann et al., 2015; Firth et al., 2016b). Concurrently, climate change is causing rising sea level and stormier seas, with increased frequency and intensity of coastal flooding and erosion (Neumann et al., 2015; Hansen et al., 2016; Vitousek et al., 2017). As a response, humans have built hard engineered coastal structures ('artificial structures') to protect valuable infrastructure and safeguard human lives at the expense of natural habitats, contributing to the irreversible modification of coastal systems globally (Thompson et al., 2002; Airoldi et al., 2005a; Halpern et al., 2008; Airoldi et al., 2009; Dugan et al., 2011). These artificial structures have contributed to "ocean sprawl" (Duarte et al., 2012) – a term that is used to describe the proliferation of man-made structures (i.e., seawalls, breakwaters, floating pontoons) in marine and coastal environments, and the subsequent modification and loss of natural habitats (also see Thompson et al., 2002; Firth et al., 2016b; Bishop et al., 2017; Heery et al., 2017).

Artificial structures typically have steep profiles and reduced surface area and topographic complexity (Moschella et al., 2005; Chapman and Underwood, 2011), and as such, they generally support different biological communities compared to analogous natural habitats (i.e., rocky shores; Knott et al., 2004; Moschella et al., 2005; Chapman and Underwood, 2011). These communities typically comprise lower numbers (Chapman, 2003; Geist and Hawkins, 2016) and abundances (Lam et al., 2009; Lai et al., 2018) of species, and many are dominated by invasive and opportunistic species (Dafforn et al., 2012; Bishop et al., 2015b; Dafforn, 2017), facilitating biotic homogenization (McKinney and Lockwood, 1999; McKinney, 2006; Bishop et al., 2017). Subsequently, artificial structures have a different ecological role in an ecosystem compared to natural habitats (Bulleri et al., 2004; Jackson et al., 2008b; Aguilera et al., 2014; Mayer-Pinto et al., 2018a; Mayer-Pinto et al., 2018b), with negative knock-on effects on ecosystem services rendered (e.g., carbon sequestration, water filtration, primary productivity).

Some of the largest cities in the world are located in coastal areas, with many of these cities ideally positioned to support global activities, such as commercial trade and transport (Nicholls, 1995; Timmerman and White, 1997; Tibbetts, 2002; Firth et al., 2016b). To facilitate these activities, large docks and associated hard engineered structures in working harbours have been built, replacing or degrading natural habitat (Chou, 2006; Firth et al., 2016b). Thus, these large working harbours represent novel ecosystems that are not encountered in the natural environment (Hobbs et al., 2006; Morse et al., 2014). These novel ecosystems have been shown to alter natural animal behaviours (Bulleri et al., 2005; Munsch et al., 2014; Munsch et al., 2017), and support different biological assemblages than analogous natural habitats (Chapman, 2003; Bulleri et al., 2005; Green et al., 2012; Lai et al., 2018). Recreational marinas – which are common features of harbours of all sizes – are typically composed of floating pontoons (docks), which are vastly different than natural habitats, as the pontoons stay fixed at the surface of the water and rise and fall with the tides (Holloway and Connell, 2002). These pontoons have been found to support non-native species (Arenas et al., 2006a; Ashton et al., 2006; Bishop et al., 2015b; Epstein and Smale, 2018), and thus, there is impetus to engineer pontoons and marinas to support a diverse assemblage of natural species, resisting biological invasion by enhancing native biodiversity (Hair and Bell, 1992; Stachowicz et al., 1999; Stachowicz et al., 2002; Paalvast et al., 2012). Ecosystems in harbours can also be enhanced by reducing pollution and improving water quality through biofiltration (Hawkins et al., 1992a; Hawkins et al., 1992b). In this way, harbours can support multiple uses and users so that there is a realistic balance between the people of the harbours and the resident marine flora and fauna (World Harbour Project, 2018).

Some ecologists are considering how to manage hard engineered structures within marinas and harbours for ecological and societal benefit (Milton, 2003; Odum and Odum, 2003; Hobbs et al., 2006; Macdonald and King, 2018). The design of such ecosystems, which combine human society with the natural environment for the benefit of both, has been labelled ecological engineering (or “eco-engineering”; Odum, 1962; Mitsch and Jorgensen, 1989; Odum and Odum, 2003). Despite ecological engineering in urban terrestrial and freshwater environments being well accepted by society, governments and scientists alike (Francis and Lorimer, 2011; Francis, 2014; Lepczyk et al., 2017; Naylor et al., 2017; Evans et al., 2019), eco-engineering of coastal and marine structures is a relatively new field. Ecologists are, however, beginning to build a robust foundation of evidence upon which to base future designs for large-scale implementation (Goff, 2010; Cordell et al., 2017; Perkol-Finkel et al., 2017), and are working to shift perceptions on multifunctionality of structures in the marine and coastal environments (Langhamer and Wilhelmsson, 2009; Zanuttigh et al., 2015;

Callaway et al., 2017; Evans et al., 2017; Evans et al., 2019) Most working harbours and marinas have practices in place to actively discourage the colonisation of artificial structures and vessels by fouling organisms (i.e., vessel hull cleaning; use of antifouling substances). Thus, experiments testing the effects of eco-engineering on organisms that can benefit marina users are urgently needed. Such experiments can target certain groups of organisms that are known to provide ecosystem services (i.e., improved water quality and photosynthesis; Ferrario et al., 2016) and discourage settlement of pest species (e.g., invasive species such as the carpet sea quirt, *Didemnum vexillum*; Coutts and Forrest, 2007). There have been many eco-engineering designs tested over the past decade, with a common emerging theme of adding habitat complexity to enhance species diversity (Moschella et al., 2005; Chapman and Underwood, 2011; Firth et al., 2014b; Strain et al., 2017a). Habitat complexity includes microtexture (< 1 cm) such as grooves and pits, and small (centimetres) and larger scale (centimetres - metres) habitats such as crevices, rock pools and gaps between boulders (Moschella et al., 2005; Firth et al., 2013b; Coombes et al., 2015; Liversage et al., 2017). At the microscale (mm), incorporating fine scale texture into built structures has been shown to increase larval recruitment and survival (Coombes et al., 2015). Interventions at the scale of centimetres to metres have included drilling pits (Chapman and Underwood, 2011; Firth et al., 2014b; Martins et al., 2016; Hall et al., 2018), creating rock pools (Chapman and Underwood, 2011; Browne and Chapman, 2014; Evans et al., 2016a; Firth et al., 2016a) and scoring grooves (Firth et al., 2014b; Hall et al., 2018) into artificial structures to enhance species diversity. Large-scale interventions (> 1 m) involve placement of precast habitat-enhancement units within the existing structure or during construction (Firth et al., 2014b; Perkol-Finkel and Sella, 2015; Sella and Perkol-Finkel, 2015). Moreover, habitat-forming species, such as mussels (World Harbour Project, 2018), corals (Ng et al., 2015) and canopy forming algae (Falace et al., 2006; Neo et al., 2009;

Perkol-Finkel et al., 2012; Ferrario et al., 2016), can be seeded on artificial structures to increase their abundance and promote greater species diversity through provision of space and enhancement of ecosystem services. This is done by targeting specific organisms such as barnacles, mussels, oysters and algae, which can have a “bioprotective effect” by enhancing the structural integrity and protecting the structure from saltwater, temperature extremes and intense wave action (Coombes et al., 2013; Naylor et al., 2017). In addition to adding support to the structure, these organisms contribute to biological complexity, which has been shown to be important for the subsequent colonising community (Bros, 1987; Pinn et al., 2008; Coombes et al., 2015). These organisms are called ecosystem engineers, as they create biological habitat that adds to the three-dimensional structure of a reef and enhances biodiversity (Borthagaray and Carranza, 2007; Romero et al., 2015) and encourages intraspecies settlement (Tamburri et al., 2008; Smee et al., 2013).

The field of eco-engineering, especially in subtidal environments, can learn from the decades of research and development on near- and offshore artificial reefs. Artificial reef programs in the Gulf of Mexico, in particular, are now well-established, having streamlined the permitting and siting processes (Stephan et al., 1990; Kaiser, 2006a), made strict regulations on materials (Stephan et al., 1990; Atlantic and Gulf States Marine Fisheries Commission, 2004; Sherman and Spieler, 2006) and developed programs on reefing of decommissioned oil and gas platforms (Stephan et al., 1990; Kaiser and Pulsipher, 2005; Kaiser, 2006b). But it was only with extensive research on the effectiveness of artificial reef designs to produce biomass and enhance fisheries (Bohnsack and Sutherland, 1985; Claisse et al., 2014; Smith et al., 2016; Streich et al., 2017; Lima et al., 2019), boosting recreational angling activities (Bohnsack et al., 1994; Streich et al., 2017), and supporting local tourism representing a vital source of income for local communities (Stephan et al., 1990; Adams et al., 2006; Stolk et al., 2007;

Rendle and Rodwell, 2014), that these artificial reef programs have become accepted by government bodies, commercial enterprises and the general public. Still, artificial reefs endure criticism. They have been blamed for mortalities of marine life (Barnette, 2017; Texas Parks and Wildlife Artificial Reefs Program, pers. comm.) and complications during trawling and bottom-fishing activities (Texas Parks and Wildlife Artificial Reefs Program, pers. comm.). There remains a contentious debate over the ability of artificial reefs to produce biomass rather than simply aggregate existing biomass in a condensed area, effectively making it easier to overfish a region (Bohnsack and Sutherland, 1985; DeMartini et al., 1994; Grossman et al., 1997; Pickering and Whitmarsh, 1997; Shipp, 1999; Brickhill et al., 2005; Smith et al., 2015). Although the field of coastal and marine eco-engineering has not seen this level of criticism, it is important for eco-engineering projects to consider these criticisms experienced by artificial reefs and implement these into early planning and design (see Introduction section 1.5.2 for more information on artificial reefs).

Localised environmental factors, such as temperature, sedimentation and light intensity can influence the colonising communities on artificial structures and natural rocky shores alike (Irving and Connell, 2002; Knott et al., 2004; Blockley and Chapman, 2006; Miller et al., 2009; Gallardo et al., 2013). Shading in particular has been shown to influence recruitment and survival of specific species and functional groups (Fitzpatrick and Kirkman, 1995; Glasby, 1999; Blockley and Chapman, 2006; Miller and Etter, 2008; Hanlon et al., 2018). There is general agreement that macroalgae and mobile invertebrates prefer unshaded substrate (Kennelly, 1989; Fitzpatrick and Kirkman, 1995; Baynes, 1999; Blockley and Chapman, 2006), while sessile invertebrates prefer shaded substrate (Blockley and Chapman, 2006; Miller and Etter, 2008; Hanlon et al., 2018). Few eco-engineering studies have formally incorporated shade as a factor in the experimental design (but see Hanlon et al., 2018), despite the need for investigation of multiple intervention types and development of site-specific methods that address local stressors (Strain et al., 2017a).

The vast majority of eco-engineering trials have been small-scale, tested in intertidal habitats and centred only in a few geographical hotspots such as the UK, US and Australia (but see Sella and Perkol-Finkel, 2015; Loke and Todd, 2016; Cordell et al., 2017; Perkol-Finkel et al., 2017). Results from experimental manipulations in the lower intertidal combined with descriptive studies (Glasby, 1998; Bulleri et al., 2005; Firth et al., 2016a) suggest that ecological engineering designs may be most effective in increasing species diversity the lower in the coastal zone the design is placed, as these areas are constantly submerged or immersed on every tidal cycle. The few studies that have successfully implemented ecological engineering interventions in the subtidal on coastal defences required heavy machinery and/or technical dive teams due to the large scale of the designs (Langhamer and Wilhelmsson, 2009; Firth et al., 2014b; Sella and Perkol-Finkel, 2015; Perkol-Finkel et al., 2017; ECOncrete Inc., 2019). For example, Sella and Perkol-Finkel (2015) installed ecologically enhanced precast ECOncrete© Antifer units that were 1 m^3 and weighed 2.3-2.5 tonnes on a subtidal breakwater, and Langhamer and Wilhelmsson (2009) deployed wave energy structure foundation units that were 3 m in diameter, 1 m high and weighed 10 tonnes. As such, the cost of interventions in the subtidal are substantially higher and likely require special licensing and permissions (Firth et al., 2014b). Research on eco-engineering in subtidal habitats is urgently needed to overcome these challenges, as most artificial structures in urbanised harbours are located within the intertidal and shallow subtidal zones (National Institute of Coastal and Marine Management of the Netherlands, 2004). Moreover, non-native species tend to be more abundant on artificial structures in the subtidal compared to the intertidal (Dafforn et al., 2012; Airoldi et al., 2015a), thus eco-engineering interventions designed to discourage non-natives in the subtidal need trialling. The long history of nearshore and offshore artificial reef installations and their general ability to enhance local biodiversity (for reviews see Baine, 2001; Lokesha et al., 2013) is encouraging for the future of subtidal eco-engineering of coastal structures. More importantly, scientists and engineers working on eco-engineering subtidal structures can learn from the decades of artificial reef trials, as there have been a multitude of studies in various environmental settings in order to optimise designs for specific ecological or societal goals (Gascon and Miller, 1981; Ogden and Ebersole, 1981; Benayahu and Loya, 1987; Bombace, 1989; Polovina and Sakai, 1989; Bortone et al., 1994; Folpp et al., 2011; Herbert et al., 2017). Despite many common threads between the eco-engineering of subtidal structures and creation of nearshore artificial reefs, I do not investigate engineering of artificial reefs in this study as the subject falls outside the remit of this thesis.

The overarching aim of this study was to test the efficacy of habitat enhancements and bivalve seeding on species diversity in subtidal habitats in two different geographic locations (Plymouth, British Isles and Tel Aviv, Israel). Both locations followed similar protocol to that designed by the World Harbour Project (see Chapter 4), thus results can be more comparable than results from experiments using different protocols. Although results between locations were not compared statistically, both locations were included here to make the point that eco-engineering experiments need to go beyond testing in one habitat (i.e., intertidal), and should involve comparisons across geographic localities to understand generalities of patterns of effects at larger scales. The effects of two additional factors on species diversity were investigated in the UK: (1) bivalve seeding using mussels (*Mytilus* spp.), as they provide habitat and refuge for algae, micro- and macroinvertebrates (O'Connor and Crowe, 2007; O'Connor and Crowe, 2008); and (2) shading using shaded and unshaded tiles. Species diversity was measured using taxon and functional richness and community composition. Complex, flat and control tiles, as well as cleared seawall plots were employed to test the following hypotheses:

1. Taxon and functional richness will be greater on, and community composition will differ between, complex tiles compared to control tiles/cleared seawall plots.
2. Taxon and functional richness will be greater on, and community composition will differ between, seeded compared to unseeded tiles (British Isles only).
3. Taxon and functional richness will be greater on, and community composition will differ between, shaded compared to unshaded tiles (British Isles only).

5.2 Materials and methods

5.2.1 Study sites

Experiments were run in Plymouth, British Isles and Tel Aviv, Israel (Figure 5-1). Experiments were undertaken in two marinas in Plymouth and one marina in Tel Aviv. The marinas in Plymouth included Mayflower Marina (50.364558, -4.172333) and Plymouth Yacht Haven (50.359619, -4.120661) in Plymouth Sound, which is located along the southwest coast of England. Both marinas provided floating pontoons with a north and a south-facing side and supported naturally occurring populations of *Mytilus* spp. Plymouth Sound is a heavily urbanised harbour with a long history of human modification (Knights et al., 2016). The Sound is flanked by sloping natural rocky shores composed of Palaeozoic shale and limestone, which extend along the west and east coasts. Along these areas, artificial structures to support human activity (i.e., fishing piers, recreational marinas, discharge pipes, breakwaters, seawalls) are interspersed among the natural rocky shores. A recent publication estimated that up to a third of Plymouth’s coastline is armoured, with most of the artificial structures being constructed from naturally-sourced rock (Knights et al., 2016).

Experiments conducted in Israel were located in a single marina in Tel Aviv (Herzliya Marina; 32.162333, 34.794083), which is positioned along the most densely populated area on the Israeli Mediterranean coast. The experimental seawall within the marina faces west. Herzliya Marina is the largest marina in the eastern Mediterranean Sea, and provides docking for tens of thousands of global visitors annually (ECOncrete Inc., 2019). Arid climate conditions coupled with its geological position in the Mediterranean Sea, results in species-poor waters off the Tel Aviv coast (Azov, 1991).

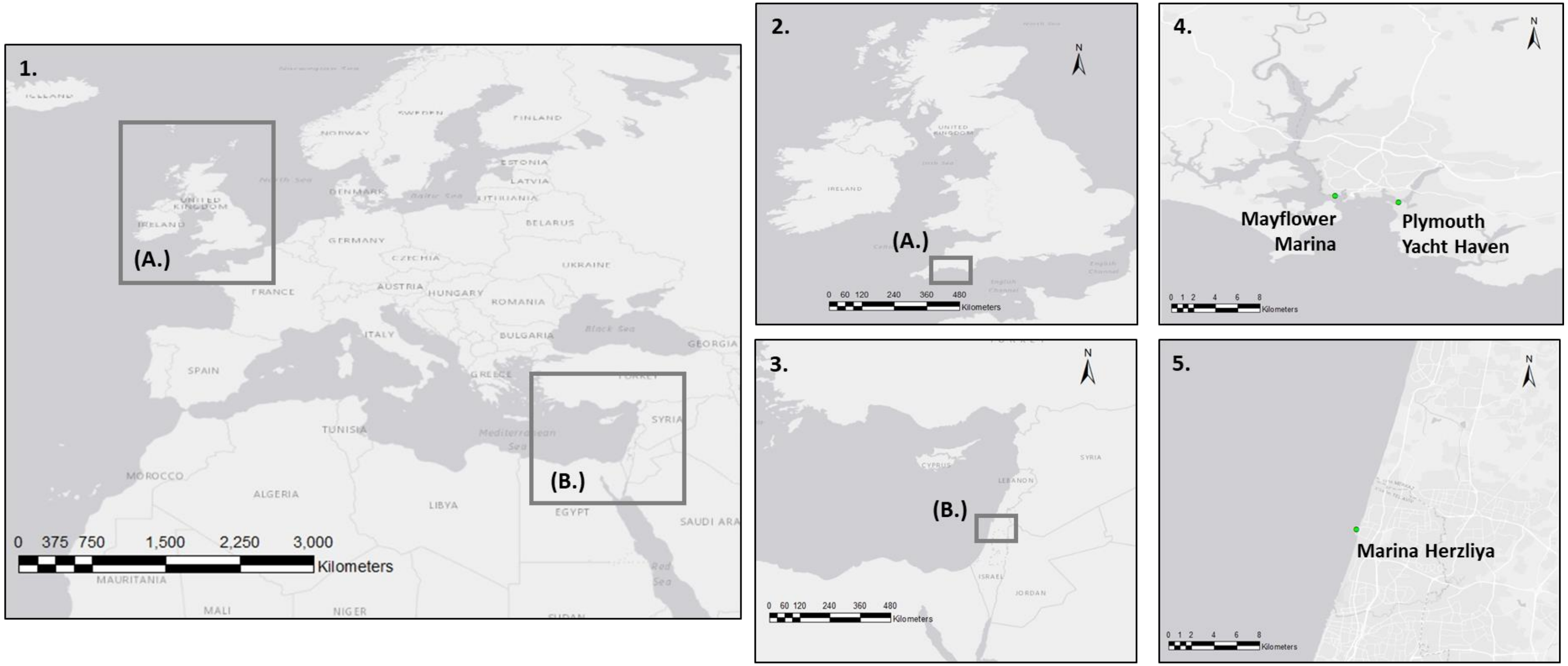


Figure 5-1. Study sites in (A.) Plymouth Sound, British Isles included Mayflower Marina and Plymouth Yacht Haven, while the study site in (B.) Tel Aviv, Israel was Marina Herzliya in the eastern Mediterranean Sea.

5.2.2 Description of experimental tiles and plots

Concrete tiles were created from moulds using 3-D printing, and were composed of sand, cement and glass fibres (Reef Design Lab, Melbourne, Australia; Figure 5-2). Experimental tiles were made with sand and glass fibres to offset the negative effects of cement in the marine environment (see section 1.5.1 for more information on effects of concrete). The World Harbour Project determined the tile design (see Chapter 4), and all study locations were required to use these specific tiles. Tile treatments included: (1) flat tiles without crevices or ridges; (2) complex tiles, with 2.5 cm high and 1.7-6.5 cm wide ridges, each separated by 1.5-5 cm wide crevices (‘2.5 cm’ treatment); and (3) complex tiles, with ridges and crevices as described for the 2.5 cm treatment, except ridges were 5 cm high (‘5 cm’ treatment). All tiles were created with fine-scale microtexture (< 1 mm grooves) on the ridges (for justification of choice of experimental tiles, see Chapter 4, section 4.2.2). For experiments in Israel, two additional treatments were used: flat control tiles without microtexture (made of 80% sand and 20% standard Portland cement) and cleared seawall plots. For experiments in Plymouth, one additional treatment was used: flat control tiles made of standard Portland cement without microtexture.

Figure 5-2. Experimental tiles showing (from left to right) the flat, 2.5 cm and 5 cm complexity treatments, with seeded tiles (mussels) shown above.

5.2.3 Seeded mussels

The mussel, *Mytilus* spp., was chosen to be seeded on British tiles because it is a habitat-forming species common on some areas of rocky intertidal habitats in Plymouth Sound (Hilbish et al., 2002). Plymouth is located within the range of the more cold-water blue mussel, *Mytilus edulis* Linnaeus, 1758, and the warm-water *Mytilus galloprovincialis* Lamarck 1819; the latter is expanding in response to climate change but has always been present in the British Isles (Seed, 1971; Ahmad and Beardmore, 1976). It is likely that that *M. galloprovincialis*, *M. edulis* and hybrids (Skibinski et al., 1978) of these two species were used in this experiment, therefore all mussel species will be referred to here as ‘mussels’ or ‘*Mytilus* spp.’

5.2.4 Experimental design

Experiments from the two geographic locations were treated separately for the following reasons: (1) experiments were implemented during different times of the year and for different lengths of time; (2) mussel seeding was added as a factor to the British Isles experiments but not the Israel experiments; (3) the control treatments differed between the locations; and (4) tiles in Plymouth were deployed off pontoons, suspended approximately 1.5 m below the surface of the water and moving with the tide, while tiles in Tel Aviv were affixed to a subtidal seawall approximately 1 m below the surface of the water. Regardless of the differences in experimental designs between countries, it is useful to informally compare localities to observe generalities in patterns of effects.

5.2.4.1 Plymouth, British Isles

At both sites, ten tiles of each of the three complexity treatments were deployed off floating pontoons (Figure 5-3). Five of the ten tiles from each treatment were seeded with 30 individuals of *Mytilus* spp. (30-35 mm shell length: 32.9 ± 0.1, mean ± 1 SE) in clusters of three individuals (five clusters in crevices; five clusters on ridges) using non-toxic Gorilla® superglue (Cincinnati, OH, USA) following World Harbour Project protocol (described in Chapter 4). The protocol stated that 30-35% of each tile needed to be covered in bivalves. The size of the mussels used in this experiment differed from those used in the intertidal experiments (Chapter 4) because all mussels of the 20-25 mm shell length were lost to predation in the previous experiments. Therefore, in order to achieve the 30-35% coverage using the larger sized mussels, 30 individuals needed to be used per tile. Clusters of mussels were used because mussels live aggregated in groups in nature. The clusters were divided equally between crevices and ridges because questions regarding the survival and effects of mussels on recruiting biota on different positions on tiles were asked for analysis done outside of this thesis. Individuals of *Mytilus* spp. were sourced from Whitsand Bay (50.346086, -4.255325). An additional six concrete tiles made of standard Portland cement were used as tile controls. Tiles were attached to 3.6 m long recycled plastic boards and hung from the south-facing sides of pontoons 1.5 m below the water's surface facing out from the pontoon. The south-facing side of pontoons was chosen to maximize light reaching the tiles. To test the effects of shading on colonisation of tiles, six concrete tiles made of standard Portland cement were hung on the same boards but facing beneath the pontoon ('shaded tiles') to compare with the light-exposed Portland cement tiles (mentioned above). All tiles were attached to boards in the same orientation (ridges running vertically), arranged in a random order and with 0.4 m spacing in between them following World Harbour Project protocol (see Chapter 4). Tiles were deployed at both sites in April 2017, and were left in place for 14 months.

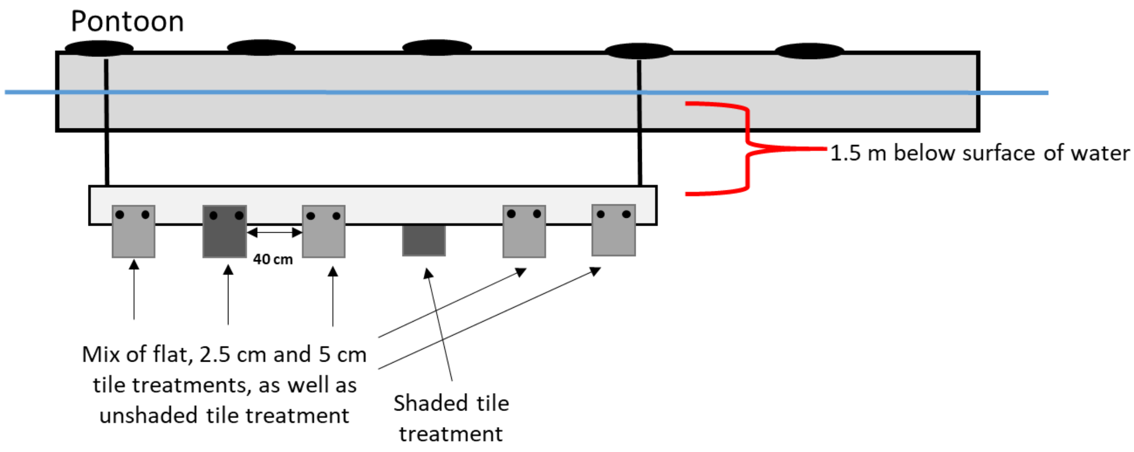


Figure 5-3. Schematic representation of the experimental design in Plymouth, British Isles. All tiles were hung on boards off floating pontoons 1.5 m below the surface of the water at two marinas.

5.2.4.2 Tel Aviv, Israel

Five tiles of each of the three complexity treatments were affixed to a subtidal seawall in a single horizontal row at approximately 1 m below the water’s surface. An additional five concrete tiles composed of the same material as the seawall (without crevices, ridges and microtexture) and five cleared plots were included amongst the experimental tiles to serve as controls. As tides in the Mediterranean Sea are on the order of centimetres (McElderry, 1963), the tiles remained fixed at approximately 1 m below the water’s surface at all times. No tiles were seeded with bivalves. Experiments commenced in August 2016, and were left in place for 12 months.

5.2.5 Sampling procedure

5.2.5.1 Plymouth, British Isles

Tiles were monitored quarterly by temporarily removing boards from the water and taking photographs of each tile. No attempt to identify and quantify taxa was made during this time because tiles supported multiple layers of organisms, many of which required microscopic analysis for positive identification. In July 2018 (after 14 months of immersion), tiles were removed from the pontoons, placed in mesh bags (< 5 mm holes) to retain all organisms, placed in cool boxes filled with ambient seawater and transported back to the laboratory. In the laboratory, organisms were kept alive until analysis (< 96 h) by storing tiles in flow-through seawater tanks at ambient conditions. Before sampling, tiles were removed from mesh bags and photographed in case organisms died before identification was possible. All organisms were removed from one crevice and one ridge on each complex tile. The same crevice and ridge were sampled across all tiles. On flat and control tiles, where crevices and ridges were absent, the same area was sampled on those tiles using a template created from the complex tiles. All organisms were identified down to the lowest taxonomic resolution possible. Hobo Pendent® temperature loggers were attached to the unshaded sides of boards (n = 2 loggers per site) using cable ties and were set to record temperature (°C) every hour. Every three months, the loggers were collected to download data and then redeployed on different boards. Salinity (psu) data were also collected during each sampling event using a refractometer (Appendix 3, Table 1).

5.2.5.2 Tel Aviv, Israel

Experimental tiles and seawall control plots were monitored at months 1, 3, 6, 9 and 12 for counts of mobile taxa and percentage cover of sessile taxa in case tiles were lost before the conclusion of the experiment. After 12 months, final data were collected by taking photographs of each tile and seawall plot in the field, and then percentage cover of sessile organisms (no mobile organisms present) was estimated using CoralNet software (Beijbom et al., 2012). Organisms were identified down to the lowest taxonomic resolution possible. Salinity (specific gravity, Sg) and temperature (°C) were measured using a hydrometer (Sera, D 52518, Heinsberg, Germany) and a temperature probe, respectively, at months 1, 3, 6, 9 and 12 (Appendix 3, Table 1).

5.2.6 Statistical analysis

5.2.6.1 Plymouth, British Isles

Species diversity was quantified using final taxon and functional diversity and community composition data from the conclusion of the experiment. To investigate differences among treatments in functional groups, taxa were classified into eight functional groups: filter feeders, omnivores, detritivores/scavengers, predators, corticated foliose algae, filamentous algae, leathery macrophytes and corticated macrophytes. Mean taxon and functional richness were quantified using univariate analysis of variance tests (ANOVA) on untransformed presence/absence data on Bray-Curtis similarity matrices. Community composition was analysed using permutational multivariate analysis of variance tests (PERMANOVA) using fourth root transformed abundance data to reduce the influence of very abundant species (Anderson, Gorley, & Clarke, 2008) after Bray-Curtis similarity matrices were computed.

To test the hypotheses about differences in taxon and functional richness and community composition among tile treatments and mussel seeding, a three-way PERMANOVA was used with factors: Site (random; 2 levels: Mayflower Marina, Plymouth Yacht Haven), Treatment (fixed; 4 levels: control, flat, 2.5 cm, 5 cm) and Mussel Seeding (fixed; 2 levels: seeded, unseeded). To test the hypothesis about differences in taxon and functional richness and community composition between shaded and unshaded tiles, a two-way PERMANOVA was used with factors: Site (random; 2 levels: Mayflower Marina, Plymouth Yacht Haven) and Shade (fixed; 2 levels: shaded, unshaded). PERMANOVAs were based on 9999 permutations of residuals under a reduced model. Post-hoc pairwise tests were employed where applicable. Where there were not enough possible permutations to perform a reasonable test, Monte Carlo tests were run to obtain more meaningful P-values (Anderson et al., 2008).

5.2.6.2 Tel Aviv, Israel

Species diversity was quantified using final taxon diversity and community composition data collected at the conclusion of the experiment. Functional richness was not assessed because there were only two functional groups present on tiles and seawall plots. Mean taxon richness was quantified using univariate analysis of variance tests (ANOVA) on untransformed presence/absence data on Bray-Curtis similarity matrices. Community composition was analysed using permutational multivariate analysis of variance tests (PERMANOVA) using square root transformed abundance data to reduce the influence of very abundant species (Anderson, Gorley, & Clarke, 2008) after Bray-Curtis similarity matrices were computed.

To test the hypothesis about differences in taxon richness and community composition among tile treatments, a one-way PERMANOVA was used with factor Treatment (fixed; 5 levels: seawall plot, control, flat, 2.5 cm, 5 cm) and was based on 9999 permutations of residuals under a reduced model. Post-hoc pairwise tests were run where applicable. Where there were not enough possible permutations to perform a reasonable test, Monte Carlo tests were run to obtain more meaningful P-values (Anderson et al., 2008).

5.2.6.3 Plymouth, British Isles and Tel Aviv, Israel

All multivariate data sets were visualised using non-metric multi-dimensional scaling (nMDS) plots. In cases where stress on the two-dimensional nMDS plot was high (~0.2), the three-dimensional solutions (lower stress) were visualised to confirm observed patterns, and the two-dimensional plots were retained. All statistical tests were run in PRIMER v6 with the PERMANOVA+ add-on (PRIMER-E Ltd, Plymouth, UK; Anderson et al., 2008) using the PERMANOVA routine, and data were visualised using the nMDS routine. Where significant differences in community composition were detected among treatments, percentage contributions of individual taxa to dissimilarities between treatments were analysed using the similarity percentage (SIMPER) routine in PRIMER v6.

5.3 Results

5.3.1 Plymouth, British Isles: General overview

Overall, 78 taxa were recorded on tiles, with 16 taxa being non-native (20% non-native; Appendix 3, Table 2). Thirteen mobile and 51 sessile animals were recorded overall, while 14 macroalgal taxa were recorded overall. Salinity ranged from 30-35 psu, while temperature ranged from 5.1-24 °C (Appendix 3, Table 1).

Tiles at Mayflower Marina supported greater numbers of total taxa (64) compared to tiles at Plymouth Yacht Haven (52 taxa). Overall, complex tiles (2.5 cm and 5 cm tiles) supported similar numbers of total taxa (58 and 56, respectively), while flat tiles supported the greatest number of total taxa (66), and control tiles supported the lowest number of total taxa (33). Seeded and unseeded tiles supported the same number of taxa (65 taxa; Appendix 3, Table 2). Eight functional groups were represented, with filter feeders being the most numerically dominant group (53 taxa). Flat and 5 cm tiles supported the greatest number of functional groups (8), while control tiles supported the fewest (5 groups; Figure 5-4). One seeded 5 cm tile at Mayflower Marina and one unseeded 5 cm tile at Plymouth Yacht Haven were lost during the experiment.

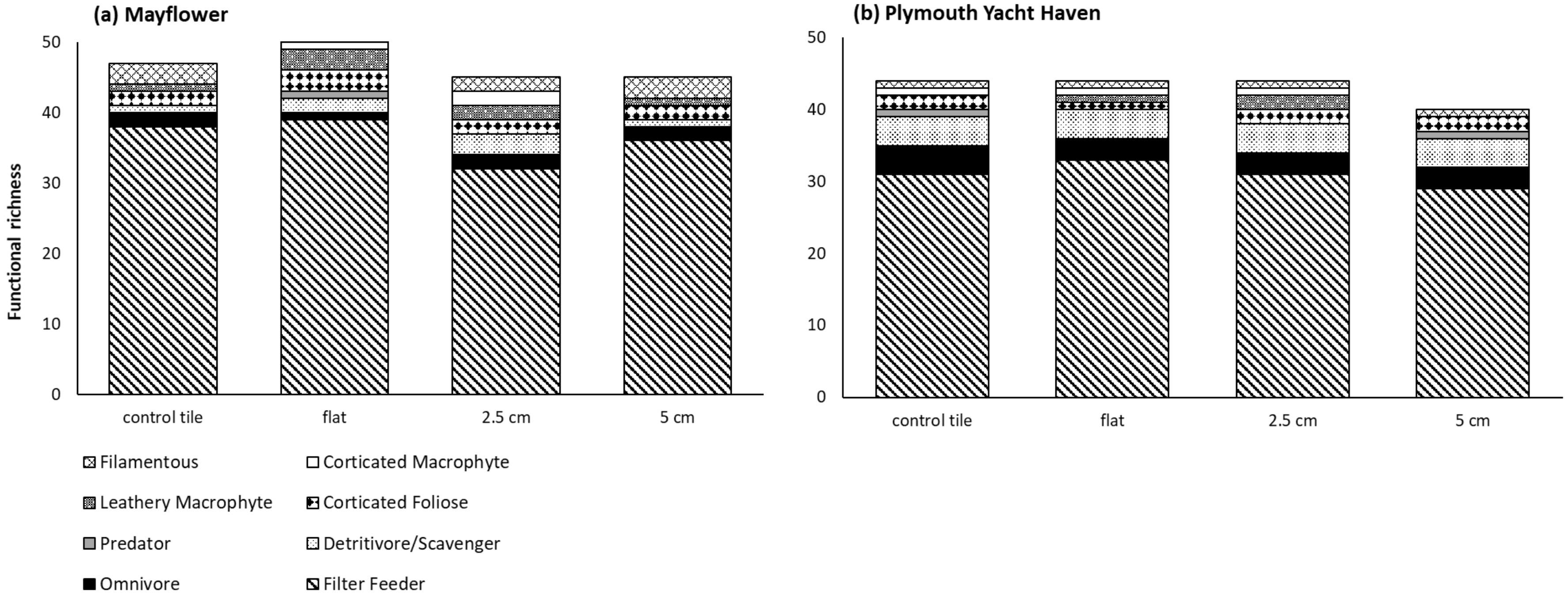


Figure 5-4. Number of taxa within each functional group by tile treatment at (a) Mayflower Marina and (b) Plymouth Yacht Haven, Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. The most numerically dominant group at both sites was the filter feeders.

5.3.2 Plymouth, British Isles: Comparison of taxon and functional richness among tile treatments and mussel seeding

There were no significant differences in mean taxon richness among tile treatments (Table 5-1a, Figure 5-5a). Mean taxon richness, however, was significantly greater on unseeded tiles compared to tiles seeded with mussels, (Table 5-1a; Figure 5-6). For mean functional richness, the effects of tile treatments differed significantly between the two study sites (Table 5-1b). At Mayflower Marina, functional richness was significantly greater on 2.5 cm tiles compared to control tiles, as well as on 2.5 cm tiles compared to 5 cm tiles (Figure 5-5b). While at Plymouth Yacht Haven, significant differences were only detected between control tiles and 2.5 cm tiles and control tiles and 5 cm tiles (Figure 5-5b), with the complex tiles supporting greater richness than controls. There was no significant difference between mussel treatments for functional richness (Table 5-1b).

Table 5-1. Three-way ANOVAs comparing mean (a) taxon and (b) functional richness among tile treatments in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Where unique permutations were < 100, Monte Carlo tests were run and P(MC) values were used to determine significance. Significant p-values are bolded.

(a) Taxon richness

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Site	1	263.82	263.82	3.037	0.086	9929	0.0814
Treatment	3	305.37	101.79	3.269	0.1433	6361	0.1627
Mussel	1	286.95	286.95	56.743	0.1684	6	**0.0438**
Si x Tr	3	93.415	31.138	0.35845	0.8017	9968	0.7983
Si x Mu	1	5.0569	5.0569	0.0582	0.8616	9918	0.8713
Tr x Mu	2	34.796	17.398	0.27758	0.7926	9968	0.8032
Si x Tr x Mu	2	125.35	62.676	0.7215	0.4919	9964	0.4919
Residual	55	4777.8	86.869				
Total	68	5757.7					
Transform:	no transformation						

(b) Functional richness

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Site	1	2439.9	2439.9	10.404	**0.0006**	9939	0.0006
Treatment	3	10757	3585.8	3.0077	0.1194	6385	0.1554
Mussel	1	1312.1	1312.1	4.8132	0.3354	6	0.2076
Si x Tr	3	3576.5	1192.2	5.0837	**0.0012**	9943	0.001
Si x Mu	1	272.6	272.6	1.1624	0.2903	9934	0.2804
Tr x Mu	2	728.53	364.26	6.8206	0.083	9972	0.0749
Si x Tr x Mu	2	106.81	53.407	0.22774	0.8706	9957	0.8734
Residual	55	12898	234.51				
Total	68	32518					
Transform:	no transformation						

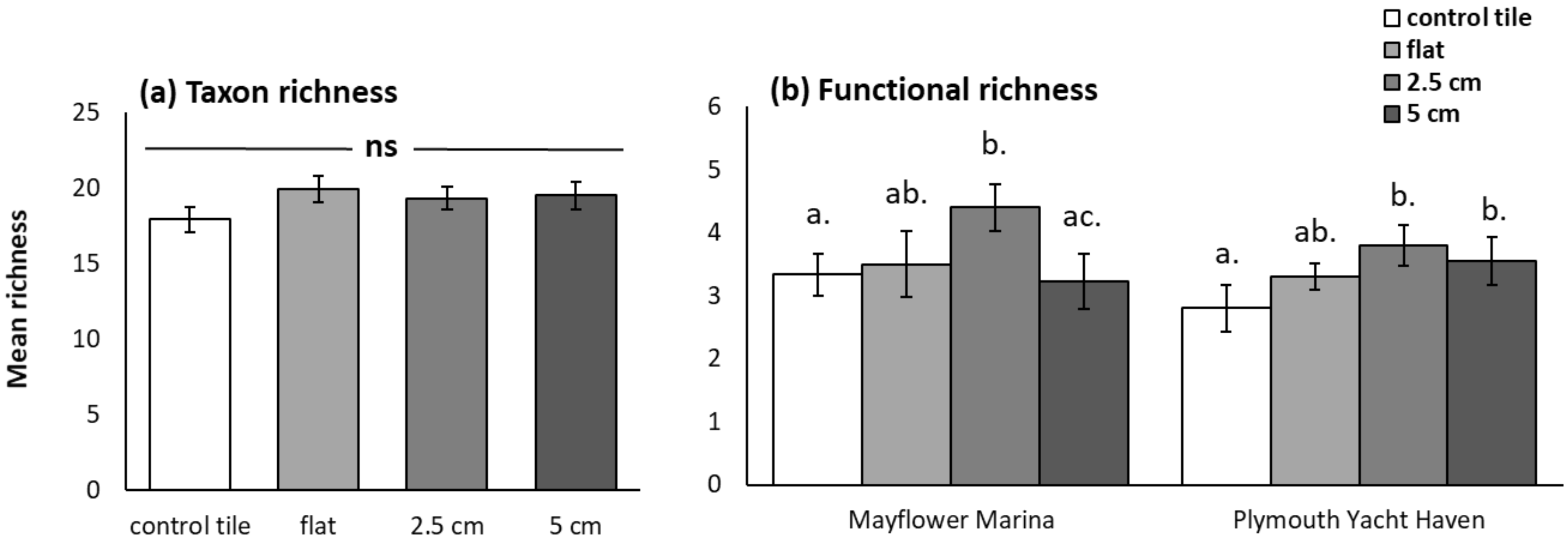


Figure 5-5. Comparison of mean (a) taxon and (b) functional richness among tile treatments at Mayflower Marina and Plymouth Yacht Haven in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. There was a significant site by treatment interaction for (b) functional richness ($p = 0.0012$). Error bars represent standard error. Letters show where there are significant differences between treatments determined by post-hoc pairwise comparisons ((a): control, $n = 12$; flat, $n = 20$; 2.5 cm, $n = 20$; 5 cm, $n = 20$; (b): control, $n = 6$; flat, $n = 10$; 2.5 cm, $n = 10$; 5 cm, $n =10$ per site). ‘ns’ indicates no significant differences among treatments in (a). There was a significant difference between control tiles and 2.5 cm tiles and 2.5 cm tiles and 5 cm tiles in (b) at Mayflower Marina. There were significant differences between control tiles and 2.5 cm tiles and control tiles and 5 cm tiles in (b) at Plymouth Yacht Haven.

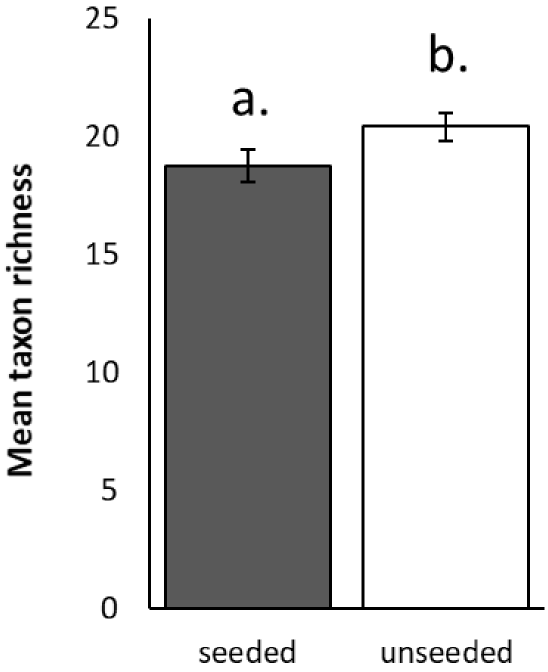


Figure 5-6. Comparison of mean taxon richness between seeded and unseeded tiles at both sites in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Error bars represent standard error. Letters show that there are significant differences between treatments (seeded, n = 30; unseeded, n = 30; p = 0.0438).

5.3.3 Plymouth, British Isles: Comparison of community composition among tile treatments and mussel seeding

There were no differences in community composition among tile treatments (Table 5-2; Figures 5-7), but community composition between mussel seeding treatments did differ significantly (Table 5-2, Figure 5-8). An analysis of the contribution from individual taxa (SIMPER) showed that many taxa contributed to the dissimilarity between seeded and unseeded tiles (Table 5-3). Approximately 45% of the dissimilarity observed was due to contributions from 14 taxa: *Ascidiella aspersa* (4.5%), *Styela clava* (3.9%), *Corella eumyota* (3.7%), *Mytilus* spp. (3.6%), *Aplidium* cf. *glabrum* (3.5%), *Cryptosula pallasiana* (3.5%), *Bugulina fulva* (3.1%), *Tricellaria inopinata* (3.1%), *Asterocarpa humilis* (3.0%), Amphipod spp. (2.8%), *Spirobranchus* sp. (2.7%), *Ciona intestinalis* (2.5%), *Conopeum reticulum* (2.5%) *and Botrylloides* *violaceus* (2.5%). *A. aspersa*, *Mytilus* spp., *Aplidium* cf. *glabrum*, *A. humilis* and *C. intestinalis* were more abundant on seeded tiles. *S. clava*, *C. pallasiana*, *B. fulva*, Amphipod spp. and *Spirobranchus* sp. were more abundant on unseeded tiles. *C. eumyota*, *T. inopinata*, *C. reticulum* and *B. violaceus* were equally abundant on seeded and unseeded tiles.

Table 5-2. Three-way PERMANOVA comparing community composition among tile treatments in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Where unique permutations were < 100, Monte Carlo tests were run and P(MC) values were used to determine significance. Significant p-values are bolded.

Community composition

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Site	1	13438	13438	15.968	**0.0001**	9917	0.0001
Treatment	3	3534	1178	1.0791	0.4588	6338	0.4094
Mussel	1	2456	2456	5.0897	0.4992	6	**0.0039**
Si x Tr	3	3275	1091.7	1.2972	0.0873	9872	0.1124
Si x Mu	1	482.54	482.54	0.57337	0.9054	9909	0.8794
Tr x Mu	2	1076.6	538.31	0.60037	0.7516	9952	0.8998
Si x Tr x Mu	2	1793.3	896.63	1.0654	0.3748	9889	0.375
Residual	55	46287	841.58				
Total	68	72973					
Transform:	fourth root						

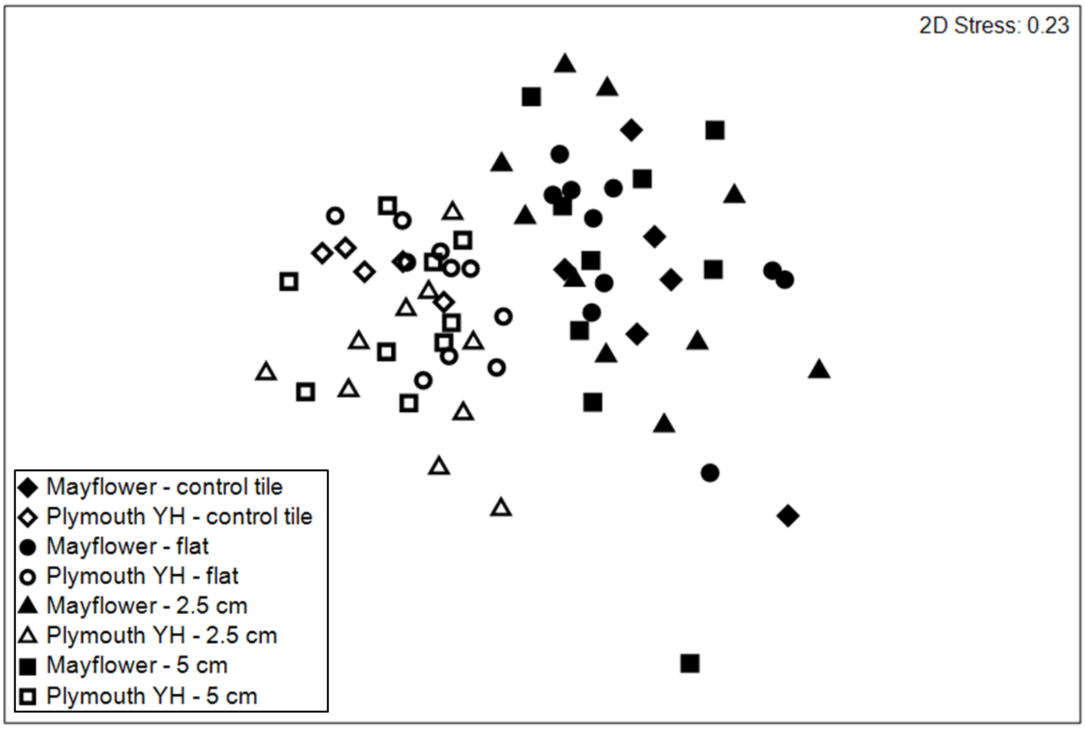


Figure 5-7. nMDS ordination plot comparing community composition among tile treatments in the Plymouth, British Isles recorded at the conclusion of the 14-month experimental period.

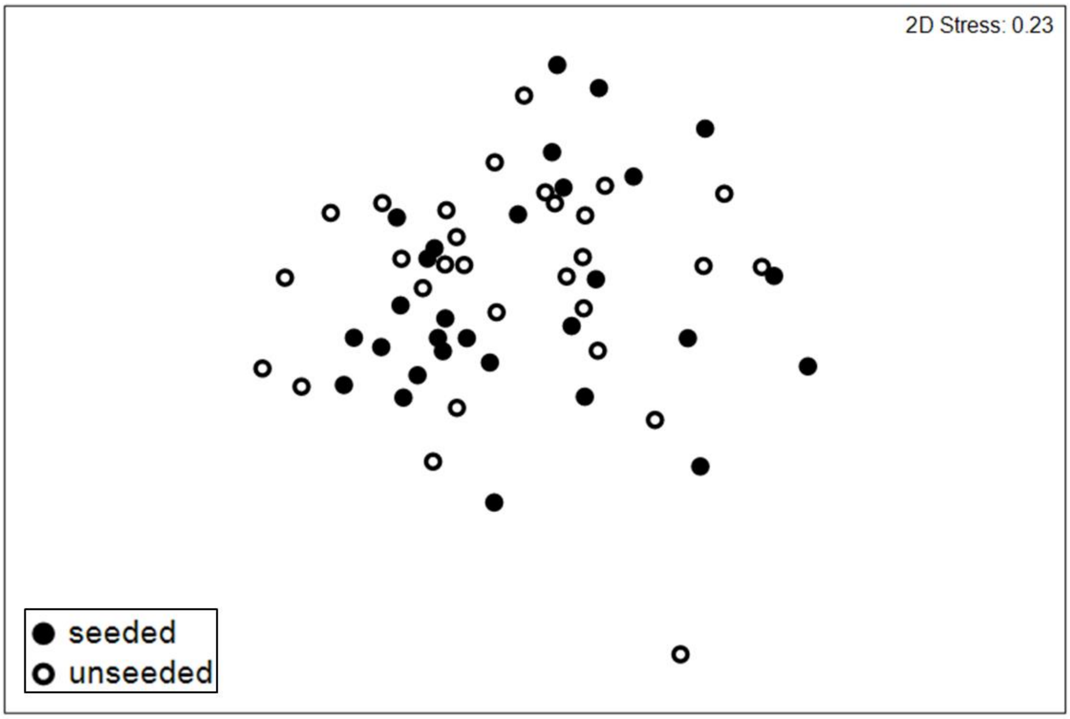


Figure 5-8. nMDS ordination plot comparing community composition between seeded and unseeded tiles in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period (p = 0.0039).

Table 5-3. Differences in average abundances (fourth root transformed; indicated by > or <) and contributions ('%' for percentage or 'c' for counts) of individual species to community composition dissimilarities between seeded and unseeded tiles in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Consistency of contribution is shown by 'Diss/SD', which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

Average dissimilarity = 45.8%	**seeded**	**>/<**	**unseeded**	**Contr%**	**Diss/SD**
Ascidiella aspersa (%)	1.7	>	1.6	4.5	1.3
Styela clava (%)	1.0	<	1.5	3.9	1.3
Corella eumyota (%)	1.2	=	1.2	3.7	1.3
Mytilus spp. (%)	2.2	>	1.6	3.6	1.1
Aplidium cf. *glabrum* (%)	1.0	>	0.9	3.5	1.3
Cryptosula pallasiana (%)	0.7	<	0.9	3.5	1.2
Bugulina fulva (%)	0.5	<	0.6	3.1	1.0
Tricellaria inopinata (%)	1.1	=	1.1	3.1	1.2
Asterocarpa humilis (%)	0.7	>	0.6	3.0	1.2
Amphipod spp. (%)	1.6	<	1.7	2.8	1.1
Spirobranchus sp. (%)	1.2	<	1.6	2.7	1.4
Ciona intestinalis (%)	2.0	>	1.9	2.5	0.9
Conopeum reticulum (%)	0.4	=	0.4	2.5	0.7
Botrylloides violaceus (%)	0.4	=	0.4	2.5	0.8
Anomia ephippium (%)	0.8	<	1.0	2.5	1.3
Molgula sp. (%)	0.5	>	0.4	2.4	1.0
Caprella spp. (c)	0.5	=	0.5	2.4	1.1
Modiolarca sp. (%)	0.6	=	0.6	2.3	1.2
Bugula neritina (%)	0.2	<	0.5	2.3	0.8
Hydroid spp. (%)	0.4	=	0.4	2.3	0.9
Watersipora subatra (%)	0.2	<	0.5	2.2	0.8
Polychaete spp. (%)	0.6	>	0.4	2.2	1.2
Polysiphonia spp. (%)	0.2	<	0.5	2.1	1.0
Orange sponge sp. 1 (%)	0.3	<	0.4	2.0	0.8
Red fan sp. (%)	0.3	=	0.3	2.0	0.8
Soft tube worms (%)	0.3	<	0.4	1.9	1.0

5.3.4 Plymouth, British Isles: Comparison of taxon and functional richness on shaded and unshaded tiles

Shaded and unshaded tiles supported equal numbers of taxa (43). Mean taxon richness did not differ significantly between shaded and unshaded tiles (Table 5-4a), but mean functional richness was significantly greater on shaded compared to unshaded tiles (Table 5-4b; Figure 5-9). One unshaded tile at Plymouth Yacht Haven was lost during the experiment.

Table 5-4. Two-way PERMANOVAs comparing mean (a) taxon and (b) functional richness between shaded and unshaded tiles in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Where unique permutations were < 100, Monte Carlo tests were run and P(MC) values were used to determine significance. Significant p-values are bolded.

(a) Taxon richness

Source	df	SS	MS	Pseudo-F	P(perm)
Site	1	996.51	996.51	9.2953	**0.0053**
Treatment	1	796.68	796.68	6.2491	0.4942
Si x Tr	1	127.49	127.49	1.1892	0.2846
Residual	19	2036.9	107.21		
Total	22	3944.2			
Transform:	no transformation				

(b) Functional richness

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Site	1	293.03	293.03	2.059	0.154	9913	0.1597
Treatment	1	2194.1	2194.1	85.433	0.3329	6	**0.0211**
Si x Tr	1	25.683	25.683	0.18046	0.7691	9934	0.7752
Residual	19	2704.1	142.32				
Total	22	5136.6					
Transform:	no transformation						

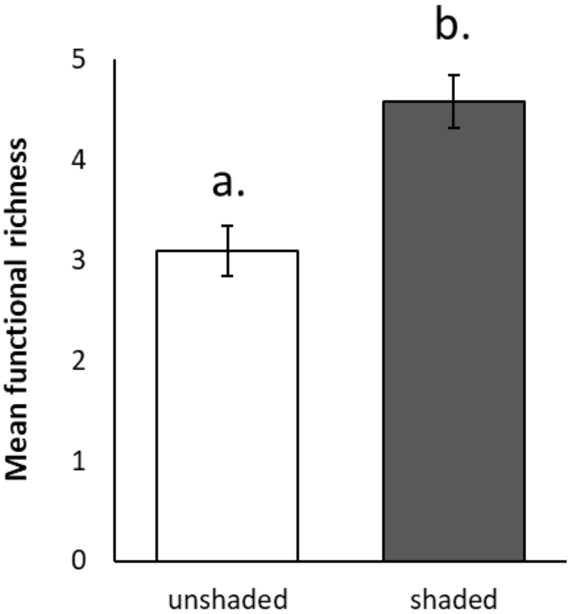


Figure 5-9. Comparison of mean functional richness between unshaded and shaded tiles in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Error bars represent standard error. Letters show that there are significant differences between treatments (unshaded tiles, n = 11; shaded tiles, n = 12; p = 0.0211).

5.3.5 Plymouth, British Isles: Comparison of community composition on shaded and unshaded tiles

Community composition between shaded and unshaded tiles was significantly different, with a significant interaction of site and shade treatment (Table 5-5; Figure 5-10). An analysis of the contribution from individual taxa (SIMPER) showed that over 10% of dissimilarity between shaded and unshaded tiles at Mayflower Marina was attributed to Amphipod spp. (11.1%), with a greater abundance on shaded compared to unshaded tiles. At Plymouth Yacht Haven, *A. aspersa* (10.3%) was the top driver of differences between the treatments, with greater abundance on unshaded compared to shaded tiles (Table 5-6). In general, unshaded tiles at both sites supported more numbers and abundances of ascidians, while shaded tiles at both sites supported greater abundances of *Polyshiphonia* spp. and Amphipod spp.

Table 5-5. Two-way PERMANOVA comparing community composition on shaded and unshaded tiles in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Where unique permutations were < 100, Monte Carlo tests were run and P(MC) values were used to determine significance. Significant p-values are bolded.

Community composition

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Site	1	6519.9	6519.9	7.3318	**0.0001**	9925	0.0002
Treatment	1	10981	10981	4.1322	0.5033	6	**0.0496**
Si x Tr	1	2657.4	2657.4	2.9883	**0.0010**	9923	0.0072
Residual	19	16896	889.27				
Total	22	36728					
Transform:	square root						

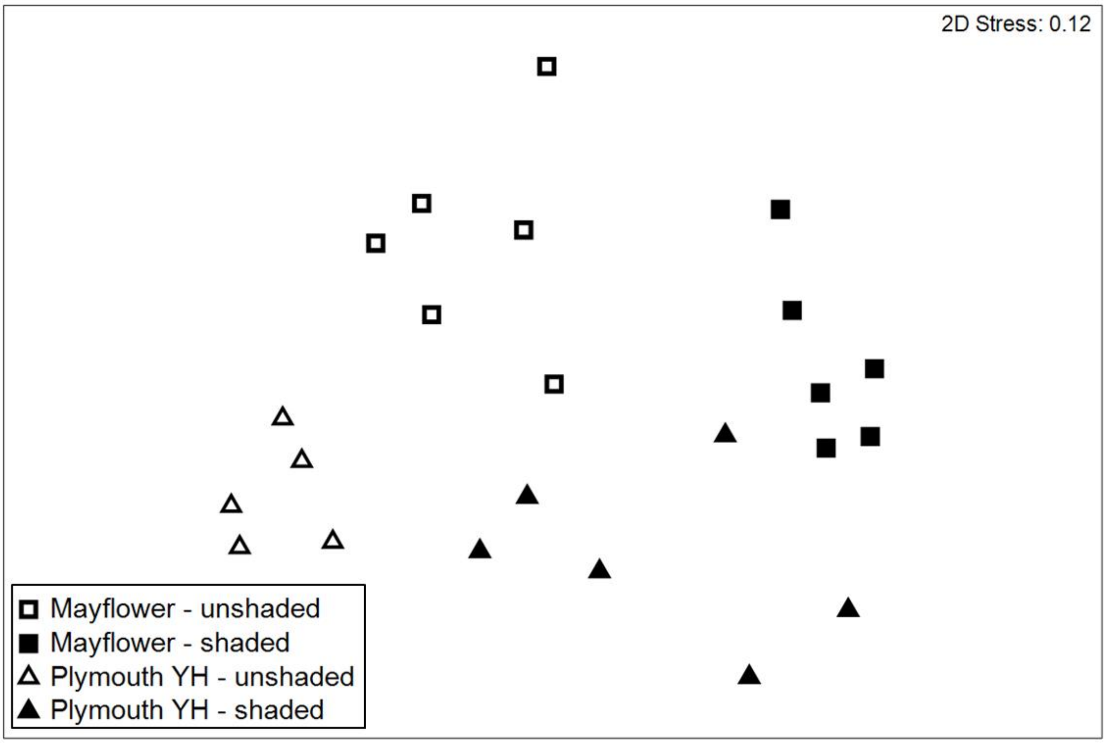


Figure 5-10. nMDS ordination plot comparing community composition between shaded and unshaded tiles at two sites in Plymouth, British Isles (p = 0.0496) recorded at the conclusion of the 14-month experimental period. There was a significant site by treatment effect (p = 0.0010).

Table 5-6. Differences in average abundances (square-root transformed; indicated by > or <) and contributions ('%' for percentage) of individual species to community composition dissimilarities between shaded and unshaded tiles at (a) Mayflower Marina and (b) Plymouth Yacht Haven in Plymouth, British Isles recorded at the conclusion of the 14-month experimental period. Consistency of contribution is shown by ‘Diss/SD’, which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(a) Mayflower Marina

Average dissimilarity = 61.7%	**Unshaded**	**>/<**	**Shaded**	**Contr%**	**Diss/SD**
Amphipod spp. (%)	3.3	<	7.3	11.1	1.7
Mytilus spp. (%)	5.6	>	2.6	7.8	1.9
Ciona intestinalis (%)	2.6	>	0.0	6.2	1.7
Diplosoma listerianum (%)	2.0	>	0.0	5.1	1.9
Styela clava (%)	2.3	>	2.0	4.6	1.3
Saccharina latissima (%)	0.0	<	1.9	4.5	1.3
Spirobranchus sp. (%)	3.7	<	4.0	4.3	1.2
Polysiphonia spp. (%)	0.5	<	2.0	4.1	1.6
Hiatella sp. (%)	0.8	<	2.4	4.1	1.8
Anomia ephippium (%)	1.9	>	0.5	4.0	2.0
Red fan sp. (%)	0.8	<	1.8	3.8	1.2
Corella eumyota (%)	1.6	>	0.0	3.7	1.1
Aplidium cf. *glabrum* (%)	1.9	>	0.5	3.7	1.5

Bugulina fulva (%)	1.4	>	0.0	3.4	1.2

(b) Plymouth Yacht Haven

Average dissimilarity = 60.5%	**Unshaded**	**>/<**	**Shaded**	**Contr%**	**Diss/SD**
Ascidiella aspersa (%)	7.0	>	2.0	10.3	1.7
Ciona intestinalis (%)	4.8	>	1.0	7.6	2.4
Diplosoma listerianum (%)	4.0	>	0.3	7.6	3.1
Corella eumyota (%)	4.0	>	0.4	7.2	3.0
Amphipod spp. (%)	3.0	<	6.2	6.6	1.7
Mytilus spp. (%)	2.3	<	2.5	4.1	1.4
Styela clava (%)	3.8	>	1.7	4.1	1.6
Polysiphonia spp. (%)	0.5	<	2.4	3.8	1.6
Watersipora subatra (%)	1.9	>	0.2	3.4	1.8
Cryptosula pallasiana (%)	1.7	>	0.5	3.3	1.4
Austrominius modestus (%)	0.1	<	1.7	3.1	1.6
Hydroid spp. (%)	1.7	>	1.4	2.5	1.4
Botrylloides violaceus (%)	1.3	>	0.6	2.4	1.1
Asterocarpa humilis (%)	1.2	>	0.0	2.4	1.2
Orange sponge sp. 1 (%)	1.5	>	0.9	2.4	1.3

5.3.6 Tel Aviv, Israel: General overview

In total, there were 13 taxa recorded on experimental tiles and controls, with one being a non-native species (8% non-native; Table 5-7). Of the thirteen taxa, 11 were sessile animals and two were macroalgae, with no mobile animals recorded. Control tiles supported the greatest number of taxa (12), while flat and 2.5 cm tiles supported the fewest number of taxa (9). Taxon richness of treatments generally increased over the 12-month experimental period (Figure 5-11).

Table 5-7. Summary table for taxa recorded by functional group on experimental tiles, control tiles and cleared seawall plots in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period. Non-native species are indicated by ‘NNS’ superscript.

Taxa	**Cleared seawall**	**Control tile**	**Flat**	**2.5 cm**	**5 cm**
Filter feeder					
Alectryonella plicatula (Gmelin, 1791)^{NNS}		✓		✓	✓
Amphibalanus amphitrite (Darwin, 1854)	✓	✓	✓	✓	✓
Crambe crambe (Schmidt, 1862)	✓	✓	✓	✓	✓
Encrusting bryozoan	✓	✓	✓	✓	✓
Ircinia sp.	✓				
Ostrea edulis Linnaeus, 1758	✓	✓	✓	✓	✓
Schizoporella sp.		✓	✓	✓	✓
Serpulidae	✓	✓	✓		✓
Spirorbidae	✓	✓	✓	✓	✓
Watersipora cucullata (Busk, 1854)	✓	✓			
Primary producer					
Crustose coralline algae	✓	✓			✓
Turf	✓	✓	✓	✓	✓
Other					
Unidentified fouling organism	✓	✓	✓	✓	
Total taxon richness	**11**	**12**	**9**	**9**	**10**

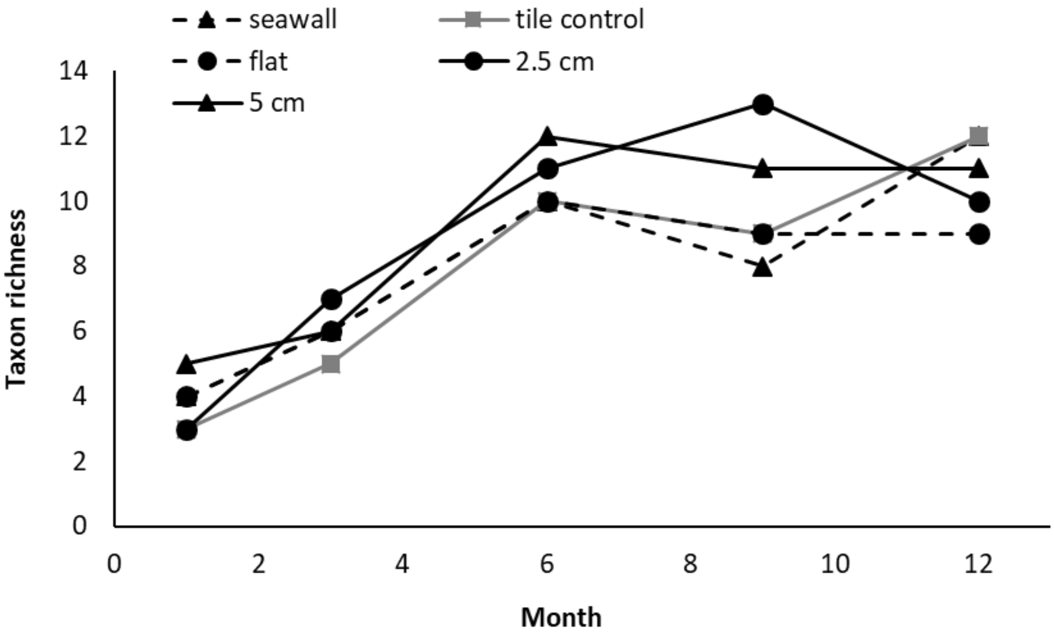


Figure 5-11. Temporal changes in taxon richness over the course of the 12-month experimental period in Tel Aviv, Israel. Taxon richness was recorded at 1, 3, 6, 9 and 12 months.

5.3.7 Tel Aviv, Israel: Comparison of taxon richness among tile treatments

There was no significant difference in mean taxon richness among tile treatments (Table 5-8a, Figure 5-12). The control tile supported the greatest mean richness (6.0 ± 0.8), while the 2.5 cm tile supported the lowest mean richness (3.8 ± 1.4).

Table 5-8. One-way ANOVAs comparing mean taxon richness among treatments in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period.

(a) Taxon richness

Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	4	3360.2	840.05	1.895	0.101
Residual	20	8866	443.3		
Total	24	12226			

Transform: no transformation

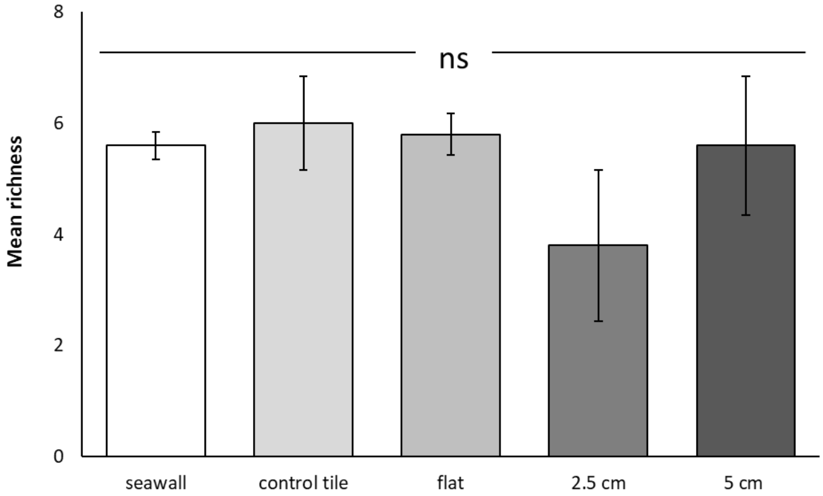


Figure 5-12. Comparison of mean taxon richness among tile treatments in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period. Error bars represent standard error (seawall, n = 5; tile control, n = 5; flat, n = 5; 2.5 cm, n = 5; 5 cm, n = 5). ‘ns’ indicates no significant difference among treatments.

5.3.8 Tel Aviv, Israel: Comparison of community composition among tile treatments

Community composition was significantly different among tile treatments (Table 5-9; Figure 5-13), with post-hoc pairwise comparisons revealing significant differences between control, flat and 2.5 cm tiles and seawall plots, as well as between control and 2.5 cm tiles. SIMPER analyses showed that, of the treatments that were significantly different from each other, the species that contributed the most to dissimilarities between seawall plots and control tiles, and seawall plots and flat tiles, was the sponge, *Crambe crambe* (24.9% and 22.8%, respectively), with abundances greater on seawall plots. The taxon that contributed the most to dissimilarities between seawall plots and 2.5 cm tiles, and control and 2.5 cm tiles, was turf algae (28.3% and 40.3%, respectively; Table 5-10), with abundances greater on seawall plots and control tiles compared to 2.5 cm tiles.

Table 5-9. One-way ANOVA comparing community composition among treatments in Tel Aviv, Israel recorded at the conclusion of the 12-month experimental period. Significant p-values are bolded.

Community composition					
Source	df	SS	MS	Pseudo-F	P(perm)
Treatment	4	14757	3689.3	3.5654	**0.0018**
Residual	20	20695	1034.7		
Total	24	35452			
Transform:	square root				

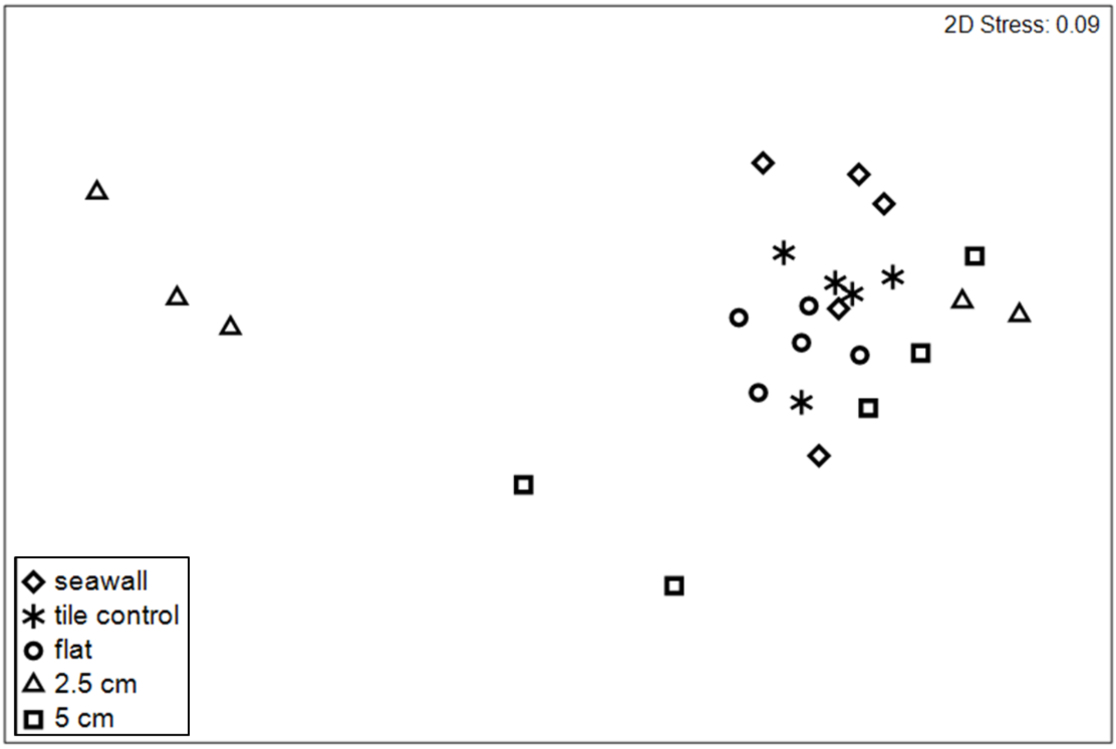


Figure 5-13. nMDS ordination plots comparing community composition among tile treatments in Tel Aviv, Israel (p = 0.0018) recorded at the conclusion of the 12-month experimental period.

Table 5-10. Differences in average abundances (square root transformed; indicated by > or <) and percent contributions ('%' for percentage) of individual species to community composition dissimilarities between tile treatments in Tel Aviv, Israel for (a) seawall compared to tile control, (b) seawall compared to flat tile, (c) seawall compared to 2.5 cm tile, (d) seawall compared to 5 cm tile, (e) tile control compared to flat tile, (f) tile control compared to 2.5 cm tile, (g) tile control compared to 5 cm tile, (h) flat tile compared to 2.5 cm tile, (i) flat tile compared to 5 cm tile and (j) 2.5 cm compared to 5 cm tile. Consistency of contribution is shown by 'Diss/SD', which is the dissimilarity divided by standard deviation of contributions across all pairs of samples.

(a)	**Average dissimilarity = 32.7%**	**seawall**	**>/<**	**tile control**	**Contr%**	**Diss/SD**
	Crambe crambe (%)	3.7	>	0.7	24.9	1.9
	Encrusting Bryozoan spp. (%)	3.6	>	3.2	14.6	1.2
	Spirorbid worms (%)	2.8	>	2.3	13.6	1.1
	Turf algae (%)	6.8	<	8.5	13.6	1.8
	Ostrea edulis (%)	1.0	<	1.8	8.1	1.4

(b)	**Average dissimilarity = 35.5%**	**seawall**	**>/<**	**flat**	**Contr%**	**Diss/SD**
	Crambe crambe (%)	3.7	>	0.7	22.8	1.9
	Encrusting Bryozoan spp. (%)	3.6	>	1.9	19.1	2.0
	Turf algae (%)	6.8	<	8.9	16.6	2.2
	Spirorbidae (%)	2.8	=	2.8	11.4	1.2
	Ostrea edulis (%)	1.0	<	1.3	7.4	1.3

(c)	**Average dissimilarity = 72.0%**	**seawall**	**>/<**	**2.5 cm**	**Contr%**	**Diss/SD**
	Turf algae (%)	6.8	>	2.3	28.3	1.4
	Crambe crambe (%)	3.7	>	0.4	18.0	1.7
	Encrusting Bryozoan spp. (%)	3.6	>	1.1	16.7	1.3
	Spirorbidae (%)	2.8	>	1.0	10.5	1.0

(d)	**Average dissimilarity = 47.4%**	**seawall**	**>/<**	**5 cm**	**Contr%**	**Diss/SD**
	Crambe crambe (%)	3.7	>	0.9	19.4	1.6
	Encrusting Bryozoan spp. (%)	3.6	>	1.6	17.4	1.3
	Turf algae (%)	6.8	>	5.1	16.2	1.0
	Spirorbidae (%)	2.8	<	3.3	13.1	1.9
	Ostrea edulis (%)	1.0	<	2.6	12.0	1.8

(e)	**Average dissimilarity = 23.5%**	**tile control**	**>/<**	**flat**	**Contr%**	**Diss/SD**
	Encrusting Bryozoan spp. (%)	3.2	>	1.9	21.8	1.6
	Spirorbid worms (%)	2.3	<	2.8	16.0	1.3

	Crambe crambe (%)	0.7	=	0.7	9.7	1.2
	Amphibalanus amphitrite (%)	0.4	<	0.7	9.6	1.3
	Spirorbidae (%)	0.3	<	0.9	9.4	1.1
	Ostrea edulis (%)	1.8	>	1.3	8.9	1.1

(f)	**Average dissimilarity = 69.3%**	**tile control**	**>/<**	**2.5 cm**	**Contr%**	**Diss/SD**
	Turf algae (%)	8.5	>	2.3	40.3	1.6
	Encrusting Bryozoan spp. (%)	3.2	>	1.1	15.3	1.4
	Ostrea edulis (%)	1.8	>	1.6	10.8	3.4
	Spirorbidae (%)	2.3	>	1.0	8.9	0.8

(g)	**Average dissimilarity = 43.7%**	**tile control**	**>/<**	**5 cm**	**Contr%**	**Diss/SD**
	Turf algae (%)	8.5	>	5.1	26.5	1.2
	Encrusting Bryozoan spp. (%)	3.2	>	1.6	15.7	1.2
	Spirorbidae (%)	2.3	<	3.3	14.8	2.2
	Ostrea edulis (%)	1.8	<	2.6	12.0	3.3
	Crambe crambe (%)	0.7	<	0.9	7.3	0.9

(h)	**Average dissimilarity = 67.9%**	**flat**	**>/<**	**2.5 cm**	**Contr%**	**Diss/SD**
	Turf algae (%)	8.9	>	2.3	46.0	1.6
	Spirorbidae (%)	2.8	>	1.0	11.1	1.4
	Ostrea edulis (%)	1.3	<	1.6	10.0	2.0
	Encrusting Bryozoan spp. (%)	1.9	>	1.1	9.8	1.2

(i)	**Average dissimilarity = 41.5%**	**flat**	**>/<**	**5 cm**	**Contr%**	**Diss/SD**
	Turf algae (%)	8.9	>	5.1	32.6	1.3
	Ostrea edulis (%)	1.3	<	2.6	13.7	2.0
	Spirorbidae (%)	2.8	<	3.3	12.2	1.7
	Encrusting Bryozoan spp. (%)	1.9	>	1.6	10.9	1.1
	Crambe crambe (%)	0.7	<	0.9	7.7	1.1

(j)	**Average dissimilarity = 68.4%**	**2.5 cm**	**>/<**	**5 cm**	**Contr%**	**Diss/SD**
	Turf algae (%)	2.3	<	5.1	27.7	1.7
	Spirorbidae (%)	1.0	<	3.3	21.2	1.3
	Ostrea edulis (%)	1.6	<	2.6	14.0	1.4
	Encrusting Bryozoan spp. (%)	1.1	<	1.6	8.3	1.1

5.4 Discussion

These experiments tested the effects of added habitat complexity on species diversity in two geologic locations. In Plymouth, British Isles, the effects of mussel seeding and shade on species diversity were also tested. It was predicted that complex tiles, tiles seeded with mussels and unshaded tiles would support greater taxon and functional richness, and different community composition than control tiles/cleared seawall plots, unseeded tiles and shaded tiles.

In Plymouth, British Isles, contrary to the prediction, habitat complexity had no effect on taxon richness and community composition. The seeding of mussels had an effect on community composition and taxon richness, with unseeded tiles supporting greater taxon richness than seeded tiles. Control tiles had lower functional richness compared to complex tiles, and at Mayflower Marina, control tiles also had lower functional richness than flat tiles. There was no effect of shade on taxon richness, but as expected, shade had an effect on community composition. Shade also had a significant effect on functional richness, with shaded tiles supporting greater numbers of functional groups compared to unshaded tiles.

In Tel Aviv, Israel, habitat complexity had no effect on taxon richness. Community composition differed among tile treatments, with differences between seawall plots and tiles, as well as control tiles and complex tiles, indicating that the presence of tiles and added habitat complexity influenced the colonising community. There were no differences in community composition between control and flat tiles, indicating that microtexture had no effect during this experiment.

In a meta-analysis of eco-engineering interventions, Strain et al. (2017a) found that in subtidal habitats, small-scale holes (≥ 5 cm deep) supported greater abundances of mobile organisms, as these depressions provided refuge from predation and wave activity for new recruits. Additionally, for abundance of sessile organisms, pits (> 1 mm to 5 cm deep) and microtexture (≤ 1 mm grooves) had significant positive effects, while crevices (> 1 mm deep) and seeding with habitat-forming taxa (e.g., oysters, mussels) had no effect. During the current study, in both countries, there were no significant effects of crevices and microtexture on numbers of taxa. In Tel Aviv, community composition was different among tile treatments, with an effect of crevice but not microtexture (control tiles did not vary from flat [textured] tiles). In Plymouth, there was an effect of mussel seeding, but the direction of effect was surprisingly negative (seeded tiles supported fewer numbers of taxa). These findings show that biotic responses to eco-engineering interventions will differ across locations and conditions.

Enhancing species diversity can also reduce the likelihood of the establishment of non-native species. Marinas provide ideal habitat for non-native species, as they are typically sheltered (Bax et al., 2002; Holloway and Connell, 2002) and provide docking for vessels from neighbouring regions and sometimes from around the world, with vessels acting as vectors for non-native species transport (Bax et al., 2002; Clarke Murray et al., 2011; Bishop et al., 2015b). Non-native species have been responsible for smothering marina pontoons and pilings (Bullard et al., 2007; Coutts and Forrest, 2007; Dafforn et al., 2009), costing marina managers and boat owners extra expenses in control and anti-fouling remedies (e.g., the carpet sea squirt, *Didemnum vexillum*; the erect bryozoan, *Tricellaria inopinata*; Coutts and Forrest, 2007; Piola et al., 2009). It is commonly accepted that diverse biological assemblages and biotic communities with habitat-forming or space-occupying species are more resilient to invasion by non-native species compared to less diverse assemblages (Stachowicz et al., 1999; Stachowicz et al., 2002; Arenas et al., 2006b; Dafforn et al., 2012). In the current experiment, non-native species were found on all tile and mussel seeding treatments in the British Isles, and the one non-native observed in Israel (*Alectryonella plicatula*) was found on control, 2.5 cm and 5 cm tiles. Although species diversity did not differ among tile treatments in the British Isles, diversity was different between seeded and unseeded tiles. Ecosystem engineers, such as oysters, mussels and reef-forming worms, provide a 3-dimensional habitat (Buschbaum et al., 2009) and have been shown to support greater numbers of associated taxa compared to areas without reef-forming taxa (Smyth and Roberts, 2010; Romero et al., 2015), which may reduce the establishment of non-native species (Stachowicz et al., 1999; Arenas et al., 2006b; Byers et al., 2006). Surprisingly, in the current study, unseeded tiles supported greater taxon richness than seeded mussels. Moreover, of the top contributing taxa to the differences in community composition between seeded and unseeded tiles, 35% were non-native species, with over 50% of those species more or equally abundant on seeded tiles. Therefore, results from our experiments do not provide evidence that habitat complexity and seeding of habitat-forming species discourage the spread of non-native species, and highlights the need for continued eco-engineering trials in marina settings.

In Plymouth, British Isles, the effects of shade on species diversity was tested by suspending tiles from floating pontoons positioned facing outward (unshaded) or facing under (shaded) the pontoons. This study had no hypothesis about sedimentation relating to shaded versus unshaded tiles and did not formally measure sedimentation. Greater accumulation of sediment on shaded compared to unshaded tiles was, however, observed at both sites. Unsurprisingly, shaded tiles supported different biological communities compared to unshaded tiles. Although the two study sites supported different communities, there were similarities in the identities of species driving the differences in communities between the treatments. Space-occupying ascidians (i.e., *Styela clava*, *Ascidiella aspersa*) were more abundant on unshaded tiles, while Amphipod spp. were more abundant on shaded tiles. Amphipods naturally live in low ambient light conditions (Meyer-Rochow and Tiang, 1979), as exposure to high intensity light has been shown to cause elevated levels of stress (Simčič and Brancelj, 2007). As these were tube-dwelling amphipods, it is possible that the animals utilized debris, organic matter and sediment to create tubes (Ulrich et al., 1995; Karez and Ludynia, 2003) which allowed them to proliferate where other taxa could not. Exposure to light has been shown to prevent settlement of certain species, thus inhibiting the development of a fully formed community (Irving and Connell, 2002; Hanlon et al., 2018), while sedimentation under shaded conditions compared to lit conditions was found to have greater negative effects on the colonising community (Irving and Connell, 2002). Many studies have investigated effects of shade on species diversity in intertidal and subtidal habitats, with a common emerging theme that shaded substrate favours fast growing sessile invertebrates (Baynes, 1999; Blockley and Chapman, 2006; Miller and Etter, 2008; Hanlon et al., 2018), such as ascidians (Kennelly, 1989; Miller and Etter, 2008; Hanlon et al., 2018) and bryozoans (Kennelly, 1989; Miller and Etter, 2008), while unshaded substrate favours macroalgae (Reed and Foster, 1984; Kennelly, 1989; Fitzpatrick and Kirkman, 1995; Baynes, 1999; Blockley and Chapman, 2006) and mobile invertebrates (Blockley and Chapman, 2006). Results from the present experiment, however, disagreed with previous studies, finding greater abundances of macroalgae on shaded tiles and greater abundances of ascidians on unshaded tiles. Many of these previous studies used substrate orientation (horizontal versus vertical; downward versus upward facing) as a proxy for shade (Baynes, 1999; Irving and Connell, 2002; Blockley and Chapman, 2006; Miller and Etter, 2008; Hanlon et al., 2018). As orientation of substrate is known to affect colonising communities due to a number of factors such as temperature, sedimentation and light (Connell, 1999; Glasby and Connell, 2001; Irving and Connell, 2002; Knott et al., 2004; Miller and Etter, 2008), results from these studies may not be directly comparable to the current study, which used only vertically oriented tiles. Grazing pressure may explain fewer macroalgae on unshaded tiles, however, very few (numbers and abundances) grazing invertebrates were found on any of the tiles in this experiment. Similarly, fish could have had an effect on controlling densities of certain algal or invertebrate species on tiles (Morris et al., 2017a; Strain et al., 2017b); however, recording fish visits was outside the remit of this experiment, and there are virtually no herbivorous fish this far north in the North Atlantic Ocean (S. Hawkins, pers. comms.). Non-biological factors might have driven community composition differences. For example, less sedimentation on the unshaded tiles suggests that these tiles experienced greater amounts of wave swash while shaded tiles were more sheltered. Although levels of exposure in the context of this experiment were probably very small, exposure levels have been found to have clear determining effects on colonising communities (Faucci and Boero, 2000; Moschella et al., 2005; Walker et al., 2008; Firth et al., 2016a). In fact, relationships between wave activity, sedimentation and available light have been documented (Madsen et al., 2001); with measurements of sedimentation being inversely related to wave exposure (Schiel et al., 2006), and with increased sedimentation causing reduction in light availability (Madsen et al., 2001). It is thus possible that the lack of light experienced by shaded tiles was further exacerbated by sediments limiting light availability to organisms living under the sediment layer. Moreover, water movement and sedimentation have been found to adversely affect species diversity (Loya, 1976) and different community assemblages have been found to result from different levels of wave exposure (Maughan and Barnes, 2000). Although level of sedimentation and water movement probably played important roles in determining the biotic community on tiles (Maughan, 2001), this experiment did not formally test either of these factors; thus, future experiments should consider testing sedimentation and record wave activity when comparing communities on shaded and unshaded tiles. Nevertheless, the current experiment demonstrated the ability of certain eco-engineering interventions (e.g., shade) to target specific species and functional groups, and highlighted the importance of teasing apart the effects of all factors of a design (Miller and Etter, 2008; Hanlon et al., 2018).

One of the goals of eco-engineering is to enhance valuable ecosystem services and improve the ecological functioning of artificial structures (Allen and Hawkins, 1993; Mayer-Pinto et al., 2018a). Experiments in Plymouth, British Isles clearly demonstrated that hard substrate placed in subtidal habitats will readily become colonised by sessile and mobile organisms, regardless of tile complexity and microtexture. The colonising communities, however, may be ephemeral or undesirable (Pratt, 1994), and so designs should strive to target specific taxa that will have beneficial effects. The majority of organisms recorded on British tiles were filter feeders (66%), which have positive knock-on effects on water filtration for the surrounding marina. In Tel Aviv, tile complexity influenced community composition, with the orange encrusting sponge (*Crambe crambe*) and an encrusting bryozoan species driving the differences between seawall plots and control and flat tiles. Interestingly, both species were more abundant on seawall plots compared to the tiles, indicating that communities living directly on the seawall were providing greater water filtration services compared to communities on tiles. Turf algae drove differences between seawall plots and 2.5 cm tiles and control tiles and 2.5 cm tiles, with abundances greater in the seawall plots and on the control tiles. Turf algae has high photosynthetic capabilities (Steneck and Dethier, 1994; Phillips, 1996) and thus may be desirable target taxa for eco-engineering designs. Moreover, turfs have been shown to be important in the diets of grazing invertebrates (Steneck and Watling, 1982; Boaventura et al., 2002), and where turf is low in abundance, there may be limitations on grazer populations (Lai et al., 2018). It is difficult, however, to make any conclusions regarding effects of turf algae abundance on biotic communities in Tel Aviv, as grazing invertebrates were absent from all tiles and seawall plots.

Experiments in this study addressed recent concerns that the majority of eco-engineering interventions examined only single types of habitat enhancing interventions under one set of environmental conditions (Strain et al., 2017a; but see Loke and Todd, 2016; Morris et al., 2017b; Hanlon et al., 2018 for studies that focussed on multiple types of habitat enhancements). This study implemented eco-engineering designs across two locations (UK and Israel) and tested multiple habitat enhancement interventions simultaneously (microtexture, crevices and mussel seeding [Plymouth only]) in an understudied habitat (subtidal) to examine effects on species diversity. By testing habitat enhancement interventions simultaneously, experiments in Tel Aviv showed that crevices but not microtexture were important in determining the colonising communities; whilst in Plymouth, results suggest there needs to be continued research to identify interventions that will have positive effects on species diversity. Strain et al. (2017a) found that the majority of eco-engineering trials were carried out over 12 months, with intervention effects on a longer time scale largely unknown. In the present study, it is possible that different results will have emerged if tiles would have been left in place longer than the 12- (Tel Aviv) and 14-month (Plymouth) experimental periods. To quantify the stabilized community, future eco-engineering trials should thus investigate colonising communities after years rather than months (Hawkins et al., 1983; Bulleri, 2005b; Firth et al., 2016a), with the best option to allow a period of “constancy” where no more major changes in response variables are observed over the course of the experiment (Menge, 1997). Duration of experiments should be defined from the onset of the project and may focus on life histories of target taxa (i.e., run the experiment for at least one life cycle; Hairston, 1989) or terminate when a mature biological community is achieved. Yet biological succession has been known to fluctuate over space and time, with individuals dying off, migrating, stabilizing and becoming grown over at timescales of months to years (Hawkins, 1981; Hawkins, 1983); these processes can change species richness and abundance over time (Connell and Slatyer, 1977; Benedetti-Cecchi, 2000; Benedetti-Cecchi et al., 2000; Maggi et al., 2011). If the community is within a highly disturbed or unstable environment, bare space may be created, thereby creating a cyclical process of succession (Oshurkov, 1992). Therefore, confidence that a climax community has been reached may only be possible in well-studied systems (Oshurkov, 1992), and thus it may be challenging to define the duration of the experiment in lesser-studied systems. The British experiment considered the life history of ascidian species, which go through a boom and bust cycle over the course of approximately 12 months in temperate waters (Stachowicz et al., 1999; Hawkins et al., 2017; A. Yunnie, pers. comm). If the experiment would have been terminated at 12 months, taxon richness would be markedly lower and community assemblage would be noticeably different, as ascidians went through a winter die-off at the 12-month mark. In this way, the results obtained likely show greater than average taxon richness experienced over the entire experimental period, with this “boom” period buffering the winter “bust” period (Levine, 2000). In seasonal temperate waters it may be important, therefore, to create a spring and autumn sampling regime to capture the full species diversity picture. Regardless, these experiments reinforced the idea that the future of eco-engineering will have to address multiple intervention types across latitudinal scales in order to build an evidence base for large-scale implementation.

5.4.1 Concluding remarks

The success of any eco-engineering design will ultimately depend on well-informed planning underpinned by sound evidence, as well as setting and monitoring of secondary management goals, which might include enhancing specific ecosystem services such as water filtration or provision of fish habitat, transplanting species of commercial or conservation interests or mitigating spread of non-native species. Moreover, it is vital to understand under which environmental conditions interventions will have the greatest positive effects so that eco-engineering can be an effective tool for achieving management goals (Dafforn et al., 2015b; Dafforn et al., 2016; Mayer-Pinto et al., 2017; Strain et al., 2017a). The present study found that: (1) under the current environmental conditions in Plymouth, there were limited effects of microtexture and crevices on species diversity; (2) in Plymouth, unseeded tiles surprisingly supported greater taxon richness than seeded tiles, and community composition differed between seeded and unseeded tiles; and (3) in Tel Aviv, despite no difference in taxon richness, community composition was influenced by crevices, but not microtexture. Thus, in Plymouth, British Isles, further testing of eco-engineering designs in subtidal habitats is necessary before interventions at the scale of entire structures can be undertaken. In Tel Aviv, Israel, however, future research can build on these effective interventions to develop site-specific approaches that match the local taxa and address the environmental conditions.

Artificial structures will never be exact surrogates for the natural habitats they replace, and even the best eco-engineering designs cannot replicate nature. However, if decision-making is well informed and secondary management goals are determined from the onset, eco-engineering interventions can support greater species diversity, therefore providing valuable ecosystem services for humans and nature. This means that interventions underpinned by a sound evidence base will be an essential prerequisite for the future of ecological engineering in coastal and marine environments.

6. CHAPTER SIX

Design catalogue for eco-engineering of marine and coastal artificial structures: a multifunctional approach for stakeholders and end-users

Abstract

Coastal urbanisation, energy extraction and food production have led to a global proliferation of artificial structures within the coastal and marine environments (*sensu* “ocean sprawl”). To mitigate impacts on natural habitats and biodiversity, the practice of eco-engineering of artificial structures has been developed over the past decade. Eco-engineering aims to create sustainable ecosystems that integrate human society with the natural environment for the benefit of both. The science of eco-engineering has grown markedly, yet synthesis of research into a user-friendly and practitioner-focused format is lacking. Feedback from stakeholders has repeatedly stated that a “photo user guide” or “manual” covering the range of eco-engineering options available for coastal and marine artificial structures would be beneficial. However, a detailed and structured “user guide” for eco-engineering in coastal and marine environments is not yet possible; therefore we present an accessible review and catalogue of possible eco-engineering options and a summary of guidance for a range of different structures tailored for stakeholders and end-users as the first step towards a structured manual. This work can thus serve as a potential template for future eco-engineering guides. Structures covered here include: (1) rock revetment, breakwaters and groynes composed of armour stones or concrete units; (2) vertical and sloping seawalls; (3) over-water structures (i.e., piers) and associated support structures; (4) tidal river walls; and (5) offshore structures (i.e., offshore energy systems). The overall aim of this paper is to suggest potential eco-engineering designs for biodiversity enhancement of coastal and marine artificial structures.

6.1. Introduction

Urbanisation, aquaculture and the increasing demand for energy are driving the drastic and irreversible modification of aquatic systems globally (Vitousek et al., 1997; Halpern et al., 2008; Knights et al., 2015). Many of these anthropogenic activities have contributed to “ocean sprawl” – a term that was recently coined to describe the proliferation of artificial structures (i.e., seawalls, breakwaters, groynes) in marine and coastal environments, and the subsequent modification and loss of natural substrata (Duarte et al., 2012; Firth et al., 2016b; Bishop et al., 2017).

Artificial structures typically have steep profiles and reduced surface area and complexity, and as such, they generally support different species assemblages than natural habitats in similar environmental settings (Knott et al., 2004; Chapman and Underwood, 2011). Any hard substrate placed in the sea will inevitably become colonised by marine organisms, which can be perceived either favourably or unfavourably depending on the environmental context and the colonising biological community (“community” is used to describe a group of interacting species in a given area). These communities are typically composed of fewer numbers of species (Chapman, 2003; Geist and Hawkins, 2016) and many are dominated by invasive species (organisms that are not native to the ecosystem) and opportunistic species (organisms that make up the initial stages of succession) compared to natural habitats (Dafforn et al., 2012; Bishop et al., 2015b; Dafforn, 2017). As a result, the functional role of artificial substrate in an ecosystem is often different to natural habitats (Bulleri et al., 2004; Jackson et al., 2008b; Aguilera et al., 2014).

Regardless of the specific ecological impacts, it is clear that human actions are leading to the development of new habitats and ecosystems without natural analogues (Hobbs et al., 2006; Morse et al., 2014). In response, some ecologists are considering how to manage these new habitats for ecological and societal benefit (Milton, 2003;

Hobbs et al., 2006; Macdonald and King, 2018). The design of such ecosystems, which integrate human society with the natural environment for the benefit of both, has been labelled ecological engineering or “eco-engineering” (Odum, 1962; Mitsch and Jorgensen, 1989; Odum and Odum, 2003). Whilst the environmental context of artificial structures is likely to be fixed, their biodiversity (i.e., the variety of living organisms; Colwell, 2009) and role in ecosystem functioning (i.e., biotic processes such as water purification) can be enhanced through eco-engineering techniques.

The field of eco-engineering is beginning to provide practitioners with options for the design and management of artificial structures in marine (in the sea), coastal (where land meets sea) and estuarine (body of water where river meets sea) environments to support biodiversity and provide desirable secondary benefits to both society and nature – often referred to as “ecosystem services” (Figure 6-1). The overall aim of eco-engineering is to promote biodiversity and enhance provision of ecosystem services whilst not compromising the primary function of a structure such as coastal defence, safe berthing in a port or energy provision by offshore renewables. The organisms that colonise artificial structures can provide important ecological and socio-economic services, such as habitat provision to support fisheries and aquaculture (Hawkins et al., 1992b; Bohnsack et al., 1994; Whitmarsh et al., 2008), water quality improvement through biofiltration (Allen et al., 1992) and education and general aesthetic appeal of biodiversity in urban areas contributing to human well-being (Figure 6-1; Airoldi et al., 2005a; Sugden et al., 2009; Mayer-Pinto et al., 2017).

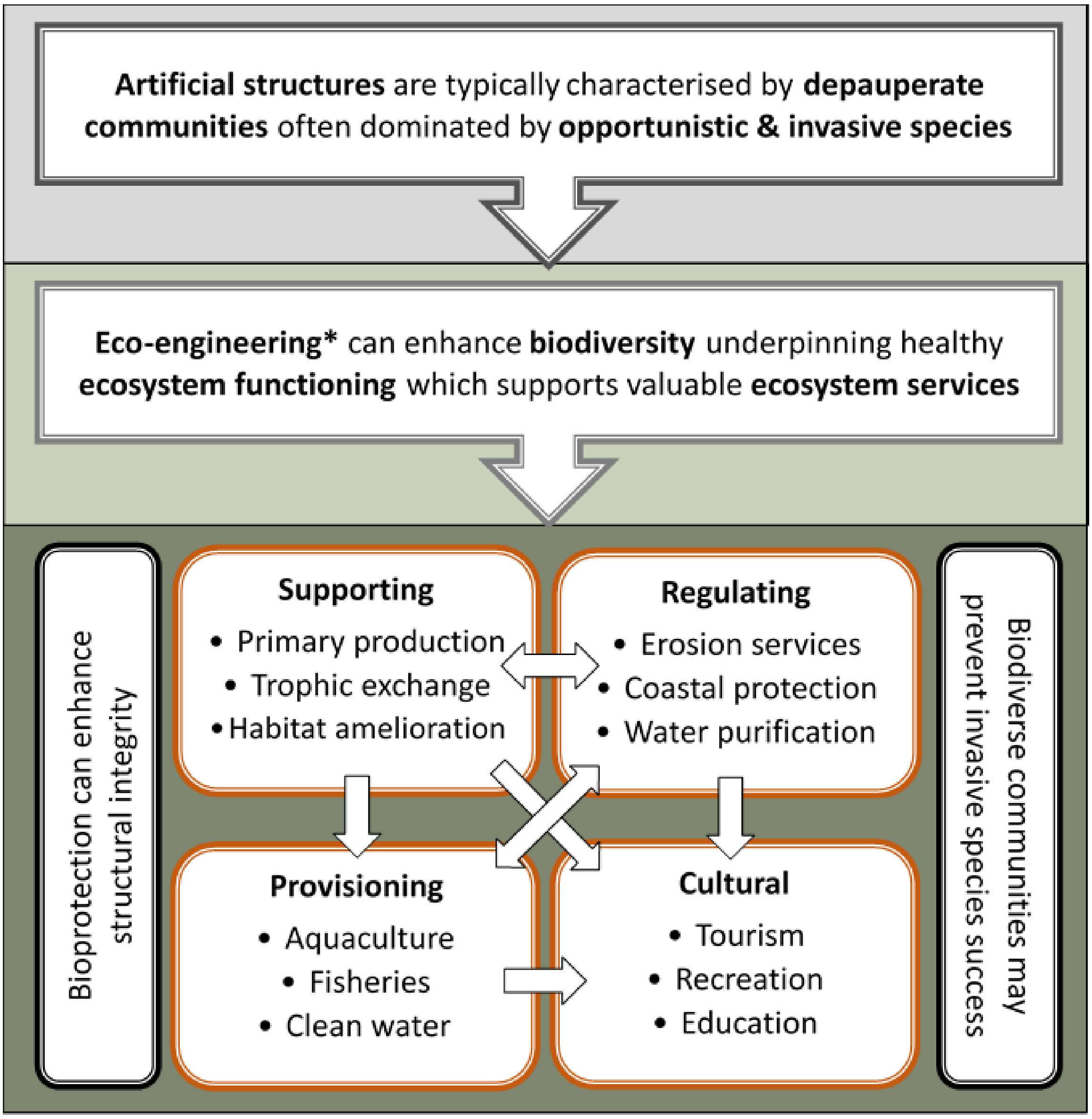


Figure 6-1. Typical characteristics of artificial structures and how eco-engineering optimises the potential ecosystem services as outlined by the Millennium Ecosystem Assessment (red boxes) (Millennium Ecosystem Assessment 2005; Everard 2017). The arrows show the potential linkages and feedbacks between services (e.g., improved fisheries [provisioning service] can have beneficial knock-on effects to recreational fishing and tourism [cultural service]). Other potential desirable outcomes of eco-engineering are highlighted in black boxes. *Eco-engineering enhances biodiversity and ecosystem services only compared to the ecological condition of the same structure without eco-engineering applications.

There is increasing impetus for eco-engineering of artificial structures to support ecosystem services. Evans et al. (2017) interviewed different stakeholder groups about their perceptions of artificial coastal defence structures and their potential to provide built-in secondary benefits. Respondents prioritised ecological benefits over economic, social and technical ones. At the same time, stakeholders have raised concerns relating to the impacts of eco-engineering interventions; engineers are concerned with impacts on the performance and durability of the structure whilst conservationists are concerned about invasive species (Dafforn et al., 2012; Evans et al., 2017; Naylor et al., 2017). Research has shown that the encouragement of certain colonising organisms such as barnacles, mussels, oysters and algae can have a positive “bioprotective effect” through physical strengthening of the materials and protection from temperature extremes and wave action (Risinger, 2012; Coombes et al., 2013; Coombes et al., 2015). Furthermore, one of the primary functions of eco-engineering is to promote diverse native biological communities that can prevent the establishment of invasive species (Figure 6-1; Stachowicz et al., 1999; Stachowicz et al., 2002; Arenas et al., 2006b).

Whilst efforts should be focused on maximising ecological benefits through eco-engineering of artificial structures, the best option is to allow natural defences to persist where possible and avoid building infrastructure and associated defences unless absolutely necessary – the “do nothing” approach (Hoggart et al., 2014). Where and when human intervention is needed for reasons of safety, infrastructure protection or energy development, the use of “soft” engineering approaches should be used (Dafforn et al., 2015a; Morris et al., 2018a). These are typically non-structural interventions that involve working with nature, such as the modification or removal of artificial structures to allow the sea to re-inundate previously reclaimed land (commonly called “managed realignment”; French, 2006; Masselink et al., 2017; Mayer-Pinto et al., 2017), or using vegetation, sand-fills and sand nourishment as coastal protection (Erdle et al., 2006; Stive et al., 2013; Hanley et al., 2014; Morris et al., 2018a). Where these soft designs are not possible, a combination of hard and soft techniques, such as the “hybrid stabilisation” approach, should be considered (Bilkovic and Mitchell, 2013; Temmerman et al., 2013; Sutton-Grier et al., 2015). Quite often in urbanised areas, however, the only feasible approach is to build hard structures due to lack of space and the immediate need to protect valuable coastal infrastructure (Chee et al., 2017). In this paper, we assume that the reader has already explored and rejected soft engineering options, leading to an informed decision to move forward with necessary eco-engineering of hard structures to provide secondary functional benefits.

Feedback from stakeholders and end-users has repeatedly informed us that a “photo user guide” or “manual” covering the range of eco-engineering options available would be much easier than having to sift through the rapidly expanding body of academic literature (see Dafforn et al., 2015a; Geist and Hawkins, 2016; Mayer-Pinto et al., 2017 for reviews). It is increasingly accepted that one role of scientists and engineers is to inform coastal managers of current research (Chapman and Underwood, 2011; Evans et al., 2017). Thus, structured guides and frameworks (e.g., Naylor et al., 2017) tailored for decision-makers will become essential for eco-engineering to progress. Therefore, in this chapter, a user-friendly, illustrated review of possible eco-engineering options and a summary of potential guidance for a range of different artificial structures is provided for practitioners involved in development of coastal and marine environments. This work can thus serve as a template or model for future guides and frameworks as the field of eco-engineering grows. Here, various types of structures are considered in turn, with guidance given on appropriate eco-engineering interventions (Appendix 4), and generic and contextual considerations on application of eco-engineering designs are discussed.

6.2. Methods

6.2.1. Literature search

Using literature identified by Strain et al. (2017a) as a foundation and supplemented with subsequent searches for scientific articles, conference papers and government reports, studies and projects on eco-engineering interventions in coastal, estuarine, tidal river and offshore systems from around the world that included measurable ecological or environmental outcomes were reviewed. The focus was only on measurable ecological effects because the vast majority of eco-engineering studies measured only these outcomes, although social, cultural and economic knock-on effects are expected (Airoldi et al., 2005a). A systematic literature review of eco-engineering studies was not done here because Strain et al. (2017a) conducted a meta-analysis on experimental eco-engineering studies in intertidal and subtidal coastal and marine environments that examined the ecological effects of adding complexity to artificial structures. Thus, this current work aimed to build on the review done by Strain et al. (2017a) and identify more recent studies and government work. Results from the literature search are displayed in Table 6-1 as intervention types for each type of artificial structure, including the number of studies that have tested each intervention. Studies from the literature search that represented the range of options for the most common types of structures were selected, and these were presented as separate tables for each type in a visual framework included in Appendix 4 (see section 6.3. for descriptions of structures). Information for each selected study includes design details, intended outcomes, success, photographs, habitats, key references and associated costs (if known). It is important to note that the cost of interventions was not scaled up or standardised across all studies presented. As much consistent information from these studies as possible was included, but only the information derived from the authors' original interpretations was used.

Table 6-1. Summary of intervention types tested by artificial structure type.

Artificial structure type	Eco-engineering intervention	No. of studies
Rock revetment, breakwaters and groynes made of armour stones or concrete units	Hybrid stabilisation	20
	Pits, holes, crevices, grooves, cuts, roughness, gaps	5
	Precast habitat enhancement units	3
	Rock/tidal pools	4
	Seeded, textured or complex tiles or panels	3
	Transplant target species	5
Vertical and sloping seawalls	Addition of natural material	1
	Gabion baskets	2
	Hybrid stabilisation	1
	Modifying seawall slope or seawall removal	4
	Pits, holes, crevices, grooves, cuts, roughness, gaps	5
	Rock/tidal pools	7
	Seeded, textured or complex tiles or panels	8
	Transplant target species	2
Over-water structures	Light-penetrating designs	7
	Seeded, textured or complex tiles or panels	2
Pier pilings	Addition of synthetic material	1
	Precast habitat enhancement units	1
	Seeded, textured or complex tiles or panels	1
	Transplant target species	1
Tidal river walls	Addition of natural material	1
	Floating island habitats	1
	Timber fenders & ledges	1
	Wall boxes	2
Offshore structures	Create artificial reefs from oil & gas platforms	2
	Pits, holes, crevices, grooves, cuts, roughness, gaps	1
Floating pontoons	Addition of synthetic material	1
	Seeded, textured or complex tiles or panels	3

6.3. What structures are covered?

A range of coastal, estuarine and offshore structures were considered: (1) *Rock revetment, breakwaters and groynes* include structures perpendicular and parallel to the shore composed of armour stones or concrete units, which are typically sloping structures that function to retain land, shelter a coastal area from incident waves or dissipate wave energy. (2) *Vertical and sloping seawalls* are solid, protective structures, including harbour walls and docks, designed to retain land and reflect wave energy. (3) *Over-water structures* include bridges and piers (and their supportive pilings). (4) *Tidal river walls* are typically vertical or sloping structures that provide flood defence and erosion mitigation where riverine freshwater meets the sea. (5) *Offshore structures* include structures associated with renewable energy and oil and gas platforms. (6) *Vulnerable, degraded and culturally valuable structures* include structures that are not permitted to be manipulated because of cultural or heritage value, or because of their state of deterioration. (7) *Floating pontoons* (or floating docks) are hollow structures used as walkways and for docking boats, most often within marinas. All of the studies reviewed consisted of interventions made to existing structures or incorporated within structures during their construction. Artificial reefs and eco-engineering of the upper reaches of rivers were not considered because comprehensive reviews on these subjects exist (e.g., Pickering et al., 1999; Baine, 2001; Palmer et al., 2005; Radspinner et al., 2010; Lokesha et al., 2013) and these habitats fall outside the remit of this paper.

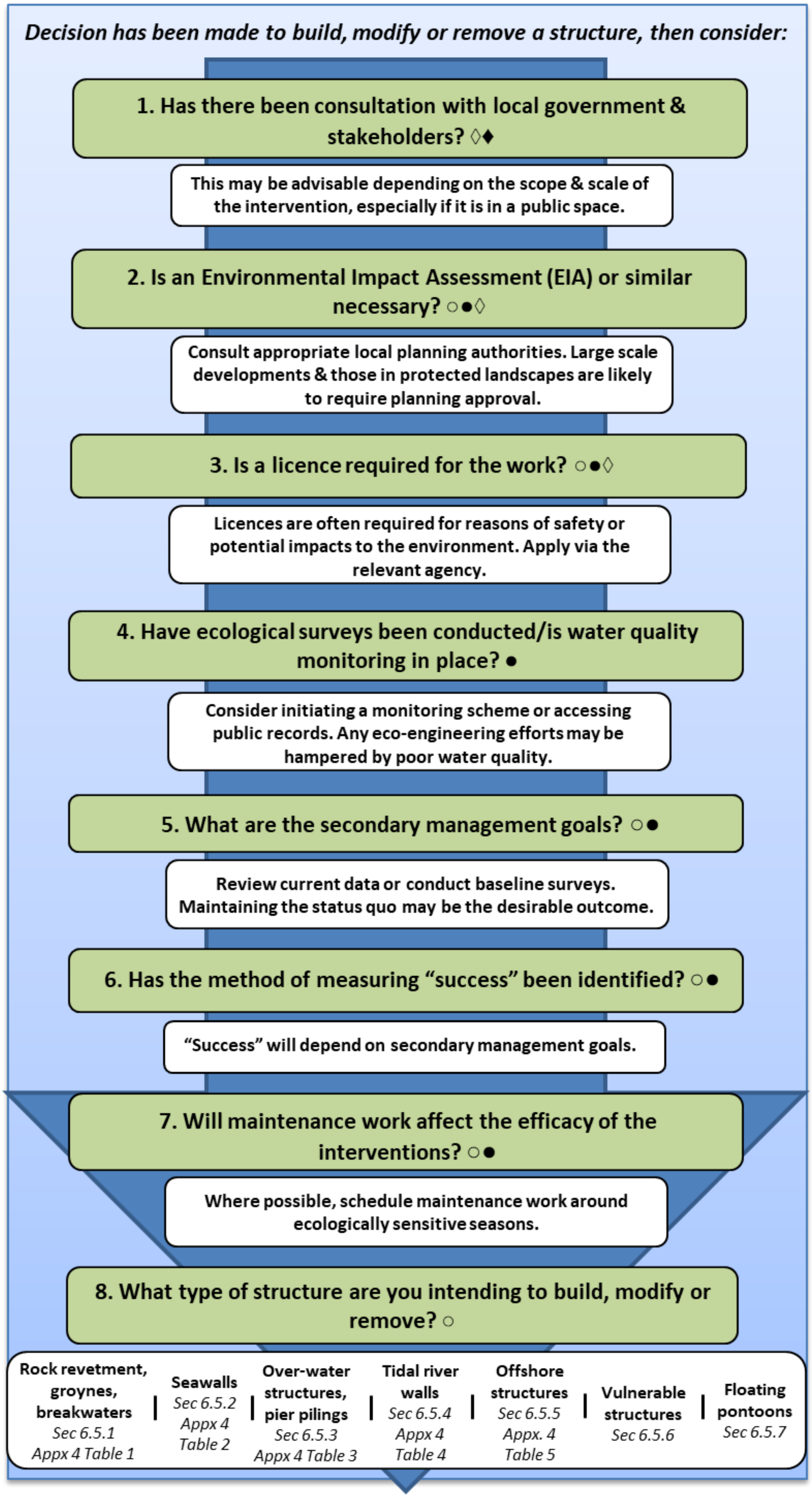
6.4. How to use this guide

Whilst it is strongly advised that the secondary management goals for any eco-engineering are clearly defined at the outset, it is understandable that managers may not be aware of the range of potential interventions (see Evans et al. (2017) for a list of potential secondary benefits of designing multi-functional engineered structures suggested by a group of stakeholders). Consequently, this chapter offers a step-by-step approach that will direct the user to relevant information and help guide the user through the range of eco-engineering options currently available.

Step 1 – Refer to Figure 6-2 which illustrates a series of questions that managers should consider in relation to incorporating eco-engineering into a planned development. The user should move through the questions sequentially, although some questions may not be applicable in every case.

Step 2 – Refer to the appropriate section and table. Figure 6-2 directs users to the appropriate section (in-text) and table (Appendix 4) containing information and photographs from previous studies for the particular structure type that they are working with. It is important to note that some enhancement designs may be applicable to structure types across multiple groups.

Step 3 – Refer to Table 6-2 which details additional generic considerations that may be applicable.



Decision has been made to build, modify or remove a structure, then consider:

1. Has there been consultation with local government & stakeholders? ◊♦

This may be advisable depending on the scope & scale of the intervention, especially if it is in a public space.

2. Is an Environmental Impact Assessment (EIA) or similar necessary? ○●◊

Consult appropriate local planning authorities. Large scale developments & those in protected landscapes are likely to require planning approval.

3. Is a licence required for the work? ○●◊

Licences are often required for reasons of safety or potential impacts to the environment. Apply via the relevant agency.

4. Have ecological surveys been conducted/is water quality monitoring in place? ●

Consider initiating a monitoring scheme or accessing public records. Any eco-engineering efforts may be hampered by poor water quality.

5. What are the secondary management goals? ○●

Review current data or conduct baseline surveys. Maintaining the status quo may be the desirable outcome.

6. Has the method of measuring "success" been identified? ○●

"Success" will depend on secondary management goals.

7. Will maintenance work affect the efficacy of the interventions? ○●

Where possible, schedule maintenance work around ecologically sensitive seasons.

8. What type of structure are you intending to build, modify or remove? ○

Rock revetment, groynes, breakwaters *Sec 6.5.1 Appx 4 Table 1* | **Seawalls** *Sec 6.5.2 Appx 4 Table 2* | **Over-water structures, pier pilings** *Sec 6.5.3 Appx 4 Table 3* | **Tidal river walls** *Sec 6.5.4 Appx 4 Table 4* | **Offshore structures** *Sec 6.5.5 Appx. 4 Table 5* | **Vulnerable structures** *Sec 6.5.6* | **Floating pontoons** *Sec 6.5.7*

Figure 6-2. Considerations for developers and managers relating to eco-engineering decisions for coastal and marine artificial structures. Question #8 prompts the user to choose the structure type of interest and refer to the associated section (in-text) and table (Appendix 4) for design details and examples. Symbols represent different consideration types: ○ Engineering, ● Environmental, ◊ Governmental, ♦ Societal.

6.5. Eco-engineering of different artificial structures

Much progress has been made in eco-engineering trials, and a wide range of options is becoming available and is provided within this paper. It is cautioned, however, that many designs have only been trialled once, or only under certain environmental conditions or regions (i.e., temperate regions), and so it is unclear whether the same results would emerge under different environmental conditions. When choosing an eco-engineering intervention, all physical (e.g., wave action, storm frequency, sediment loading, turbidity), chemical (e.g., salinity regime, nutrient supply, pollution loading) and biological factors (e.g., pool of potential colonising species, larval supply, proximity to point of introduction of invasive species) should be considered. It is crucial that developers and engineers engage with local ecologists, oceanographers and experts to discuss the feasibility of options so that valuable resources are not wasted and the outcomes of eco-engineering installations maximised.

6.5.1. Rock revetment, breakwaters and groynes made of armour stones or concrete units (Appendix 4, Table 1)

There are many options for eco-engineering these structures. Small-scale physical modifications involve drilling pits and rock pools (Firth et al., 2014b; Evans et al., 2016a; Hall et al., 2018). Large-scale physical interventions involve placement of precast habitat-enhancement units within the existing structure or during construction (Firth et al., 2014b; Perkol-Finkel and Sella, 2015; Sella and Perkol-Finkel, 2015).

Biological modifications include transplanting target species to the structure for habitat enhancement or conservation purposes (Perkol-Finkel et al., 2012; Ng et al., 2015; Ferrario et al., 2016). Hybrid methods consist of combining planted vegetation (e.g., saltmarsh cordgrass, mangrove trees) or reef-forming animals (e.g., oysters, coral) with built structures to mitigate erosion and rehabilitate coastal habitat (Hashim et al., 2010; Kamali et al., 2010; Bilkovic and Mitchell, 2013).

6.5.2. Vertical and sloping seawalls (Appendix 4, Table 2)

Options for eco-engineering seawalls include drilling pits into pre-existing seawalls (Martins et al., 2010; Martins et al., 2016), manipulating wet mortar to create grooves and pits in new seawalls (Firth et al., 2014b; Jackson, 2015) and transplanting target species or species of conservation concern directly onto seawalls (Perkol-Finkel et al., 2012; Ng et al., 2015). Structural complexity can be added by attaching eco-friendly concrete panels to seawalls (Loke and Todd, 2016; Cordell et al., 2017; Perkol-Finkel et al., 2017; World Harbour Project, 2019), and water-retaining features can be created by retro-fitting precast concrete units on seawalls or replacing blocks with cavities during seawall construction (Chapman and Blockley, 2009; Browne and Chapman, 2014; Morris et al., 2018b).

6.5.3. Over-water structures, such as bridges and piers, and their associated supporting pilings (Appendix 4, Table 3)

Over-water structures and their associated foundational support structures may alter physical characteristics, such as hydrodynamics, sediment movement and light penetration in the immediate area (Smith and Mezich, 1999; Shafer, 2002; Gaston et al., 2013; Li et al., 2014). These physical modifications result in changes to ecosystem functioning, including fish migration behaviour (Ono and Simenstad, 2014; Munsch et al., 2017) and seagrass survival (Blanton et al., 2002; Shafer, 2002). To alleviate some of the negative effects associated with over-water structures, ecologists have experimented with light-penetrating materials (Shafer and Lundin, 1999; Alexander, 2012; Cordell et al., 2017) and artificial lighting (Ono and Simenstad, 2014). Ecological encasement jackets and synthetic free-hanging ropes have been trialled on pier pilings (Paalvast et al., 2012; Perkol-Finkel and Sella, 2015), which had positive effects on biodiversity and local water quality through biofiltration, and without compromising the functional integrity of pilings.

6.5.4. Tidal river walls and embankments (Appendix 4, Table 4)

Tidal rivers and estuaries are among the most degraded and altered aquatic ecosystems in the world (Malmqvist and Rundle, 2002; Lotze et al., 2006), yet there has been a paucity of eco-engineering interventions attempted in these systems (but see Francis et al., 2008; Francis, 2009; Hoggart and Francis, 2014). Eco-engineering options for tidal river walls include attachment of timber fenders, wall modules and wire mesh to river walls. These can act as roughness elements, reducing flow velocity and facilitating seed trapping and germination of vegetation (Steele, 1999; Schanze et al., 2004; Hoggart and Francis, 2014). The use of floating structures such as fish hotels is not a direct enhancement to an artificial structure, but such designs do facilitate recruitment of riparian vegetation and invertebrate species, as well as provide shelter and habitat for fish and haul-out sites for seals (Francis, 2009; Yellin, 2014).

6.5.5. Offshore structures (Appendix 4, Table 5)

Offshore renewable and non-renewable energy exploration has led to the construction of tens of thousands of platforms worldwide (Francois, 1993; Parente et al., 2006), which often involve multiple structures spanning several square kilometres (International Energy Agency, 2007). These structures have been referred to as "*de facto* marine protected areas", as their very presence makes it problematic for other marine activities to take place (e.g., aggregate extraction and trawling; Schroeder and Love, 2004; Inger et al., 2009; Ashley et al., 2014). These structures therefore have the potential to passively "benefit" the surrounding environment by providing habitat for marine life and refuges from fishing pressure (Sammarco et al., 2004; Wilhelmsson et al., 2006; Pearce et al., 2014). With the increasing recognition of the expense of their removal and their potential to support a wide range of ecosystem services, programmes such as Rigs-to-Reefs in the Gulf of Mexico (Kaiser and Pulsipher, 2005; Kaiser, 2006b; Kaiser, 2006a) and the more recent concept of "renewables-to-reefs" (Smyth et al., 2015), are being developed to manage platform decommissioning and create artificial reefs.

The continued development of petroleum platforms and the emerging field of offshore renewable energy (see Firth et al., 2016b for global map of existing and proposed wind farms) means it will be important to develop methods for eco-engineering these types of structures to minimise impacts on the receiving environment and maximise ecological benefit (Zanuttigh et al., 2015). To date, only one study has tested the effects of eco-engineering offshore energy structures. Langhamer and Wilhelmsson (2009) created large pits in foundation units of wave energy structures to enhance the abundance of local fish and crustaceans. Coastal interventions, such as the use of precast habitat enhancement units (e.g., Reefballs^{TM}; Reef Ball Foundation, Inc., 2017) or boulders (Liversage et al., 2017), have the potential to be applied to the base of offshore structures for protection whilst also functioning as habitat for marine life.

6.5.6. Vulnerable, degraded and culturally valuable artificial structures on which manipulations are not permitted

Some artificial structures are degraded or have cultural or heritage value, which can make it challenging to obtain permissions for retrofitting eco-engineering interventions, especially interventions that involve drilling or attaching heavy materials. For example, Plymouth Breakwater, built between 1812-1841, is a 1.6 km long structure (Southward and Orton, 1954; Hawkins et al., 1983) that is considered a historic monument (Knights et al., 2016) and that is not permitted to be manipulated. As the original structure has become undermined over the years, sacrificial concrete wave-breaker blocks (100 tonne) are systematically placed on the seaward side of the breakwater as an additional form of protection from wave action. These blocks may function similarly to boulders or rubble placed at the base of seawalls, in that they create additional habitat that supports species that do not live on the original structure itself (Chapman, 2012; Firth et al., 2014b; Jackson, 2015; Chapman, 2017).

To our knowledge, formal tests to enhance biodiversity on vulnerable structures have not been conducted, thus information contained within this section consists only of suggested interventions, and a guidance table on eco-engineering approaches has not been offered. Nevertheless, designs that have been trialled for other structures have the potential to be implemented in front of vulnerable structures for protection and provision of habitat for marine life. For example, if the goal is to provide a secondary form of protection for the structure and enhance the habitat potential, artificial boulder fields (Chapman, 2012; Chapman, 2017) or precast armouring units (Firth et al., 2014b; Sella and Perkol-Finkel, 2015; Reef Ball Foundation, Inc., 2017; ARC Marine, 2019) could be placed in front of the structure. If located within a sheltered environment, vegetation (i.e., saltmarsh cordgrass, mangrove trees) could be planted in front of the structure, or combined with a hard stabilising structure for extra protection (i.e., hybrid stabilisation; Hashim et al., 2010; Bilkovic and Mitchell, 2013).

6.5.7. Floating pontoons

Floating pontoons (also known as floating docks) are some of the most ubiquitous artificial structures in urban harbours. They are hollow structures made of materials such as concrete or fibreglass which are used as walkways and for berthing boats, and also inevitably provide substrate for biotic colonisation (Connell, 2001; Toh et al., 2017). There are no natural analogues to pontoons, as they stay fixed in relation to the water level (they rise and fall with the tide so that the water depth below them varies), provide permanent shading and are typically located within enclosed environments (i.e., marinas; Hair and Bell, 1992; Glasby and Connell, 2001; Holloway and Connell, 2002).

To date, descriptive work on pontoons has characterised the biological assemblages and has shown that these structures support invasive species (Arenas et al., 2006a; Perkol-Finkel et al., 2008; Bishop et al., 2015a; Toh et al., 2017), although few eco-engineering studies have been carried out on pontoons (but see Hair and Bell, 1992; Stachowicz et al., 2002; Paalvast et al., 2012). This knowledge gap is reflected in the absence of a guidance table on eco-engineering approaches to pontoons in this paper. It is important to note that eco-engineering pontoons may be undesirable for marina operators because additional material on pontoons may affect buoyancy of pontoons and impede mooring of boats, and the associated organisms typically cover boat hulls and marina equipment (Connell, 2001). In particular, invasive species (e.g., the carpet sea squirt) have been responsible for smothering pontoons, marina equipment and boat hulls and engines, costing marina managers and boat owners extra expenses in anti-fouling remedies (Coutts and Forrest, 2007; Piola et al., 2009; Bishop et al., 2015b). Thus, trials are urgently needed to test eco-engineering interventions that will support native biodiversity, thereby offsetting the success of invasive species.

Table 6-2. Checklist for additional generic considerations that may be applicable to the chosen eco-engineering intervention

Considerations	**References**
☑ **Implementation**	
Implementation of design can be during construction or retrofitted	
- During construction: Designs may be covered by the licence for the construction work, be more creative, less expensive & implemented on a larger scale than if fitted retrospectively	Firth et al. 2014b; Sella & Perkol-Finkel 2015
- Retrofitting existing structures: Cost-effective options are available, such as affixing additional material, drilling pits, grooves & pools & transplanting desirable habitats or species	Browne & Chapman 2011; Perkol-Finkel et al. 2012; Evans et al. 2016; Strain et al. 2017b
☑ **Materials**	
Geological origin of material used can affect colonising communities, therefore try to:	
- Use material local to the region	Burcharth & Lamberti 2007; Green et al. 2012
- Use eco-friendly or natural material	ECOncrete Inc.; Dennis et al. 2017
- Use cement replacements (ground granulated blast-furnace slag)	McManus et al. 2017
☑ **Placement**	
Performance of eco-engineering designs may be influenced by:	
- Immersion gradient	
Subtidal and lower intertidal: Placement of interventions here yields markedly greater biodiversity as this area is immersed on every tidal cycle & the potential pool of colonising species is greater; however the risk of sand scour is greater, which may result in loss of the intervention	Browne & Chapman 2011; Firth et al. 2016a
Middle and high intertidal: Placement of interventions here may help extend the area of suitable habitat , which is normally compressed & greatly reduced compared to the intertidal zone in natural rocky shore	Perkol-Finkel & Sella 2015
- Exposure gradient	
Sheltered sites: Design may becoming inundated with sediment	Evans et al. 2016; Firth et al. 2016a
Exposed sites: Design may be lost to currents & waves	Francis et al. 2008; Browne & Chapman 2014
- Aspect	
Directionality (north vs. south in particular) determines the magnitude of shading & thermal stress a structure receives	Chapman & Blockley 2009 Chapman & Underwood 2011
- Inclination	
Substrate slope may determine the colonising community, as survivability on horizontal vs. vertical substrate is species-specific, & thus might influence success of invasive species	Francis & Hoggart 2008; Dafforn et al. 2012
☑ **Timing of installation**	
Timing of installation of eco-engineering interventions is important, as recruitment periods of marine life & subsequent community development vary throughout the year	Airoldi & Bulleri 2011; Evans 2016
☑ **Maintenance of structure**	
Maintenance can result in disturbance, often creating bare space where dense biological assemblages occurred previously, increasing the risk of colonisation by invasive species	Stachowicz et al. 1999; Airoldi & Bulleri 2011
☑ **Uncontrollable factors**	
The precise effects of eco-engineering interventions are difficult to predict because coastal & marine systems are highly variable, with many uncontrollable conditions	
- Local conditions: Consider the success of past designs in similar locations & conditions	
- Extreme weather events: Use information on weather trends in the region	
- Obtaining permissions to install a design: Many structural design features of artificial structures are non-negotiable because of their primary function & cost restrictions	

6.6. Concluding remarks

Artificial structures in the coastal, estuarine and marine environments are not equivalent surrogates for the natural habitats they replace; even the best eco-engineering designs cannot replicate nature. The best option for maintaining biodiversity and healthy ecosystem functioning is to minimise intervention and work with natural habitats whenever possible (e.g., sand banks, saltmarshes, mangroves; Airoldi et al., 2005a; Hanley et al., 2014; Morris et al., 2018a).

The future of eco-engineering will necessarily include a wider ecosystem perspective; this will include combining “hard” and “soft” engineering (Bilkovic and Mitchell, 2013; Temmerman et al., 2013; Hanley et al., 2014; Chee et al., 2017), and will involve a multifunctional approach to design structures that can synergistically support aquaculture, energy production, diverse biological communities and healthy ecosystems (Zanuttigh et al., 2015; Evans et al., 2017). As a response, ecologists have developed a wide range of eco-engineering options and are beginning to develop user-friendly frameworks and guidelines for coastal managers, government bodies and other practitioners (Dafforn et al., 2015b; Dyson and Yocom, 2015; Mayer-Pinto et al., 2017); but we caution that significant knowledge gaps remain regarding the applicability of these techniques outside the environmental scenarios in which they were trialled, and all designs carry with them an associated risk. As Bulleri and Chapman (2010) warned, it is not yet possible to provide a full “recipe book” of interventions from which engineers and developers may select the best approach with absolute confidence to possible outcomes (see also Evans et al., 2017). To inform sound eco-engineering practice, there is a need for wider testing of existing designs in different environmental settings, and to develop the predictive capability to forecast ecological outcomes (Airoldi et al., 2005a; Hulme, 2014; Evans, 2016). Meticulous planning, informed decision-making and setting and measuring secondary management goals are vital in maximising the ecological and societal benefits of eco-engineering (Russell et al., 1983; Hawkins et al., 1992a). Collaboration between developers, ecologists and engineers is an essential prerequisite for maximising biodiversity gains and minimising ecological impacts of coastal development (Department for Communities and Local Government, 2012).

Ecologists should acknowledge concerns from engineers, coastal managers and government bodies at the onset of any eco-engineering project. Although managers are typically concerned with the elevated costs of using eco-engineering in the design of coastal development, Strain et al. (2019b) found that this group was supportive of eco-engineering for lessening the effects of pollution and enhancing biodiversity in harbours. Civil and construction engineers hesitate to incorporate ecological design into new developments because these are unconventional concepts that go against “business as usual”, and working with natural processes is not part of the curriculum in most engineering education programs (Pioch et al., 2018). Additionally, societal, economic and structural considerations still hold precedent over environmental concerns (Pioch et al., 2018). Mitsch (2014) argued that eco-engineering will become part of routine practice only when ecologists learn about engineering, and engineers learn about ecology. Recently, government bodies have shown interest in building coastal artificial structures with secondary ecological benefits, and policies are evolving to reflect this shift in perception (Naylor et al., 2012; Evans et al., 2017; Evans et al., 2019); yet governments have limited access to academic journals and lack the time and resources to research and implement relevant designs. (Evans et al., 2019; Welsh Government, pers. comm.). Although formal economic assessments of eco-engineering coastal artificial structures are yet to be done, the field of eco-engineering can learn from concerns raised about and assessments done on the economic value of artificial reefs (Kawasaki, 1984; Bohnsack, 1991; Adams et al., 2006; Macreadie et al., 2011).

Arguably more is learnt from failure than from success (see Firth et al., 2016a), and we advocate that reporting of failure is imperative. Reflecting the restricted distribution of these trials grouped in a few geographical hotspots (i.e., Australia, Italy, Singapore, UK, USA; Firth et al., 2016b; Strain et al., 2017a) and limited types of structures studied (i.e., limited research on pontoons, offshore and subtidal structures), we caution against unconsidered implementation of these recommendations without full consideration of the environmental context, overall management goals and desired target effects. With careful planning and consultation with the appropriate team of experts – local ecologists, engineers and societal stakeholders – even heavily stressed coastal and marine ecosystems can support greater biodiversity, enhancing functioning, thereby providing valuable ecosystem services for both nature and society.

7. CHAPTER SEVEN

General Discussion

7.1. Thesis overview

This thesis addressed five key knowledge gaps in the current eco-engineering literature: (1) understanding of occurrence and patterns of non-native species in intertidal natural and artificial habitats along the south coast of England (an invasion hotspot; Chapter 2); (2) looking beyond conventional measures (α-diversity) of species diversity to better understand the differences in communities between natural and artificial habitats at multiple spatial scales (Chapter 3); (3) comparing how topographic complexity shapes species diversity in both intertidal and subtidal habitats (Chapters 4 and 5); (4) seeking generality of patterns of eco-engineering interventions across geographic localities (Chapters 4 and 5); and (5) making the outcomes of eco-engineering research accessible in a user-friendly and practitioner-focussed format for stakeholders and end-users (Chapter 6). In this chapter, main findings of this research is summarized in the context of these knowledge gaps (Section 7.1.) and this is put in the context of information necessary for eco-engineering to become routine practice at larger scales (Section 7.2.). The areas that need further attention are identified and suggestions for future work are discussed (Section 7.3.). This chapter then concludes with some final remarks (Section 7.4.).

7.1.1. Understanding the occurrence and patterns of non-native species in intertidal natural and artificial habitats along the south coast of England.

Many studies in the British Isles have documented non-native species in subtidal habitats (i.e., floating pontoons; Ashton et al., 2006; Griffith et al., 2009; Bishop et al., 2013; Foster et al., 2016), with the south coast of England being particularly well-studied (Arenas et al., 2006a; Bishop et al., 2015a; Bishop et al., 2015b; Wood et al., 2015). These studies did not survey intertidal habitats and natural rocky shores, thus, there remained a gap in the understanding of the full non-native species picture along the south coast of England. This thesis showed that the Central region of the south coast of England (Poole, Southampton, Portsmouth) supported more non-native species than the West (Falmouth, Looe, Plymouth, Salcombe, Torbay) and the East (Shoreham, Folkestone, Dover), agreeing with results from previous surveys in the same geographic region (Bishop et al., 2015a; Bishop et al., 2015b). These results may be explained by vessel traffic arriving in ports, as vessels are known vectors of non-native introductions (Carlton and Geller, 1993; Ruiz et al., 1997; Gollasch, 2002; Gollasch, 2008; Molnar et al., 2008; Clarke Murray et al., 2011). Unsurprisingly, the number of non-native species was positively correlated with the number of vessel arrivals in the region. Additionally, non-native species assemblage composition differed between natural and artificial habitats, with most of the non-natives that were more abundant in natural found almost exclusively in rock pools (e.g., *Grateloupia turuturu*, *Sargassum muticum*, *Undaria pinnatifida*). These organisms are lower intertidal and shallow subtidal algal species (Bunker et al., 2017) and are common in assemblages found on floating pontoons (Arenas et al., 2006a; Epstein and Smale, 2018). These species, therefore, are opportunistically taking advantage of any available submerged substrate, and thus the probability of further spread out from invaded marinas is likely (Epstein and Smale, 2018). Knowledge gained from these surveys can contribute immensely to the understanding of the “invasibility” of a structure (see Section 7.3.1. of this chapter; Alpert et al., 2000; Arenas et al., 2006b; Dafforn et al., 2012). Although Rapid Assessment Surveys (RAS) are a common and effective method for quantifying non-native species presence and abundance (Bishop et al., 2015b), there are limitations to the area which surveyors can realistically cover during a low tide. It is therefore important to acknowledge that non-native species reports here are likely conservative ones; the absence of a species from any report does not necessarily equate to real absence in the ecosystem.

7.1.2. Looking beyond conventional measures (α-diversity) of species diversity to better understand the differences in communities between natural and artificial habitats at multiple spatial scales

This thesis showed that taxon richness (α-diversity) – a common measurement of species diversity in marine and coastal ecology (e.g., Chapman, 2003; Firth et al., 2013b; Firth et al., 2014a) – was greater in natural compared to artificial habitats at two spatial scales. However, patterns of β-diversity (the measure of the variation in identities of species among sampling units in a given area; Anderson et al., 2011) were different depending on the scale examined. As expected, variation in taxon richness (β-diversity) was greater in natural compared to artificial habitats at the within-site scale. Surprisingly, the variation in taxon richness (β-diversity) at the among-site scale, however, was greater in artificial compared to natural habitats. If α-diversity were chosen as the only measure of species diversity in this study, valuable landscape scale information would have been overlooked. Taking a landscape scale approach is not a new concept in assessing species diversity in terrestrial systems (Noss, 1983; Knopf and Samson, 1994; Duelli, 1997; Brockway, 1998; Gabriel et al., 2006; Lawrence et al., 2018). Importantly, management plans for conservation sites and species are often determined by these assessments (Siderits and Radtke, 1977; Margules and Usher, 1981; Smith and Theberge, 1986; Asaad et al., 2017). Noss (1983) stated that all ecosystems are open, and that biotic (e.g., organisms) and abiotic (e.g., nutrients) factors are constantly exchanged among neighbouring ecosystems. Thus, determining the appropriate spatial scale and units of measurement for quantifying patterns in species diversity is difficult; consequently, landscape scale approaches are not commonly used in coastal ecology studies (but see Jenkins et al., 2001; Johnson et al., 2003; Jenkins et al., 2005; Coleman et al., 2006; Porter et al., 2018). Findings from this study show that diversity values may be perceived differently based on how they are quantified; this has clear implications for determining species and habitat management priorities.

7.1.3. Understanding how topographic complexity shapes species diversity in intertidal and subtidal habitats across geographic localities

The effects of added habitat complexity on species diversity was measured in different habitats (intertidal, subtidal) in two different geographic localities (Plymouth, British Isles and Tel Aviv, Israel). Results differed depending on habitat and location. In general, in intertidal habitats in Plymouth, habitat complexity had no effect on taxon richness (differences were between seawall plots and tiles only), while habitat complexity had an effect on community composition. In intertidal habitats in Tel Aviv, Israel, complex tiles supported greater taxon richness and different community composition compared to flat tiles and seawall plots. In subtidal habitats in Plymouth, habitat complexity had no effect on taxon richness or community composition, while in Tel Aviv, habitat complexity had no effect on taxon richness but did effect community composition.

A notable result was that complexity had no effect on taxon richness but did influence community composition in intertidal habitats in Plymouth. This is of interest, as it may be favourable to target a specific colonising community or species of conservation (Perkol-Finkel et al., 2012; Ferrario et al., 2016) or commercial (Martins et al., 2010; Martins et al., 2016) interest through the application of eco-engineering. In this case, differences between seawall plots and complex tiles were driven by abundances of *Austrominius modestus*, a non-native barnacle (albeit “ubiquitous”; Crisp, 1958; Tøttrup et al., 2010; Gallagher et al., 2015 in the British Isles), and *Ulva* spp., an ephemeral opportunistic green alga, with both generally being more abundant on complex tiles. Differences in community composition were also driven by the common limpet, *Patella vulgata*, which was more abundant on complex tiles compared to seawall plots. As *A. modestus* and *Ulva* spp. are both undesirable species, these interventions would probably not be chosen for large scale implementation in Plymouth Sound. On the other hand, these interventions enhanced abundance of mobile grazers, which are known to be in low abundances on artificial structures compared to natural rocky shores (Chapman, 2003; Martin et al., 2005; Moreira et al., 2006; Lam et al., 2009). In fact, grazing organisms are essential in controlling abundances of micro- (Hawkins et al., 1989; Skov et al., 2011) and macroalgae (Hawkins, 1983b; Hawkins, 1983a), which influence the trophic structure of natural rocky shores (Hawkins, 1983b; Hawkins, 1983a; Arrontes et al., 2004; Coleman et al., 2006). Thus, it is possible with modification of design and continued trials, interventions may be optimised for addressing the need to increase grazing organisms on seawalls in Plymouth. The differential results obtained highlight the need to design interventions that are site- (and therefore, condition-) specific (Strain et al., 2017a). Future designs in Plymouth Sound (and indeed worldwide) might therefore aim to quantify environmental conditions such as turbidity or water velocity as part of the sampling regime in order to catalogue performance of intervention under various conditions. These experiments demonstrate that eco-engineering of coastal structures in subtidal habitats is very much in the "experimental" phase. Engineering in subtidal habitats for the purpose of enhancing species diversity is not new; humans have been creating artificial reefs to improve fisheries in nearshore and offshore waters for hundreds of years (reviewed in Bohnsack and Sutherland, 1985). This means much can be learned from the decades-long research and development of artificial reefs (Gascon and Miller, 1981; Bohnsack et al., 1994; Carr and Hixon, 1997; Burt et al., 2009; Harris, 2009; Folpp et al., 2011; Herbert et al., 2017), including offshore oil and gas platforms converted to reefs (e.g., Rigs-to-Reefs Program; Kaiser and Pulsipher, 2005; Kaiser, 2006a), as well as early discussions on eco-engineering of renewable energy structures (i.e., wind turbines, wave and tidal harnessing devices; Zanuttigh et al., 2015; Callaway et al., 2017).

7.2. Knowledge gaps and application of research

This research will contribute to information necessary for eco-engineering to become routine practice at larger scales. This thesis provides a benchmark of intertidal biological community data in Plymouth Sound and intertidal non-native species assemblages across the south of England that can be used for assessment of suitability of eco-engineering interventions. This work also provides information about performance of eco-engineering interventions tested in different habitats and locations. Lastly, this work fills a key knowledge gap by addressing how to make eco-engineering evidence available to practitioners. This information is discussed in detail below.

7.2.1. Potential for biological community survey data to be used for assessment of suitability and success of eco-engineering interventions

Strategic planning (Mayer-Pinto et al., 2017) informed decision-making (Dafforn et al., 2015a; Mayer-Pinto et al., 2017; Chapman et al., 2018), setting and measuring secondary (ecological) management goals (Hobbs and Norton, 1996; Cairns Jr, 2000; Coen and Luckenbach, 2000; Chapman et al., 2018) and an understanding of local environmental and ecological conditions (Coen and Luckenbach, 2000; Mayer-Pinto et al., 2017) are vital in maximising the ecological and societal benefits of any restoration effort. In particular, comprehensive baseline surveys measuring relevant response variables based on overall management goals are essential for informing strategic planning at the initiation of the project (Mayer-Pinto et al., 2017). Baseline data available for eco-engineering (Chee et al., 2017) and wider conservation and restoration (Legg and Nagy, 2006) planning is often lacking, which can hamper management efforts. Even when this information is available, restoring a particular system to a historical baseline is extremely challenging, as natural ecosystems are in constant flux of biotic and abiotic change (Kloor, 2000; Harris et al., 2006; Stewart, 2010; Alagona et al., 2012). For any restoration effort, ecologists need to understand the biotic communities that existed before degradation or loss of habitat, how communities have changed in response to this loss of habitat and what the new communities should look like after intervention (Kloor, 2000; Dafforn et al., 2015b; Mayer-Pinto et al., 2017; Chapman et al., 2018).

Biological survey data, coupled with physical site data, collected at the initiation of eco-engineering projects can assist in determining which structures are ecologically capable of delivering specific secondary management goals (Mayer-Pinto et al., 2017). This can reveal which artificial structure(s) in particular has the most potential to support a particular suite of species or one target species based on the existing biotic community and physical factors. In Chapter 3 of this thesis, multiple diversity measures were employed to show that community composition among artificial structures in Plymouth Sound varied markedly (high β-diversity), suggesting that biotic communities on different structures would respond differently to eco-engineering interventions and therefore ecological goals may have to be site- (or structure-) specific to accommodate different taxa (Strain et al., 2017a). For instance, if the ecological goal were to enhance habitat by transplanting canopy-forming algae, the ideal structure for implementation would be one with physical conditions that mimic structures that support reproductive populations of macroalgae of the same species or functional group. Additionally, the structure of interest should be close enough to a reproducing population so as to receive a sufficient supply of propagules (e.g., close to natural rocky shores; Sousa, 1984). Propagule supply to a particular location within a harbour could be predicted with a high level of confidence using hydrodynamic and particle tracking models (Gilbert et al., 2010; Hall, 2018) or *in situ* assessments (McQuaid and Phillips, 2000).

Considerations for assessing the suitability of an intervention should include physical and environmental factors (Mayer-Pinto et al., 2017), taking note of which factors are uncontrollable and based on local conditions (Figure 7-1; Firth et al., 2014b). For example, it is important to note biogeographic range edges and distance from major shipping ports, which often facilitate non-native species introductions (Carlton, 1996b; Ruiz et al., 1997; Ruiz et al., 2000), and thus eco-engineering designs may inadvertently assist in the migration of invasive species (Airoldi et al., 2015b; Bishop et al., 2017; Chapman et al., 2018). Physical environmental gradients, such as exposure (wave-exposed or sheltered), tidal height (low-, mid-, upper-intertidal zones) and bathymetry (in the subtidal zone), although largely uncontrollable, should be assessed prior to implementation to maximise ecological benefits of the design (Moschella et al., 2005; Burcharth and Lamberti, 2007; Firth et al., 2014b; Dafforn et al., 2016). There will always be a degree of environmental variation that cannot be controlled (Firth et al., 2014b), but considering all controllable and uncontrollable factors will at least give a more comprehensive view of how the eco-engineering intervention will perform under the known conditions.

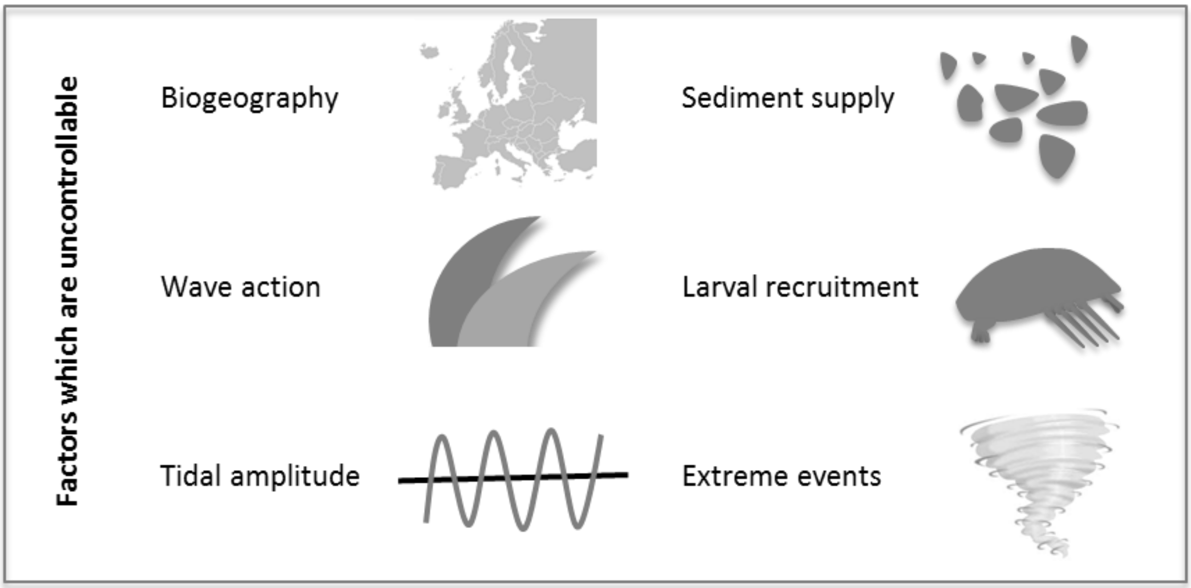


Figure 7-1. It is important that managers and engineers understand what factors are uncontrollable (context-dependent) when considering eco-engineering designs, as this will help determine the level of intervention. The above examples are common uncontrollable factors, but may vary based on the location of the artificial structure.

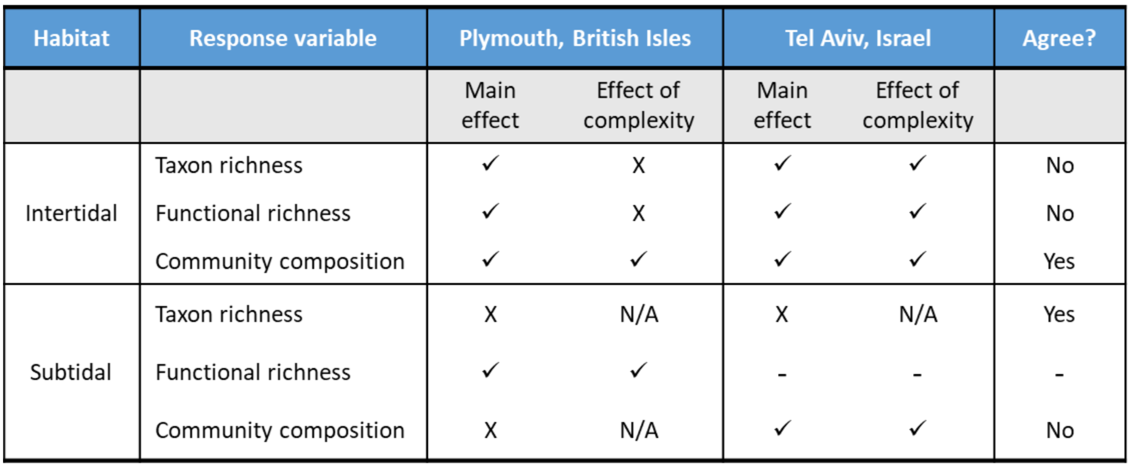
In Chapter 2 of this thesis, the need for baseline survey data in the context of non-native species was addressed. Occurrence of non-native species in intertidal habitats (both artificial and natural) along the south coast of England were recorded. The majority of the non-native species recorded in these surveys from natural rocky shores (i.e., *Sargassum muticum*, *Grateloupia turuturu*, *Colpomenia peregrina*) were regularly observed within rock pools or other water-retaining features. This may be of particular concern for eco-engineering interventions that incorporate water-retaining features, such as attachment of flowerpots to seawalls (Browne and Chapman, 2014; Hall, 2018; Morris et al., 2018b), drill-cored rock pools in a breakwater (Evans et al., 2016a), in-filled cores in a boulder breakwater (Firth et al., 2014b), pools in precast habitat enhancement units (Firth et al., 2014b; Perkol-Finkel and Sella, 2015), cavities in a seawall (Chapman and Blockley, 2009; Chapman and Underwood, 2011), drilled pits in a wave breaker unit (Firth et al., 2014b; Jackson, 2015) and creation of pools in wave energy-dissipating units (Firth et al., 2016a). Of all of these studies, only two reported on non-native species (Firth et al., 2016a; Morris et al., 2018b), with Morris et al. (2018b) specifically testing the ability of eco-engineering interventions to discourage native species settlement. Additionally, there are very few eco-engineering designs in general with specific objectives concerning discouraging non-native species settlement (but see Paalvast et al., 2012; Sella and Perkol-Finkel, 2015; McManus et al., 2017; Morris et al., 2017b). This affirms the concerns of Strain et al. (2017a) and Chapman et al. (2018) regarding an inadequate number of eco-engineering experiments reporting the proportion of native to non-native species colonising eco-engineered designs. There is concern that eco-engineering may facilitate the spread of non-native species (Naylor et al., 2017; Chapman et al., 2018); thus, it is essential to gather data to serve as a benchmark of current non-native species pre-installation, with continued monitoring post-installation.

The positive correlation between numbers of non-native species and vessel arrivals per day in the current study has clear implications for application of eco-engineering interventions in heavily trafficked harbours. Extra care must be taken in these harbours to avoid facilitating the spread of non-native species via eco-engineering interventions (Chapman et al., 2018). This could be done by limiting the amount of additional hard substrate placed in the sea (difficult in practice) or avoiding the use of substrate preferred by specific non-native species of high priority (i.e., species that cause a noticeably negative impact; e.g., *Didemnum vexillum*; Bullard et al., 2007). A recent study examining colonising communities on substrate made of different chemical composition found that, although all substrate treatments supported non-native species, the non-native barnacle, *A. modestus* was unique only to the ground granulated blast-furnace slag (GGBS) treatment and the mixed treatment (GGBS and pulverized fly ash (PFA); McManus et al., 2017). Moreover, Glasby et al. (2007) found greater numbers of non-native species on fibreglass and concrete pontoons compared to wooden structures, sandstone seawalls and natural rocky reefs in Sydney Harbour. In fact, of all the artificial structures examined, sandstone seawalls supported the lowest number of non-natives (Glasby et al., 2007), suggesting eco-engineering designs should consider using sandstone material over concrete. Hall (2018), however, found no significant difference in number of non-native species between wooden and rock groynes along the south of England, indicating that species responses vary by geographic location. Any hard substrate placed in the sea will likely become colonised by marine life, regardless of intention of the substrate. For example, artificial surf reefs such as the Boscombe Artificial Surf Reef in the south of England, are built to enhance the surfing experience, with positive knock-on effects on tourism (Fletcher et al., 2011; Rendle and Rodwell, 2014). However, this new bare substrate placed in the sea can easily be colonised by non-native species (Herbert et al., 2017), facilitating the ‘stepping stone’ effect (Airoldi et al., 2005a; Dafforn et al., 2009; Floerl et al., 2009). It is largely unknown what the role is for eco-engineering to facilitate non-native species, but it is a real concern for mangers and conservationists (L. Firth, pers. comm.; Evans et al., 2017; Chapman et al., 2018), and therefore it is crucial to measure presence and abundance of non-native species during assessment surveys and eco-engineering monitoring.

7.2.2. Importance of testing eco-engineering interventions in the same environmental and ecological context of desired large-scale installation

In contrast to a range of other studies that found that increasing complexity supported greater species diversity (Moschella et al., 2005; Chapman and Underwood, 2011; Firth et al., 2014b; Loke and Todd, 2016; Perkol-Finkel et al., 2017; Strain et al., 2017a), this research found that species response (colonisation) to varying levels of complexity and mussel seeding differed depending on geographic location (i.e., Britain, Israel) and habitat (i.e., intertidal, subtidal; Chapters 4 and 5). Results were very context-dependent, suggesting that documenting physical and chemical environmental conditions will be imperative in explaining biological differences across localities. General comparisons between the two locations showed only some commonalities in species response to added habitat complexity, with response variables from the locations agreeing in only two out of the five common tests (Table 7-1). For example, in intertidal habitats there was a main effect of treatment for taxon richness in both locations, but in Plymouth, the effect was simply from the presence of the tiles compared to bare seawall (i.e., there were no difference in taxon richness among tile treatments). Whereas in Tel Aviv, the differences in taxon richness among treatments was attributable to the complexity of tiles. Thus, with the current state of knowledge, it would be difficult to draw sweeping inferences concerning effects of added habitat complexity on species diversity across these two geographic locations. Nevertheless, these tests highlight the importance of replicating eco-engineering experiments in many different locations and habitats.

Table 7-1. Informal comparison of effects of added habitat complexity in intertidal and subtidal habitats in Plymouth, British Isles and Tel Aviv, Israel. 'Main effect' indicates if there were significant differences in species diversity among any of the treatments. 'Effect of complexity' indicates if there were differences in species diversity among tile treatments (i.e., not just differences between seawall plots and tiles). 'Agree?' indicates if results from the two locations concurred. A dash (-) represents where no test was run.



Habitat	Response variable	Plymouth, British Isles		Tel Aviv, Israel		Agree?
		Main effect	Effect of complexity	Main effect	Effect of complexity	
Intertidal	Taxon richness	✓	X	✓	✓	No
	Functional richness	✓	X	✓	✓	No
	Community composition	✓	✓	✓	✓	Yes
Subtidal	Taxon richness	X	N/A	X	N/A	Yes
	Functional richness	✓	✓	-	-	-
	Community composition	X	N/A	✓	✓	No

Results from the eco-engineering experiments in this thesis shed light on the need for carefully thought-out bespoke experimental trials in the same environmental and ecological conditions as those where they intend to be implemented, and with clear secondary (ecological) management goals identified at the commencement of the project (Mayer-Pinto et al., 2017; Strain et al., 2017a). For example, along the waterfront of Seattle in the USA, large-scale eco-engineered seawalls were installed in 2017 as part of a larger waterfront regeneration project (Seattle Office of the Waterfront and Civic Projects, 2019). The waterfront seawall installations (Cordell et al., 2017) were based on eco-engineering trials of bespoke designs at a small scale (see Goff, 2010 for the small scale trials). Similarly, in Sydney (Australia), the ‘Living Seawalls’ project

(Living Seawalls, 2019) – an initiative that uses retrofitted habitats on existing seawalls to enhance and improve the ecological performance of artificial structures – is a product of extensive eco-engineering trials in the same location as the large-scale ecological enhancements (Strain et al., 2017b; World Harbour Project; Strain et al., 2019b). Moreover, these designs were shaped by years of structured assessments of biotic communities on seawalls compared to natural habitats in Sydney Harbour (see Chapman, 2003; Chapman and Bulleri, 2003; Knott et al., 2004; Bulleri et al., 2005; Blockley and Chapman, 2006; Chapman, 2006; Moreira et al., 2007; Chapman and Underwood, 2011).

7.2.3. Potential for the application of eco-engineering in coastal development

The field of eco-engineering is beginning to provide practitioners with a variety of proof-of-concept options for the design and management of artificial structures in marine and coastal environments to support biodiversity and provide desirable ecological benefits to both society and nature (Dafforn et al., 2016; Naylor et al., 2017; Strain et al., 2017a; Evans et al., 2019). Stakeholder support for eco-engineering at the theoretical level is high (Evans et al., 2017), however there are still barriers to ecologically sensitive designs becoming part of real practice: (1) policy concerning the use of nature based solutions (e.g., eco-engineering) during coastal development in the UK is non-statutory (UK Parliament, 2009; Welsh Government, 2016; Welsh Government, 2017a); and (2) evidence to support eco-engineering is locked away in academic literature which is inaccessible to practitioners; the synthesis of research into a practitioner-focused format is lacking (McNie, 2007; Holmes and Clark, 2008; Evans et al., 2019; but see Naylor et al. 2017 for a freely available framework for integrated green-grey infrastructure).

In Wales, there is a clear "policy push" (Naylor et al., 2012) to find nature based solutions for both terrestrial and coastal adaptation to climate change (Welsh Government, 2016; Welsh Government, 2017a; Welsh Government, 2017b). Members of the Welsh Government (WG) Flood and Coastal Erosion Risk Management (FCERM) team have communicated, however, that the limited availability of information about ecologically sensitive designs in coastal engineering has discouraged them from pursuing alternative options. It is, therefore, essential that ecologists provide scientific evidence in a usable and freely accessible format if practitioners are expected to transition from traditional techniques to nature based methods. This is even more imperative if ecologists advocate for new policies to include statutory guidelines for eco-engineering (McNie, 2007; Holmes and Clark, 2008; Evans, 2016; Evans et al., 2019). Evans (2016) suggested that key eco-engineering research could be communicated to practitioners through an evolving catalogue of design options with associated ecological outcomes ranked by level of confidence in delivering ecological goals. Furthermore, Evans et al (2019) suggested that "*packaging the evidence in a useful form to support planning and decision-making*" would aid in the "uptake" of eco-engineering by practitioners. Chapter 6 of this thesis addressed this need by providing a template for future eco-engineering "user guides" tailored for coastal developers, government bodies and stakeholders. Although this "user guide" is a step in the right direction, it is clearly a small contribution to wider efforts that are needed for eco-engineering to become part of routine practice in coastal developments. There is one project, however, that has recently been initiated to address this very issue. The Ecostrucure Project – a collaborative project among eco-engineering researchers in Ireland and Wales – provides coastal developers and regulators with free on-line tools and access to a reliable evidence base for eco-engineering solutions for coastal adaptation globally (Ecostructure, 2019). Although still in the development stage, Ecostructure will translate useful scientific evidence from the eco-engineering literature into a user-friendly catalogue format. Ideally, freely accessible resources like the ones provided by Ecostructure will develop in tandem with evolving scientific research in various locations globally, and will include a wide range of nature based solution options (e.g., soft, hybrid, hard) for coastal developers and mangers.

7.3. Future work

This research filled important knowledge gaps concerning the ecological role of artificial structures and their ability to be ecologically enhanced for beneficial ecological outcomes. This research, however, brought to light more questions and revealed areas that need further attention. These areas are addressed below.

7.3.1. Non-native species management

Surveys documenting non-native species introduction and spread are becoming increasingly common (Cohen, 2005; Pederson et al., 2005; Arenas et al., 2006a; Minchin, 2007; Bishop et al., 2013; Bishop et al., 2015a; Bishop et al., 2015b; Wood et al., 2015; Foster et al., 2016). Attention now needs to turn to assessing the factors that affect the degree of “invasibility” of a habitat (Alpert et al., 2000; Dafforn et al., 2012). Whilst the concept is well developed in terrestrial habitats (especially amongst plant species; e.g., Robinson et al., 1995; Brooks, 1999; Lonsdale, 1999; Richardson and Pyšek, 2006), assessing the “invasibility” of a habitat in coastal environments is comparatively understudied (but see Arenas et al., 2006b; Wang et al., 2006; Dafforn et al., 2012; Simkanin et al., 2017 for marine and coastal examples). Highly “invasible” habitats are typically lacking in biodiversity (Osman et al., 1992; Stachowicz et al., 1999; Levine et al., 2004; Dafforn et al., 2012), highly disturbed (Airoldi, 2000; Alpert et al., 2000; Airoldi and Bulleri, 2011) and have high resource availability (Dukes and Mooney, 1999; Alpert et al., 2000). In the context of coastal artificial structures, “invasible” factors might also include material composition of the structure (e.g., wood, concrete, metal, fibreglass; Glasby et al., 2007; Hall, 2018), habitat (e.g., hard bottom, sandy shores; Airoldi et al., 2015a), tidal height (i.e., low-, mid-, high-intertidal, subtidal) and level of exposure (i.e., sheltered, exposed; Bulleri and Airoldi, 2005). Horizon scanning techniques could benefit substantially from being able to predict the colonising community based on a suite of factors, as efforts could target specific "invasible" habitats (Mehta et al., 2007; Roy et al., 2014). Evans (2016) showed that broad community structure could be predicted with 60% confidence based on a suite of environmental and physical factors. Thus, in concert with expert and historical knowledge, there is scope for the use of predictive models for the future of non-native species management.

7.3.2. Biodiversity monitoring

Despite the growing urgency to develop timely and inexpensive methods to measure biodiversity, the value of expert knowledge, effective sampling techniques and use of appropriate analyses cannot be overstated. In this thesis, the analysis of species diversity between natural and artificial habitats at multiple spatial scales using a variety of different analyses revealed differential results based on the resolution of observation and metric used. This exposed the realisation that the way ecologists interpret biodiversity can have major implications for conservation management of ecosystems and future eco-engineering interventions. It is crucial that future biodiversity surveys carefully consider the appropriate method and scale of sampling and analysis for the overall ecological goal at the onset of the study.

7.3.3. Eco-engineering

Even the best eco-engineering intervention cannot replicate nature. Where there is an option to do nothing, that option should be thoroughly explored (Hoggart et al., 2014). Moreover, there is growing concern that eco-engineering might be used as a strategy for gaining consent for potentially harmful new developments in under- or undeveloped areas (Firth et al., in prep). These previously undeveloped coastal areas should rather be protected and preserved in their current state. If, however, construction is proceeding anyway, or the area of interest is located in an already degraded environment (e.g., heavily urbanised harbours, disused docks), then there are methods to influence the design so as to achieve ecologically beneficial outcomes. For example, the Liverpool Docks in the River Mersey fell into disuse in the 1970s with the onset of containerisation, providing opportunities for urban renewal projects in the 1970s and 1980s (Russell et al., 1983; Allen et al., 1992; Hawkins et al., 1992a). An airlift water circulation and aerator system was installed to promote oxygenation and mixing of the water column (Russell et al., 1983; Hawkins et al., 1992a) and a mussel culture was created within the docks to help improve water quality which provided a favourable environment for biodiversity (Hawkins et al., 1992b; Allen and Hawkins, 1993). Due to the significant ecological improvements, the Liverpool Docks has successfully been developed for luxury accommodation, restaurants, museums, office space and frequently used for water sports (Hawkins et al., 1992a). This example can therefore be looked upon for future development of degraded environments in order to add in valuable ecosystem services where they would otherwise be lacking.

The future of eco-engineering will probably feature a wider approach where multifunctional structures with built-in secondary benefits (e.g., structures simultaneously supporting renewable energy, aquaculture and transport; Zanuttigh et al., 2015; Callaway et al., 2017) or natural structures and ecosystem engineers (e.g., saltmarsh, mangrove forests, oyster reefs) will be used for coastal protection (Temmerman et al., 2013; Morris et al., 2018a). In the context of biodiversity and the wider ecosystem, the use of “soft” engineering approaches is favoured over “hard” approaches (Narayan et al., 2016; Morris et al., 2018a); they are typically non-structural and involve complete removal of artificial structures to allow the sea to re-inundate previously reclaimed land (commonly called “managed realignment”; French, 2006; Chapman and Underwood, 2011; Mayer-Pinto et al., 2017). Other “soft” engineering techniques involve using vegetative plantings or sand nourishment as coastal protection (Erdle et al., 2006; Stive et al., 2013; Hanley et al., 2014). Where these soft designs are not possible, a combination of hard engineering (i.e., built structures) and soft techniques should be considered (i.e., hybrid designs). The “hybrid stabilisation” approach involves planting vegetation (e.g., salt marsh, mangrove forest) on the landward side of a stabilising structure (e.g., stone sill or breakwater) to allow for sedimentation and subsequent habitat stabilisation (Hashim et al., 2010; Kamali et al., 2010; Bilkovic and Mitchell, 2013; Temmerman et al., 2013).

Although “soft” approaches and hybrid designs for coastal adaptation and protection are preferred (Temmerman et al., 2013; Morris et al., 2018a), quite often in urbanised areas, it is necessary to build hard structures due to lack of space and the urgent need to protect coastal infrastructure (Borsje et al., 2011; Chee et al., 2017; Morris et al., 2018a). As a response, equivalent eco-engineering designs in different geographic locations (British Isles, Israel) and habitats (intertidal, subtidal) were tested as part of the current research with the aim to increase species diversity. A surprising result was that there was no effect of topographic complexity on species diversity under some scenarios (dependent on location, habitat and response variable). This raised two important questions: First, was the duration of experiments long enough to allow for full community development in order to measure effects of treatments? Secondly, what is the proportion of all eco-engineering designs that result in no effect of treatment? These experiments were run for 12-14 months, which is a common timeframe for eco-engineering experiments (Strain et al., 2017a; but see Martins et al., 2016; Perkol-Finkel et al., 2017; Hall, 2018 for longer trials). In the restoration ecology literature, concerns have been raised regarding the appropriate timescale in which to measure the “success” of an effort (Simenstad and Thom, 1996; Grayson et al., 1999; Irving et al., 2010; Bell et al., 2014), as the time allocated to measuring success usually falls short of the ecologically relevant timeframe in which to detect improvements (Fonseca et al., 2004; Irving et al., 2010; Bell et al., 2014). Premature cessation of monitoring efforts before ecological changes can be detected will therefore influence how success is evaluated (Grayson et al., 1999; Bell et al., 2014). For example, Jackson et al. (1995) maintained that, although positive effects of wetland restoration can be detected within a decade, evidence of improved wetland functioning would not be observed for 10-50 years. This is a concern in the field of eco-engineering as well (Chapman et al., 2018). For example, an experiment run to test the effects of eco-engineering enhancements on species diversity in energy dissipating units on a causeway, found differential results between sampling conducted at 12 and 24 months, with almost 4 times the number of species observed during the latter sampling (Firth et al., 2016a). Few eco-engineering experiments with a result of no effect or a failed design have been documented in the scientific literature (but see Firth et al., 2016a; Morris et al., 2017b; Morris et al., 2018b). This may be due to the reluctance of scientific journals to accept papers reporting negative results or no effects (Browman, 1999). This stigma, however, needs to be overcome, as the reporting of a failed design or negative or no effect of treatment in the field of eco-engineering is imperative in order to build a substantial evidence base upon which we can make confident recommendations to practitioners (Chapman et al., 2018) and prevent money wastage and future failures. Moreover, the method of communicating these results should be freely available (see Ecostructure, 2019); information should not be locked away in inaccessible academic literature (Evans et al., 2019). In fact, the process of designing optimal eco-engineering interventions is iterative, learning from and building on past successes and failures. The future of eco-engineering should therefore include a central cataloguing of eco-engineering results (including successful and failed designs) with specific design details, intended and actual outcomes and environmental conditions under which the design was tested in order to conserve efforts across institutions, encourage global collaboration and thereby advance the field of eco-engineering substantially.

7.4. Concluding remarks

The need to mitigate the effects of ocean sprawl will undoubtedly increase with the certainty of sea level rise and increase in coastal urbanisation. Eco-engineering is a tool to sustainably assist in managing some of the negative impacts of ocean sprawl; but more trials testing a variety of interventions in a range of geographic locations and habitats are still urgently needed. Small-scale experiments need to be scaled up to full-scale demonstration projects, ideally with replicate reference and/or control areas (Chapman et al., 2018). Meanwhile, surveys monitoring biotic communities, and specifically non-native species, will be vital in assessing the suitability of any proposed intervention. The reporting of failed designs and interventions with no effects is of critical value to strengthen the evidence base.

The future of eco-engineering of coastal structures will depend on evolving policies, building a strong evidence base ensuring accessibility and usability of academic research. A joined-up approach among ecologists, engineers, government bodies and coastal managers will be imperative not only for large-scale implementation, but also to facilitate a cultural shift in perception from traditional hard engineering to working with nature. The human population is projected to increase, with subsequent increases in coastal development and hence consequences for the natural environment. It is time to be pragmatic and come up with solutions to lessen the negative effects of ocean sprawl. Moreover, as scientists, we need to communicate a clear and comprehensive message to engineers, coastal managers, the public and importantly, decision-makers about the sustainable options for coastal adaptation and explain the consequences of accepting the status quo (i.e., hard built structures). With strategic planning and informed decision-making, eco-engineering has the potential to compensate and even mitigate the impacts of ocean sprawl, thereby preserving biodiversity and safeguarding valuable ecosystem services for future generations.

Appendix 1. Chapter 2 Supplementary Information

Table 1. Details of harbours surveyed along the south coast of England. Harbours were separated into regions based on their geographic location. Average number of vessel arrivals per day was obtained from Marine Traffic (2019). The last column shows number of surveys conducted in artificial compared to natural habitat. Natural habitat was only surveyed west of Torbay because natural rocky shore is rare or absent east of Torbay. All surveys were made in the intertidal zone. Harbours were categorised following Bishop et al. (2015b).

Harbour code	Harbour/City	Harbour coordinates	Region	Date of surveys	No. of surveys	No. of surveys by art:nat
FAL	Falmouth	50.1619, -5.072497	West	June 2018	9	5:4
LOE	Looe	50.354117, -4.455525	West	May 2018	2	1:1
PLY	Plymouth	50.360558, -4.142894	West	June 2018	7	3:4
SAL	Salcombe	50.232272, -3.769097	West	June 2018	1	1:0
TOR	Torbay	50.455153, -3.524844	West	July 2018	2	1:1
POL	Poole	50.708906, -1.979533	Central	Sept 2018	7	7:0
SHN	Southampton	50.877867, -1.387653	Central	Aug 2018	8	8:0
PMH	Portsmouth	50.788908, -1.110833	Central	July 2018	11	11:0
SHM	Shoreham	50.827919, -0.248131	East	Aug 2018	1	1:0
FOL	Folkestone	51.079289, 1.189525	East	Oct 2018	1	1:0
DOV	Dover	51.122417, 1.318406	East	Oct 2018	4	5:0

Table 2. Site and environmental information for each structure surveyed. A dash (-) under 'Composition of structure' indicates natural rocky shore. Wave exposure was ranked from 1-3 with 3 being the most exposed. A dash under all other columns indicates unknown information. See Table 1 in this appendix for Harbour codes.

SITE INFORMATION				ENVIRONMENTAL INFORMATION		
Harbour	**Site coordinates**	**Structure type**	**Composition of structure**	**Temperature (°C)**	**Salinity (psu)**	**Wave exposure**
FAL	50.153245, -5.066497	seawall	small-medium natural stone	18.5	35	1
FAL	50.154978, -5.067719	seawall	large Portland cement blocks	18.5	35	1
FAL	50.156368, -5.070065	seawall	large natural stone	18.5	35	1
FAL	50.139167, -5.076108	natural rocky shore	-	-	35	2
FAL	50.140339, -5.073469	natural rocky shore	-	-	35	2
FAL	50.144278, -5.041606	natural rocky shore	-	15.5	35	2
FAL	50.145106, -5.042689	natural rocky shore	-	15.5	35	2
FAL	50.161253, -5.073419	seawall	small-medium natural stone	18.4	35	1
FAL	50.1588, -5.072547	seawall	small-medium natural stone	18.4	35	1
LOE	50.350933, -4.450969	seawall	large natural stone	12.5	30	2
LOE	50.352639, -4.448383	natural rocky shore	-	12.5	30	2
PLY	50.363908, -4.162949	seawall	large natural stone	17.2	35	1
PLY	50.363339, -4.139722	natural rocky shore	-	-	35	2
PLY	50.363439, -4.139903	seawall	large natural stone	15.9	35	1
PLY	50.360728, -4.129425	seawall	large natural stone	-	-	1
PLY	50.356944, -4.127864	natural rocky shore	-	16.4	35	2
PLY	50.333383, -4.121997	natural rocky shore	-	-	35	2
PYL	50.334306, -4.199042	natural rocky shore	-	-	35	2
SAL	50.234670, -3.768665	seawall	large natural stone	-	-	1
TOR	50.4595, -3.502197	natural rocky shore	-	20.1	35	2

TOR	50.461575, -3.531375	seawall	large natural stone	21.5	35	2
POL	50.688717, -1.947217	marina wave breaker wall	wooden	20.3	35	1
POL	50.688439, -1.9456	marina wave breaker wall	wooden	20.3	35	1
POL	50.713506, -2.024911	pier	wooden	20.1	35	1
POL	50.700472, -1.941967	pier	wooden	18.8	35	1
POL	50.702722, -1.944408	discharge pipe	metal	18.8	35	1
POL	50.709644, -2.004792	groyne	wooden	-	-	1
POL	50.682808, -1.945619	groyne	natural rock boulders	19.2	35	1
SHN	50.895386, -1.408497	disused pier	metal	20.9	32	2
SHN	50.855592, -1.330786	pipe	metal	21.7	33	2
SHN	50.850481, -1.325708	pier	metal	21.7	33	2
SHN	50.8955, -1.403469	seawall	metal sheet piling	20.7	30	1
SHN	50.897994, -1.428567	pier	metal	25.2	30	2
SHN	50.890117, -1.387633	pier	wooden	20.1	32	1
SHN	50.852108, -1.30745	boat dock	wooden	20.8	32	2
SHN	50.914406, -1.386164	bridge support structure	concrete	-	24	1
PMH	50.777724, -1.086395	seawall	Portland cement mixed with stone	21.8	35	3
PMH	50.777507, -1.089037	seawall	Portland cement mixed with stone	21.8	35	3
PMH	50.792878, -1.109184	side of boat ramp	large natural stone	20.8	35	1
PMH	50.792291, -1.108191	seawall	metal sheet piling	20.8	35	1
PMH	50.796040, -1.024988	side of boat ramp	metal sheet piling	24.5	35	1
PMH	50.796061, -1.024617	side of boat ramp	concrete	24.5	35	1
PMH	50.788900, -1.028503	disused pier	reinforced concrete	22.4	35	2
PMH	50.789168, -1.107047	disused pier	reinforced concrete	19.8	35	2
PMH	50.786188, -1.102138	wharf	reinforced concrete	19.8	35	2

PMH	50.792991, -1.11692	marina wave breaker wall	metal sheet piling	21	35	2
PMH	50.797481, -1.109744	breakwater	concrete	21	35	2
SHM	50.829339, -0.248061	pier	metal sheet piling	20.8	35	2
FOL	51.078806, 1.189825	tetrapods	concrete	-	-	2
DOV	51.1247, 1.322469	breakwater	large natural stone	-	35	2
DOV	51.125328, 1.327475	old boat ramp	concrete	-	30	2
DOV	51.122769, 1.317124	groyne	natural rock boulders	-	35	2
DOV	51.121348, 1.315813	groyne	natural rock boulders	-	35	2
DOV	51.120142, 1.314172	groyne	natural rock boulders	-	35	2

Table 3. Summary of non-native species recorded in each harbour along the south coast of England. See Table 1 in this Appendix for harbour codes. NNS within natural and artificial habitats are included. New species records are indicated with an asterisk (*).

Site	FAL	LOE	PLY	SAL	TOR	POL	SHN	PMH	SHM	FOL	DOV
Bryozoan											
Watersipora subatra (Ortmann, 1890)	✓		✓		✓	✓	✓	✓	✓		
Tricellaria inopinata d'Hondt & Occhipinti Ambrogi, 1985	✓					✓	✓	✓	✓		
Bugulina stolonifera (Ryland, 1960)						✓	✓				
Bugulina simplex (Hincks, 1886)								✓			
Bugula neritina (Linnaeus, 1758)						✓	✓	✓			
Ascidian											
Didemnum vexillum Kott, 2002						✓*		✓			
Botrylloides diegensis Ritter & Forsyth, 1917						✓	✓	✓			
Botrylloides violaceus Oka, 1927						✓	✓	✓			
Botrylloides sp. indet.†	✓							✓	✓		
Aplidium cf. *glabrum (*Verrill, 1871)					✓*	✓*					
Styela clava Herdman, 1881					✓	✓	✓	✓	✓		✓
Corella eumyota Traustedt, 1882											✓
Mollusca											
Magallana gigas (Thunberg, 1793)	✓*	✓	✓	✓	✓*	✓	✓	✓	✓		✓*
Crepidula fornicata (Linnaeus, 1758)	✓			✓			✓	✓			✓*
Cnidaria											
Diadumene lineata (Verrill, 1869)							✓*				
Arthropoda											
Austrominius modestus (Darwin, 1854)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓*
Annelida											
Ficopomatus enigmaticus (Fauvel, 1923)						✓	✓				
Ochrophyta											
Undaria pinnatifida (Harvey) Suringar, 1873			✓		✓	✓					
Sargassum muticum (Yendo) Fensholt, 1955	✓	✓	✓	✓	✓*			✓			
Colpomenia peregrina Sauvageau, 1927	✓*		✓		✓			✓			

Rhodophyta											
Grateloupia turuturu Yamada, 1941			✓					✓			
Chrysymenia wrightii (Harvey) Yamada, 1932								✓*			
Caulacanthus okamurae Yamada, 1933	✓*	✓	✓*		✓*	✓*		✓*		✓	✓*
Bonnemaisonia hamifera Hariot, 1891	✓*										
Asparagopsis armata Harvey, 1855	✓										
Chlorophyta											
Codium fragile subsp. fragile (Suringar) Hariot, 1889											
Total number of species	**11**	**4**	**8**	**4**	**9**	**14**	**12**	**17**	**6**	**2**	**6**

†*Botrylloides* sp. indet. represents a *Botrylloides* spp. that is likely either *B. diegensis* or *B. violaceus* but could not be positively distinguished between the two.

Appendix 2. Chapter 3 Supplementary Information

Table 1. Details of 54 survey sites. Under ‘Habitat Type’, ‘A’ represents artificial and ‘N’ represents natural habitats. ‘Exposure’ indicates level of wave exposure (1-3; with 3 being the most exposed).

Date Surveyed	Site Name	Coordinates		Habitat Type	Exposure	Artificial Structure Type	Composition of Artificial Structure
13-May-17	Turnchapel_1	50.35935	-4.11782	A	1	seawall	medium stone blocks
13-May-17	Turnchapel_2	50.35878	-4.11822	A	1	seawall	medium stone blocks
11-Jul-17	Hooe Lake	50.35654	-4.11285	A	1	seawall	large stone blocks
13-Jul-17	East of Devil's Point	50.35904	-4.16381	N	3	-	-
22-Jul-17	Richmond Walk	50.36497	-4.16948	A	1	seawall	medium stone blocks
25-Jul-17	Oreston_1	50.36598	-4.10883	A	1	seawall	large stone blocks
27-Jul-17	Laira Bridge	50.36835	-4.10782	A	1	seawall	large stone blocks
07-Sep-17	Millbay Docks_1	50.36524	-4.15495	A	1	stone armour revetment	large stone blocks
07-Sep-17	Waterfront Café_1	50.36288	-4.14791	N	2	-	-
07-Sep-17	Millbay Docks_2	50.36587	-4.15382	A	1	seawall	medium stone blocks
09-Sep-17	Fort Bovisand	50.33756	-4.12749	A	1	seawall	large stone blocks
11-Sep-17	Fort Picklecombe_1	50.34435	-4.17000	A	1	seawall	medium stone blocks
12-Sep-17	Waterfront Café_2	50.36271	-4.14820	N	2	-	-
17-Sep-17	Bovisand Beach_1	50.33371	-4.12154	N	3	-	-
17-Sep-17	Bovisand Beach_2	50.33491	-4.12075	N	2	-	-
19-Sep-17	Mount Batten Pier_2	50.35917	-4.13149	N	3	-	-
19-Sep-17	Mount Batten Pier_1	50.35933	-4.13224	A	3	stone armour revetment	large stone boulders
19-Sep-17	Mount Batten Watersports_1	50.35997	-4.12684	A	1	seawall	small and medium stone blocks
20-Sep-17	Queen Anne's Battery	50.36456	-4.12770	A	2	stone armour revetment	large stone blocks
20-Sep-17	Oreston_2	50.36563	-4.10889	A	1	seawall	large stone blocks
22-Sep-17	Torpoint_1	50.37324	-4.19391	A	1	seawall	large stone blocks
22-Sep-17	Torpoint_2	50.37443	-4.19304	A	1	seawall	medium stone blocks
02-Oct-17	Penlee Point_1	50.31833	-4.18880	N	2	-	-
04-Oct-17	Plymouth Seafront Natural_1	50.36322	-4.13804	N	2	-	-

04-Oct-17	Plymouth Seafront Natural_2	50.36332	-4.13935	N	2	-	-
06-Oct-17	West of Devil's Point	50.35957	-4.16652	N	3	-	-
06-Oct-17	Firestone Bay_1	50.36108	-4.15814	N	3	-	-
06-Oct-17	Firestone Bay_2	50.36112	-4.15703	N	3	-	-
09-Oct-17	Kingsand Beach_1	50.33443	-4.19847	N	2	-	-
09-Oct-17	Kingsand Wall	50.33254	-4.20072	A	2	seawall	large stone blocks
09-Oct-17	Cawsand Beach	50.33046	-4.20072	N	2	-	-
12-Oct-17	Plymouth Seafront Natural_3	50.36415	-4.14559	N	2	-	-
12-Oct-17	Plymouth Seafront Natural_4	50.36404	-4.14466	N	2	-	-
23-Oct-17	Plymouth Breakwater_1	50.33314	-4.14707	A	3	breakwater/seawall	large stone blocks
23-Oct-17	Plymouth Breakwater_2	50.33369	-4.13753	A	1	breakwater/seawall	large stone blocks
24-Oct-17	Mount Wise_1	50.36503	-4.17663	A	2	seawall	flat concrete
26-Oct-17	Bovisand Beach_3	50.32840	-4.12150	N	2	-	-
06-Nov-17	Mount Batten Beach_2	50.35606	-4.12607	N	2	-	-
06-Nov-17	Mount Batten Beach_3	50.35719	-4.12699	N	2	-	-
19-Nov-17	Cremyll	50.36069	-4.17516	A	1	seawall	medium stone blocks
19-Nov-17	Mount Edgecumbe_1	50.35899	-4.17164	N	2	-	-
20-Nov-17	Drake's Island_1	50.35629	-4.15648	N	2	-	-
04-Dec-17	Kingsand Beach_2	50.33541	-4.19704	N	2	-	-
04-Dec-17	Kingsand Beach_3	50.33936	-4.19045	N	2	-	-
07-Dec-17	Rum Bay_1	50.35227	-4.12390	N	3	-	-
07-Dec-17	Jennycliff Beach_2	50.34898	-4.12218	N	3	-	-
07-Dec-17	Jennycliff Beach_3	50.34817	-4.12241	N	3	-	-
08-Dec-17	Heybrook Bay_1	50.31930	-4.11971	N	3	-	-
08-Dec-17	Heybrook Bay_2	50.31813	-4.11352	N	3	-	-
09-Dec-17	Mount Edgecumbe_2	50.35185	-4.16693	N	3	-	-
11-Jun-18	Admiral's Hard	50.36485	-4.16342	A	1	seawall	medium stone blocks
11-Jun-18	Freedom Walk	50.36362	-4.16310	A	1	seawall	large stone blocks
16-Jun-18	Plymouth Seafront Artificial_3	50.36359	-4.13997	A	2	seawall	medium stone blocks
28-Jun-18	Plymouth Seafront Artificial_4	50.36372	-4.14625	A	2	seawall	medium stone blocks

Table 2. Summary of taxa recorded in natural and artificial habitat listed by functional group. 'NNS' following a species name indicates a non-native species.

	Habitat	
Taxa	**Natural**	**Artificial**
Grazer/herbivore		
Asterina sp.		✓
Littorina littorea (Linnaeus, 1758)	✓	✓
Littorina saxatilis (Olivi, 1792)		✓
Littorina obtusata (Linnaeus, 1758)*/L. fabalis* (W. Turton, 1825)	✓	✓
Melarhaphe neritoides (Linnaeus, 1758)		✓
Patella depressa Pennant, 1777	✓	✓
Patella vulgata Linnaeus, 1758	✓	✓
Phorcus lineatus (da Costa, 1778)	✓	✓
Polyplacophora sp.	✓	
Steromphala umbilicalis (da Costa, 1778)	✓	✓
Steromphala cineraria (Linnaeus, 1758)		✓
Predator		
Nucella lapillus (Linnaeus, 1758)	✓	✓
Omnivore		
Carcinus maenas (Linnaeus, 1758)		✓
Filter feeder		
Actinia equina (Linnaeus, 1758)	✓	
Austrominius modestus (Darwin, 1854)$^{\text{NNS}}$	✓	✓
Botryllus schlosseri (Pallas, 1766)	✓	
Chthamalus montagui Southward, 1976	✓	✓
Chthamalus stellatus (Poli, 1791)	✓	✓
Cryptosula pallasiana (Moll, 1803)	✓	✓
Diadumene lineata (Verrill, 1869)$^{\text{NNS}}$	✓	
Dynamena pumila (Linnaeus, 1758)	✓	✓
Halichondria panicea (Pallas, 1766)	✓	✓
Hymeniacidon perlevis (Montagu, 1814)	✓	✓
Magallana gigas (Thunberg, 1793)$^{\text{NNS}}$	✓	✓
Mytilus sp. Linnaeus, 1758	✓	✓
Neodexiospira sp. Pillai, 1970	✓	✓
Perforatus perforatus (Bruguière, 1789)	✓	✓
Semibalanus balanoides (Linnaeus, 1767)	✓	✓
Spirobranchus sp. Blainville, 1818	✓	✓
Watersipora subatra (Ortmann, 1890)	✓	✓
Lichen		
Lichina pygmaea (Lightf.) C. Agardh, 1817	✓	
Verrucaria mucosa Wahlenberg, 1803	✓	
Thin filamentous		
Ceramium sp. Roth, 1797	✓	✓
Cladophora rupestris (Linnaeus) Kützing, 1843	✓	✓
Ectocarpus sp. Lyngbye, 1819		✓

Polysiphonia sp. Greville, 1823	✓	✓
Rhodothamniella floridula (Dillwyn) Feldmann, 1978	✓	
Vertebrata lanosa (Linnaeus) T.A. Christensen, 1967	✓	✓
Foliose		
Palmaria palmata (Linnaeus) Weber & Mohr, 1805	✓	✓
Porphyra sp. C. Agardh, 1824	✓	✓
Ulva spp. Linnaeus, 1753	✓	✓
Corticated macrophyte		
Catenella caespitosa (Withering) L.M. Irvine, 1976	✓	✓
Caulacanthus ustulatus (Mertens ex Turner) Kützing, 1843	✓	✓
Chondrus crispus Stackhouse, 1797	✓	✓
Gelidium sp. abbottiorum R.E. Norris, 1990	✓	✓
Lomentaria articulata (Hudson) Lyngbye, 1819	✓	
Mastocarpus stellatus (Stackhouse) Guiry, 1984	✓	✓
Osmundea sp. Stackhouse, 1809	✓	✓
Plumaria plumosa (Hudson) Kuntze, 1891	✓	
Leathery macrophyte		
Ascophyllum nodosum (Linnaeus) Le Jolis, 1863	✓	✓
Fucus serratus Linnaeus, 1753	✓	✓
Fucus spiralis Linnaeus, 1753	✓	✓
Fucus vesiculosus Linnaeus, 1753	✓	✓
Himanthalia elongata (Linnaeus) S.F. Gray, 1821	✓	
Articulated calcareous		
Corallina officinalis Linnaeus, 1758	✓	✓
Crustose		
Corallinaceae crust	✓	✓
Other algae		
non-calcareous encrusting red		✓
red slimy film		✓
Cyanobacteria		
Oscillatoria sp. Vaucher ex Gomont, 1892		✓

Appendix 3. Chapters 4 and 5 Supplementary Information

Table 1. Environmental variables measured during the intertidal (IT) and subtidal (ST) tile experiments Tel-Aviv, Israel and Plymouth, British Isles. Maximum (MAX) and minimum (MIN) values are shown for dissolved oxygen (DO), salinity, pH and water temperature. Salinity was recorded in practical salinity units (psu) in the British Isles and in specific gravity (Sg) in Israel. A dash (-) indicates where data was not recorded. Intertidal and subtidal data in Israel were recorded at the same time because tidal range in the Mediterranean Sea is on the order of centimetres.

Tidal Height	Country	Site	MAX/MIN	DO (%)	Salinity (psu)	Salinity (Sg)	pH	Temperature °C
IT & ST	Israel	Marina Hertzelia	MAX	-	-	1.0266	8.1	30.4
			MIN	-	-	1.0248	8.0	15.7
IT	UK	Mayflower Marina	MAX	100	35	-	8.5	18.4
IT			MIN	73	30	-	7.7	9.5
IT		Turnchapel Wharf	MAX	100	36	-	7.9	19.2
IT			MIN	72	25	-	6.8	7.7
ST	UK	Mayflower Marina	MAX	-	35	-	-	24.0
ST			MIN	-	30	-	-	5.1
ST		Plymouth Yacht Haven	MAX	-	35	-	-	19.8
ST			MIN	-	30	-	-	5.2

Table 2. Summary table for taxa recorded on subtidal tiles in Plymouth, British Isles. Non-native species are indicated by the superscript 'NNS'.

	Tile Treatment				**Mussel Treatment**		**Site**	
Taxa	**control**	**flat**	**2.5 cm**	**5 cm**	**mussel**	**no mussel**	**Mayflower Marina**	**Plymouth Yacht Haven**
Filter feeder								
Corella eumyota$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓	✓	✓
Ascidiella aspersa	✓	✓	✓	✓	✓	✓	✓	✓
Ciona intestinalis	✓	✓	✓	✓	✓	✓	✓	✓
Clavelina lepadiformis			✓	✓	✓	✓	✓	
Asterocarpa humilis$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓	✓	✓
Styela clava$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓	✓	✓
Dendrodoa grossularia		✓		✓		✓	✓	
Molgula sp.		✓	✓	✓	✓	✓	✓	✓
Botrylloides violaceus$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓	✓	✓
Botrylloides leachii		✓	✓	✓	✓	✓	✓	✓
Botryllus schlosseri		✓	✓	✓	✓	✓	✓	✓
Diplosoma listerianum	✓	✓	✓	✓	✓	✓	✓	✓
Lissoclinum perforatum	✓	✓	✓	✓	✓			✓
Didemnum spp.	✓		✓		✓			✓
Aplidium cf. *glabrum*$^{\text{NNS}}$		✓	✓	✓	✓	✓	✓	✓
Didemnum vexillum$^{\text{NNS}}$		✓			✓			✓
Botrylloides spp.	✓	✓	✓	✓	✓	✓	✓	✓
Polychlinid sp.		✓				✓	✓	
Tricellaria inopinata$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓	✓	✓
Bugula neritina$^{\text{NNS}}$		✓	✓	✓	✓	✓	✓	✓
Bugulina simplex$^{\text{NNS}}$		✓			✓		✓	
Bugulina stolonifera$^{\text{NNS}}$		✓			✓		✓	
Bugulina avicularia	✓	✓				✓	✓	
Bugulina fulva	✓	✓	✓	✓	✓	✓	✓	✓

Crisularia plumosa			✓	✓	✓		✓	
Bugulina flabellata			✓		✓		✓	
Scrupocellaria scruposa				✓		✓	✓	
Watersipora subatra$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓	✓	✓
Cryptosula pallisiana	✓	✓	✓	✓	✓	✓	✓	✓
Electra pilosa		✓	✓	✓	✓	✓	✓	
Conopeum reticulum		✓	✓	✓	✓	✓	✓	✓
Celleporella hyalina		✓		✓	✓		✓	
Unknown encrusting Bryozoan spp.		✓	✓	✓	✓	✓	✓	
Grantia compressa		✓		✓		✓	✓	✓
Sycon ciliatum	✓	✓	✓	✓	✓	✓		✓
Orange sponge sp. 1	✓	✓	✓	✓	✓	✓	✓	✓
Austrominius modestus$^{\text{NNS}}$	✓	✓	✓	✓	✓	✓	✓	✓
Perforatus perforatus				✓		✓		✓
Balanus crenatus		✓			✓	✓		✓
Spirobranchus sp.	✓	✓	✓	✓	✓	✓	✓	✓
soft tube worms	✓	✓	✓	✓	✓	✓	✓	✓
Polycheate spp.	✓	✓	✓	✓	✓	✓	✓	✓
Terebellid sp.	✓	✓	✓	✓	✓	✓		✓
Hydroid spp.	✓	✓	✓	✓	✓	✓		✓
Tubularia sp.		✓			✓	✓	✓	
Red anemone		✓	✓	✓	✓	✓	✓	
Grey anemone		✓	✓		✓	✓	✓	
Mytilus edulis/galloprovincialis	✓	✓	✓	✓	✓	✓	✓	✓
Anomia ephippium	✓	✓	✓	✓	✓	✓	✓	✓
Modiolarca sp.	✓	✓	✓	✓	✓	✓	✓	✓
Hiatella sp.	✓	✓	✓	✓	✓	✓	✓	✓
Crinoid sp.		✓	✓	✓	✓	✓	✓	
Crepidula fornicata$^{\text{NNS}}$		✓				✓	✓	
Detritivore and scavenger								
Amphipod spp.	✓	✓	✓	✓	✓	✓	✓	✓
Platyhelminthes sp.		✓	✓	✓	✓	✓	✓	✓

Petrolisthes sp.	✓	✓	✓	✓	✓	✓		✓
Pilumnus hirtellus	✓	✓	✓	✓	✓	✓	✓	✓
Omnivore								
Echinidae	✓							✓
Pycnogonid sp.			✓		✓		✓	
Caprella mutica$^{\text{NNS}}$		✓	✓	✓	✓	✓		✓
Caprella spp		✓	✓	✓	✓	✓	✓	✓
Carcinus meanus		✓	✓	✓	✓	✓	✓	✓
Predator								
Cancer pagurus				✓		✓		✓
Ophiuridae spp.		✓			✓		✓	
Corticated foliose								
Red fan sp.		✓	✓	✓	✓	✓	✓	✓
Rhodomenia delicatula		✓			✓		✓	
Ulva spp.		✓	✓	✓	✓	✓	✓	✓
Corticated macrophyte								
Strappy red sp.	✓		✓		✓	✓	✓	✓
Wirey red sp.		✓	✓		✓	✓		✓
Griffithsia sp.		✓	✓		✓	✓	✓	
Filamentous								
Chlorophyta spp. 1				✓		✓	✓	
Polysiphonia spp.	✓	✓	✓	✓	✓	✓	✓	✓
Ceramium spp.		✓	✓	✓	✓	✓	✓	
Leathery macrophyte								
Saccharina latissima			✓			✓	✓	✓
Undaria pinnatifida$^{\text{NNS}}$		✓	✓		✓	✓		✓
Fucus spp.		✓		✓	✓	✓	✓	
Ascophyllum nodosum		✓	✓			✓	✓	
Sargassum muticum$^{\text{NNS}}$		✓				✓	✓	
Total taxon richness	**33**	**66**	**58**	**56**	**65**	**65**	**64**	**52**

Appendix 4. Chapter 6 Supplemental Information

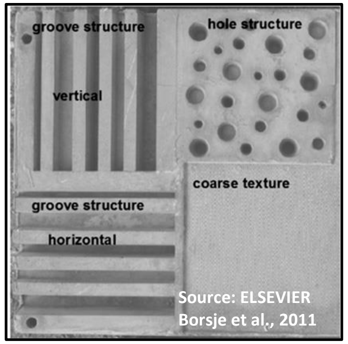
Table 1. Ecological engineering design details for **rock revetment (riprap), breakwaters and groynes made of armour stones or concrete units.** “Type” refers to the general type of eco-engineering. Within each “type”, designs are listed from small to large scale where applicable. Success of designs was based on the authors’ own interpretations. “DC or R” describes whether implementation of design can be during construction (“DC”) or added retrospectively (“R”). “Habitat” includes 3 pieces of key information about the environmental context in which the design was placed: a. intertidal or subtidal zones; b. sheltered or exposed habitats; c. type of shore where artificial structure was positioned. We include the climate where the design was tested next to the reference: *temperate, †subtropical, ‡tropical. The key reference is indicated by ^{KR}, and is the primary source of information for the design or study. The cost column includes only the cost of experiments, and costs were not scaled-up or standardised across studies. A dash (-) in any column indicates an unknown.

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
a. Precast habitat enhancement units	Precast rock pools (59 L) were incorporated into a coastal defence structure composed of rock armour.	To vertically extend habitat in which marine life can live. To increase number of species & live cover of marine life compared to adjacent boulders.	*Yes*: The design successfully mimicked natural high shore rock pool conditions. Live cover accounted for 89-100% of water-retaining sections.		DC	a. Intertidal (mean higher high water zone) b. - c. -	(Perkol-Finkel and Sella, 2015)*^{KR}, (ECOncrete Inc., 2019)$^{*/\dagger}$	-
	A precast concrete BIOBLOCK (1.5 x 1.5 x 1.1 m; 5.4 t) was placed within a rock armour (boulder) groyne in front of a seawall. It comprised multiple habitat types including rock pools, pits & ledges.	To test whether the BIOBLOCK would support more species compared to adjacent boulders.	*Yes*: BIOBLOCK supported over twice as many species as adjacent boulders (12 months).		R	a. Intertidal b. - c. Sandy shore	(Firth et al., 2014b)*^{KR}	Approx. £2000 for mould, concrete & delivery.

	Ecologically enhanced precast ECOncrete© Antifer (EA) units (1 m^3; 2.3-2.5 t) with complex surfaces including pits & crevices, composed of 3 different concrete matrices, were placed within a breakwater made of standard concrete Antifer (SA) units.	To test whether EA units would support more species, greater abundance of species & fewer invasive species compared to adjacent breakwater SA units.	*Yes*: The number of species & abundance of invertebrates & fish were higher. Numbers of invasive species were lower on EA compared to SA.	 ECOncrete	DC	a. Subtidal b. - c. -	(Sella and Perkol-Finkel, 2015)†[KR], (ECOncrete Inc., 2019)†	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
b. Artificial rock pools	Drill-cored rock pools of 2 depths (5 cm, 12 cm; both 15 cm diameter) were added on the horizontal surfaces of granite boulders on a breakwater.	To increase number of species in drill-cored rock pools compared to adjacent freely-draining rock surfaces on the boulders. To mimic natural rock pools on adjacent shores.	*Yes*: Artificial pools supported greater number of species compared to adjacent surfaces. Pools supported comparable number of species to natural rock pools; *No*: Artificial pools supported different communities of marine life compared to natural rock pools.	 A J Evans	R	a. Intertidal b. Exposed (seaward side of breakwater) c. Sandy shore	(Evans et al., 2016a)*^{KR}, (Firth et al., 2014b)*	Approx. £2000 which included 2 workers, 4 days & 40 drilled pools.
	In-filled cores with concrete to create rock pools (10 cm deep) on an intertidal breakwater. Cores were originally created by engineers to test boulder density.	To increase number of species in the pools compared to the adjacent free-draining surfaces of the boulders by providing habitat.	*Yes*: Pools supported significantly greater number of species than adjacent surfaces. *Note*: This was a demonstration project with few replicates.	 L B Firth	DC – cores drilled in boulders; R – cores then in-filled with concrete	a. Intertidal b. - c. Sandy shore	(Firth et al., 2014b)*^{KR}	< £3 per core. It took 2 workers approx. 2 h to in-fill 9 cores.
	Rock pools were created by pouring concrete into wave energy-dissipating units around buckets at high & low shore heights. These units were located along a causeway that had exposed & sheltered sides.	To compare number of species & functional groups among pools. Pools high on the shore & sheltered pools were expected to fail, whilst lower & exposed pools were expected to succeed.	*Yes*: Total number of species & functional groups: lower shore > upper shore. *No*: Mean number of species were similar between lower & upper.	 L B Firth	DC – cores drilled in boulders; R – cores then in-filled with concrete	a. Intertidal (low & high) b. Exposed & sheltered c. Mixed sandy & boulder shore	(Firth et al., 2016a)*^{KR}	Pools (80) were created using a digger, truck & cement mixer over 5 days; approx. €38 per pool.

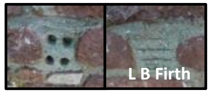
Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
c. Drilled pits	Pits (14 & 22 mm diameter; 25 mm depth) were drilled into vertical sides of 100 t wave-breaker units that were deployed on a breakwater. Each pit was drilled at a slight angle to retain water. Plots of equivalent area with no pits were used as controls.	To increase number of species in & around pits compared to control plots with no drilled pits.	*Yes*: Greater number of species in & around pits compared to control plots.		R – after blocks were cast but during the hardening process when concrete was still soft	a. Intertidal b. Exposed (seaward side of breakwater) c. Artificial boulders surrounded by deep water	(Firth et al., 2014b)*, (Jackson, 2015)*^{KR}	This is a low-cost option. University staff drilled 100 pits in 1 h.
d. Modifying slope	Replaced a structure composed of rock armour with a pocket beach comprising pebbles & cobbles (approx. 100 m).	To provide a case study for increasing habitat for invertebrate animals & larval & juvenile fish.	*Yes*: Greater number of species of invertebrates, & increased densities of larval fish & juvenile salmon within the pocket beach. *Note*: As this was a case study, there was only one replicate.		R	a. Intertidal b. - c. Shore composed of mixed sand & gravel sediments	(Toft et al., 2013)*^{KR}	This design was part of a larger project that consisted of reinforcement of existing seawall & associated habitat enhancements (Total = US $5.5 mil).

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
e. Precast panels	Concrete panels (30 x 30 cm) were attached to horizontal & vertical surfaces on an intertidal breakwater. Panels had 6 large pits (30 mm diameter, 20 mm depth), 13 small pits (15 mm diameter, 20 mm depth) or 4 large & 4 small pits. Smooth panels were used as controls.	To test if artificially enhanced complexity at a scale of < 10 cm could increase number of species compared to controls.	*Yes*: Total number of species was significantly higher on panels with pits compared to control panels.	 P S Moschella	R	a. Intertidal (mean tide level) b. Exposed c. Sandy shore	(Moschella et al., 2005)*^{KR}, (Witt et al., 2012)*	-
	Concrete panels (75 x 30 cm) divided into 6 sections (25 x 25 cm) were attached to a breakwater composed of 22- & 30-tonne blocks embedded in asphalt. The 6 sections (treatments) varied in geometric shape & texture: (1) horizontal grooves, (2) vertical grooves, (3) pits, (4) coarse texture, (5) fine texture & (6) smooth texture.	To investigate colonisation by marine life of panels consisting of different geometric shapes & textures.	*Yes*: Initially, sections with pits & fine & coarse textures supported more green algae than the sections with smooth texture. Sections with grooves & pits supported mussels & winkles. In general, panels in the low & middle intertidal were colonised quicker than panels in the high intertidal.	 Source: ELSEVIER Borsje et al., 2011	R	a. Intertidal (low, mid, high) b. Sheltered & exposed c. -	(Borsje et al., 2011)*^{KR}	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
f. Living shorelines/hybrid designs	'Hybrid stabilization.' This is a technique that converts a degraded intertidal salt marsh & associated subtidal areas to a sand fill with a planted marsh. A stabilising structure (low-profile stone sill) is constructed parallel to & on the channel side of the marsh.	To investigate changes in biological community structure, marsh plants & sediment of marsh sills were compared to natural fringing marshes, unvegetated tidal flats & riprap revetments.	*Partially*: Results varied depending on site & tidal zone (intertidal versus subtidal). Marsh sills lagged in primary production & biogeochemical processes by 5-10 yrs. In general, however, marsh sills were found to be a viable option for erosion mitigation & enhancing habitat & water quality.	 K Duhring, CCRM-VIMS	DC	a. Intertidal & shallow subtidal b. Sheltered c. Salt marsh	(Bilkovic and Mitchell, 2013)*^{KR}	-
	Mangrove seedlings were transplanted on the landward side of breakwaters. Breakwaters dissipated wave energy & promoted sedimentation, which facilitated mangrove growth.	To stabilise the coastline for mangrove seedling settlement & establishment. This should promote mangrove development & protect the eroding coastline.	*Yes*: The presence of the breakwater resulted in sediment deposition, & substrate elevation increased to a height appropriate for mangrove growth.	 R Hashim	DC	a. Intertidal b. - c. Mud flat & mangrove fringe	(Hashim et al., 2010)‡^{KR}, (Kamali et al., 2010)‡	Approx. US \$142,000 ha^{-1} which included restoration, training, monitoring, construction & maintenance.
	Mangroves were reared in a nursery (15 months) & then transplanted to sheltered & exposed field sites within armoured concrete cultivator pots.	To test a new technique for the restoration of mangroves in exposed environments.	*Partially*: Mortality rates after 2 direct hurricane hits was 57% & 26% at the exposed & sheltered sites, respectively. The fully sheltered control mangroves suffered 19% mortality.	 J Krumholz	-	a. Intertidal b. Exposed & sheltered c. Mud flat & mangrove fringe	(Krumholz and Jadot, 2009)‡^{KR}	-

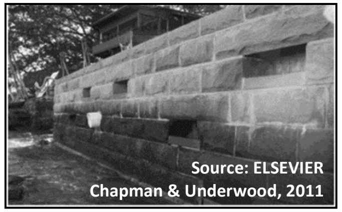
Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
g. Transplant	Transplanted juveniles of a threatened canopy-forming algae from degraded sites – where severe habitat loss was occurring – onto a breakwater (landward & seaward sides), natural habitat (boulders > 10 m^3) & native habitat (area from which juveniles were initially collected). Algae attached to small, fragmented, loose boulders were collected from the degraded sites & epoxied to substrate in the new habitats.	To test establishment success of algae on natural habitats & on landward (sheltered) & seaward (exposed) sides of breakwaters compared to degraded sites.	Greater mortality of algae on the seaward side compared to the landward side of the breakwater. Greater mortality (nearly 100%) in the degraded native sites compared to the breakwater & natural habitat. *Note*: If implementing this method on a large scale, consider cultivating the target species in the laboratory.		R	a. Subtidal b. Sheltered (landward) & exposed (seaward) c. Degraded sites – rocky shore; transplanted sites – breakwater on sandy shore	(Perkol-Finkel et al., 2012)†^{KR}, (Ferrario et al., 2016)†	-
h. Reviews	(Subramanian et al., 2008; Firth et al., 2014b; Dafforn et al., 2015a; Dafforn et al., 2015b; Dyson and Yocom, 2015; Dafforn et al., 2016; Firth et al., 2016b; Narayan et al., 2016; Mayer-Pinto et al., 2017; Munsch et al., 2017)							

Table 2. Ecological engineering design details for **vertical and sloping seawalls.** “Type” refers to the general type of eco-engineering. Within each “type”, designs are listed from small to large scale where applicable. Success of designs was based on the authors’ own interpretations. “DC or R” describes whether implementation of design can be during construction (“DC”) or added retrospectively (“R”). “Habitat” includes 3 pieces of key information about the environmental context in which the design was placed: a. intertidal or subtidal zones; b. sheltered or exposed habitats; c. type of shore where artificial structure was positioned. We include the climate where the design was tested next to the reference: *temperate, †subtropical, ‡tropical. The key reference is indicated by [KR], and is the primary source of information for the design or study. The cost column includes only the cost of experiments, and costs were not scaled-up or standardised across studies. A dash (-) in any column indicates an unknown.

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
a. Pits, grooves & crevices	Small (12 mm diameter, 10 mm depth) & large (24 mm diameter, 10 mm depth) pits were drilled into a basalt seawall (25 x 25 cm areas). Evenly spaced pits were drilled in 2 density treatments: high density (16 pits) & low density (8 pits).	To increase abundance of overexploited limpets in & around drilled pits compared to control areas of a seawall.	*Yes*: 10x as many limpets were observed in & around pits. Seven years after installation, limpets were more abundant in all enhanced treatments except the small pit diameter & lesser pit density.	 G Martins	R	a. Intertidal b. - c. Boulder shore	(Martins et al., 2010)*[KR], (Martins et al., 2016)*	< €600 total. The drilling took 5 days (1 worker).
	Six treatments of pits were drilled into a seawall: (i) no pits, (ii) 16 small pits (2.5 cm diameter, 0.5 cm deep), (iii) 16 large pits (5 cm diameter, 0.5 cm deep), (iv) 4 large pits, (v) 16 grooves (1 cm wide, 5 cm long, 0.5 cm deep), (vi) mixture of grooves, small & large pits.	To compare abundance of sessile (attached) & mobileinvertebrates & algae among: (1) pit sizes, (2) pit shapes, (3) experimental pits compared to mixture of habitat, (4) exp’l pits compared to control areas of without pits.	*Yes*: Small & large pits & grooved habitats supported higher density of chitons, & grooves & small pits supported greater numbers of limpets compared to controls during some times of sampling. Over time, however, effects lessened as the pits were filled with sessile species.	 Source: ELSEVIER Chapman & Underwood,	R	a. Intertidal b. Sheltered c. -	(Chapman and Underwood, 2011)*/† [KR]	-
	Wet mortar was manipulated to create grooves, pits & crevices in a newly constructed seawall.	To increase number of species compared to untreated areas of mortar.	*Yes*: Crevices supported greater number of species compared to grooves, pits & control plots.	 L B Firth	DC	a. Intertidal b. - c. Sandy shore	(Naylor et al., 2012; Firth et al., 2014b)*, (Jackson, 2015)* [KR]	Pits and grooves were created while mortar was still wet.

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
b. Precast panels	Concrete panels (400 x 400 x 32 mm) of 2 levels of complexity (complex & simple) comprised of 4 sub-panels (200 mm x 200 mm x 32 mm) each with different structure types (holes, towers, grooves, darts) were deployed at 2 heights on seawalls at 2 sites. The software program, *CASU*, was used to create the panels while controlling for surface area. Granite panels were used as controls.	To test the independent effects of complexity & different structural component types among treatments & controls in order to increase number of species, abundance & community composition.	*Yes*: Complex panels supported greater number of species & different biological community composition independent of surface area compared to simple panels & controls. Panels with holes supported greatest abundance & number of species. Structure type had an effect on number of species that was independent of complexity.		R	a. Intertidal b. 2 sites: 1 sheltered; 1 exposed c. Sandy shore	(Loke et al., 2014)‡, (Loke and Todd, 2016)‡^{KR}	-
	Three treatments of habitat enhancement test panels (1.5 x 2.3 m; flat, finned, stepped) with 2 textures (smooth & cobbled) were added to a seawall.	To compare number & abundance of species among the test panels.	*Yes*: The finned design & the cobbled texture panels supported greater species abundance. This experiment functioned as the foundation study for construction of seawall panels with added benches in Seattle, WA, USA (seen in photo).		R – test panels DC – seawall panels & benches	a. Intertidal b. - c. -	(Cordell et al., 2017)* ^{KR}	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
c. Artificial rock pools	Precast concrete “Vertipools” (5 L) were attached to a seawall.	To promote recruitment of species that are typically missing from seawalls by adding water-retaining features.	*Yes*: Additional species (incl. species of crabs & blennies) were recorded in the Vertipools that were not present on the seawall & within natural pools. Overall, the Vertipools supported greater number of species than the seawall. *Note*: Vertipools should only be affixed to seawalls in sheltered environments.		R	a. Intertidal (mid & high) b. - c. -	(Artecology)*^{KR}, (Hall, 2018)*	£500-1000/ unit for construction & installation depending on environment.
	Precast concrete flowerpots (6 L, 10 L) were fixed to seawalls. The pots were submerged at high tide & retained water during low tide.	To support species found in natural rock pools but which are typically missing from seawalls by incorporating water-retaining features into the seawall. To compare species abundance between seawalls with pots & seawalls with no pots.	*Yes*: 25 species colonised pots that were not found on the adjacent seawall. Pots also supported greater live cover & density of marine life compared to established assemblages on seawalls. Shallower pots & those at mid-shore supported greater abundances & number of species than deeper pots at high shore levels (7 months). At certain times, some fish were more abundant at the seawall with flowerpots, but results varied throughout the year.		R	a. Intertidal (mid & high) b. - c. -	(Browne and Chapman, 2011)*/†^{KR}, (Browne and Chapman, 2014; Morris et al., 2017a; Morris et al., 2018b)*/†	AU $300 per flowerpot for manufacture & installation.

	Addition of round-bottom cavities into a seawall by using sandbags in place of blocks during wall repairs, after which, bags were removed. Cavities held water at low tide.	To provide habitat for larger species of organisms that are rare on featureless seawalls by incorporating water-retaining features.	*Yes*: Increased rock pool species that are not normally found on featureless seawalls (i.e., octopuses & urchins).	 Source: ELSEVIER Chapman & Underwood, 2011	DC (repairs)	a. Intertidal b. - c. -	(Chapman and Underwood, 2011)$^{*/\dagger \mathrm{KR}}$	-
	Omitted sandstone blocks during seawall construction to create cavities (30 x 30 x 60 cm) with outer lips (5 cm high barrier) to retain water	To increase abundance & number of species. To compare number of species in cavities to external façade of wall & within natural pools.	*Yes*: Greater number of species of algae & sessile & mobile invertebrates in cavities at all tidal heights compared to external façade, & expanded species distribution over a greater tidal range. The cavities also provided	 Source: ELSEVIER Chapman & Underwood, 2011	DC	a. Intertidal (low, mid, high) b. - c. -	(Chapman and Blockley, 2009)$^{*/\dagger \mathrm{KR}}$, (Chapman and Underwood, 2011)$^{*/\dagger}$	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
d. Modified seawall slope & seawall removal	Replaced a vertical metal wall with a stepped slope (vertical & horizontal surfaces) of rocks to reduce the slope.	To increase abundance & number of species in an industrial area.	*No*: No observed increase in abundance & number of species, but did observe more species on vertical compared to horizontal stepped surfaces.		DC	a. Intertidal b. Sheltered c. -	(Chapman and Underwood, 2011)*/†^{KR}	-
	Replaced vertical seawalls with sloping unconsolidated boulders in an industrial area. A large horizontal area at the low tide level was included at 2 of these seawalls.	To increase slope & expanse of the intertidal zone. To compare abundance & number of species on the slope of the unconsolidated seawall to the original, & to compare abundance & number of species on a horizontal area to a sloping area over the same tidal height.	*No*: No observed increase in abundance & number of species. This was a sheltered & biodiversity-poor shore with high levels of human disturbance. This design should work if it can be done in a more exposed area, as it offers rare boulder habitat.		R	a. Intertidal b. Sheltered c. -	(Chapman and Underwood, 2011)*/†^{KR}	-
	A low-terrace habitat bench (approx. 290 m) was placed in front of an existing seawall. The bench was composed of coarse rocky substrate.	To provide a case study for increasing habitat for invertebrates, & larval & juvenile fish.	*Yes*: The habitat bench area supported greater number of species of invertebrates, & increased densities of larval fish & juvenile salmon. As this was a case study, there was only one replicate.		DC	a. Intertidal b. - c. Mixed sand & gravel sediments	(Toft et al., 2013)*^{KR}	-
	Complete seawall removal (including sloping riprap & gabion baskets). Replaced with a gradual beach slope composed of gravel & cobble sediment as well as riparian vegetation in the upland. A nearby natural beach was used as a control.	To measure response of macroinvertebrates at 3 tidal heights (mid, upper, supratidal) post restoration, & provide a case study for future seawall removal & beach restoration projects.	*Yes*: Macroinvertebrates in the area directly affected by seawall removal (supratidal) responded more positively than those in the mid- & high intertidal. Restored beach functions as & resembles a natural beach.	**Before** **After** 		a. Intertidal (mid, high, supratidal [splash zone]) b. - c. Sandy shore	(Toft et al., 2014)*^{KR}	-

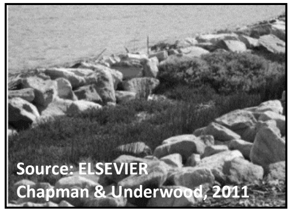
Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
e. Transplant	Transplanted hard & soft corals & sponges onto a seawall. Animal fragments were collected from local reefs & reared in a mariculture facility (1 month) & then self-attachment to cement tiles was facilitated for the soft corals & sponges (hard corals were attached directly to seawall). Cement tiles were then attached to a seawall with marine epoxy.	To test survivorship of corals & sponges after transplantation onto seawalls.	*Yes*: Results were mixed, but generally, massive & encrusting species were more successful at establishing on the seawall, & these species provided food & shelter to fish & gastropods. *Note*: Water quality may affect survival of sensitive coral species.	 L Ng	R	a. Intertidal (low) b. - c. -	(Ng et al., 2015)‡^{KR}	-
f. Gardening	A seawall was partitioned into 2 sections, & within it, a salt marsh was planted as a horizontal garden.	To observe if a salt marsh could persist & grow on a seawall, & increase abundance & number of species. However, there were no natural marshes in the area for comparison.	Many salt marsh plants continued to grow after planting, but little monitoring has been conducted since planting.	 Source: ELSEVIER Chapman & Underwood, 2011	R	a. Intertidal b. - c. -	(Chapman and Underwood, 2011)$^{*/\dagger KR}$	-
g. Placement in front of seawall	No formal study to date; this is a suggested intervention. Artificial boulders of varying boulder sizes can be placed in front of a seawall if preserving the structural integrity of the seawall is the objective.	Boulder fields in nature provide habitat for marine life. If enhanced through addition of gaps, crevices or grooves, or by infilling density cores (see Firth et al., 2014b), artificial boulders could function to support a wider	*Note*: Boulders are typically constructed to be very smooth, which offers poor habitat for marine life. This design increases the footprint of the structure, thus	 K A O'Shaughnessy	-	a. Intertidal & subtidal possible b. Typically used on exposed	(Pister, 2009)*, (Chapman, 2012)$^{*/\dagger}$, (Liversage et al., 2017)$^{*/\dagger KR}$	-
h. Reviews	(Chapman and Underwood, 2011; Dafforn et al., 2015a; Dafforn et al., 2015b; Dyson and Yocom, 2015; Dafforn et al., 2016; Firth et al., 2016b; Mayer-Pinto et al., 2017; Munsch et al., 2017)							

Table 3: Ecological engineering design details for **over-water structures and their associated supporting pilings.** "Type" refers to the general type of eco-engineering. Within each "type", designs are listed from small to large scale where applicable. Success of designs was based on the authors' own interpretations. "DC or R" describes whether implementation of design can be during construction ("DC") or added retrospectively ("R"). "Habitat" includes 3 pieces of key information about the environmental context in which the design was placed: a. intertidal or subtidal zones; b. sheltered or exposed habitats; c. type of shore where artificial structure was positioned. We include the climate where the design was tested next to the reference: *temperate, †subtropical, ‡tropical. The key reference is indicated by ^{KR}, and is the primary source of information for the design or study. The cost column includes only the cost of experiments, and costs were not scaled-up or standardised across studies. A dash (-) in any column indicates an unknown.

Type	Specific Design	Intended Outcome	Successful?	Photograph		Habitat	Ref	Cost
a. Light-penetrating designs	Over-water platforms (2.4 x 3.7 m) made from fibreglass grating material were constructed 1.2 & 1.5 m above mean high water.	To compare the effects of platform height on seagrass survival by measuring light penetration compared to an unshaded control.	*Yes*: Although fibreglass grating allowed significantly less light to penetrate compared to the unshaded control, grating material at both heights promoted sufficient light penetration for seagrass persistence. Current regulatory guidelines now recommend construction of piers over seagrass beds be made with fibreglass grid materials.	 Source: WRAP Shafer & Robinson, 2001	DC	a. 1.2 & 1.5 m above mean high water b. Sheltered c. Positioned above a sandy shore	(Shafer and Lundin, 1999)†^{KR}, (Shafer and Robinson, 2001)†, (Shafer, 2002)†	-
	®Sunlight Direct fibre optic lighting system was installed on one side of a ferry terminal (105 x 36 m). Each light cable illuminated a 1.5 x 7 m area of the water. The system collected ambient natural light from above & transmitted it to below the terminal.	To alleviate dock edge shadow so that juvenile salmon would swim under the terminal.	*Yes*: When artificial light was used to mitigate dock edge shadow, salmon swam closer to the dock. *No*: When artificial light was used on a non-shaded area of water, salmon avoided the area. *Note*: Artificial light may negatively impact other marine life (see Gaston et al., 2013; Davies et al., 2014).	 Source: ELSEVIER Ono & Simenstad, 2014	R	a. - b. - c. -	(Ono and Simenstad, 2014)*^{KR}	-

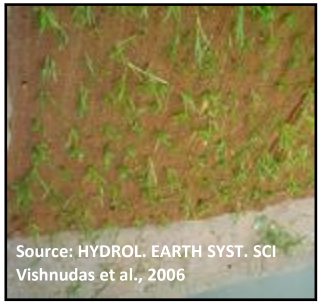
Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
a. Light-penetrating designs (continued)	Conducted field trials with off-the-shelf products (SunTunnel©, deck prisms, a metal halide greenhouse light, metal gratings) that promote light passage through over-water structures.	To determine alternative means to increase light intensity under ferry terminals by measuring minimum photosynthetically active radiation for eelgrass primary production.	*Yes*: If built ≤ 3 m above eelgrass, all products allowed enough light to penetrate for eelgrass growth. Highest to lowest light-penetrating material: metal gratings, SunTunnel©, metal halide greenhouse light, dock prisms.	 Source: WA STATE DPT. OF TRANSPORTATION Blanton et al., 2002	DC	a. Approx. 3 m above mean water level b. - c. -	(Blanton et al., 2002)*^{KR}	-
	Light-penetrating walkways made of glass brick were installed along a waterfront area as part of a larger ecosystem restoration project.	To allow enough light to pass through an overwater structure to facilitate improvement to a salmon migration corridor & increase ecosystem-wide productivity.	At the time of writing, this design was in the construction phase.	 J Toft	DC	a. - b. - c. -	(Cordell et al., 2017)*^{KR}	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
b. Pier piling enhancements	Synthetic, free-hanging ropes (“pole-hulas”, 55 cm long, 6 cm diameter) attached to high-quality canvass bands were wrapped around metal & wooden pier pilings.	To test techniques to increase abundance & number of species, & reduce invasive species abundance on pier pilings.	*Yes*: Abundance & number of species increased on the experimental pier pilings. The invasive oyster did not recruit to the pole hulas. *Note*: This design may potentially add plastic to the environment.	 P Paalvast	R	a. Intertidal & subtidal b. - c. -	(Paalvast et al., 2012)*^{KR}	-
	Ecological concrete encasement ("jacket“) positioned around deteriorating pier pilings. Jackets were composed of concrete with added texture to the surface, which has previously shown to enhance recruitment & growth of marine life.	To increase live cover on ecological jackets compared to control fibreglass jackets. To incorporate ecologically-sensitive designs into construction of an urban waterfront structure.	*Yes*: Jackets showed 70-100% live cover of marine life compared to 20-50% on controls (3 months). Jackets showed 90-100% live cover of marine life compared to 40-85% on controls (14 months).	 ECOncrete	R	a. Intertidal b. - c. -	(Perkol-Finkel and Sella, 2015)*^{KR}, (ECOncrete Inc., 2019)*$^{/†}$	-
c. Reviews	(Shafer, 2002; Dyson and Yocom, 2015; Geist and Hawkins, 2016; Munsch et al., 2017)							

Table 4: Ecological engineering design details for flood defence and erosion mitigating structures in **tidal rivers.** "Type" refers to the general type of eco-engineering. Within each "type", designs are listed from small to large scale where applicable. Success of designs was based on the authors' own interpretations. "DC or R" describes whether implementation of design can be during construction ("DC") or added retrospectively ("R"). "Habitat" includes 3 pieces of key information about the environmental context in which the design was placed: a. intertidal or subtidal zones; b. sheltered or exposed habitats; c. type of shore where artificial structure was positioned. We include the climate where the design was tested next to the reference: *temperate, †subtropical, ‡tropical. The key reference is indicated by ^{KR}, and is the primary source of information for the design or study. The cost column includes only the cost of experiments, and costs were not scaled-up or standardised across studies. A dash (-) in any column indicates an unknown.

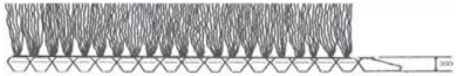
Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
a. Wall manipulations	Green wall modules: Plastic modules filled with soil & faced with coir (coconut fibre) & wire mesh. Designed for use on steep intertidal embankment walls.	To increase vegetative cover along intertidal embankment walls.	*Yes*: Successful recruitment & colonisation of plants in the modules. Greatest colonisation was seen in more sheltered locations. *Note*: If possible, use stainless steel brackets, as these have a longer lifetime & less risk of dislodgement & plastic pollution.		R	a. Intertidal b. - c. -	(Francis, 2009)*, (Francis et al., 2015)*^{KR}	< £4000 for 40 modules.
	Timber fenders & ledges were installed on sheet piling crenellations.	To trap more sediment & seeds compared to an adjacent concrete river wall.	*Yes*: Fenders & ledges trapped seeds & subsequently supported plant communities typical of natural intertidal rivers.		R	a. Intertidal b. - c. -	(Steele, 1999)*^{KR}, (Francis et al., 2008)*	-

	Coir roll (coconut fibres) seed traps were affixed to flood defence walls at 12 sites. At each site, 15 coir rolls were attached in horizontal & vertical orientations. Rolls were installed Jun/Jul 2008 & removed Jan/Feb 2009.	To determine the number of species of seeds caught in the traps: (1) at different trap heights; (2) downstream versus upstream; (3) vertical versus horizontal orientation; & (4) compared to seeds spontaneously colonising the wall.	*Yes*: Number of species of seeds was higher in coir rolls compared to river wall, & some of the seeds had germinated. Number of species of seeds was higher in coir rolls at lower tidal height & further upstream. No difference in number of species of seeds was observed between vertical & horizontal trap orientations. *Note*: If possible, use stainless steel mesh, as it has a longer lifespan & less risk of dislodgement & plastic pollution.	 S P G Hoggart	R	a. Intertidal (2 levels around mean high water) b. - c. -	(Hoggart and Francis, 2014)*^{KR}	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
b. Suggested interventions from other systems	Along a pond embankment, 3 treatments were deployed: (1) coir (coconut fibre) geotextile with planted grass, (2) coir geotextile alone & (3) control plot. Although this design was within a pond, it could be applied to low-energy tidal river embankments.	To determine the effectiveness of coir geotextiles for slope protection & to reduce soil erosion, increase vegetation growth & increase soil moisture compared to non-coir control.	*Yes*: Coir geotextiles planted with grass stabilised slopes, reduced erosion, promoted grass growth & retained moisture & nutrients compared to control plot. Coir geotextile alone had similar effects but not as significant.	 Source: HYDROL. EARTH SYST. SCI Vishnudas et al., 2006	R	a. Not tidally-influenced b. Sheltered c. Pond embankment, but application for tidal river embankment possible in low-flow areas	(Vishnudas et al., 2006)†/‡KR	-
	Vetiver – a tropical clumping grass that can filter sediment, strengthen soil & mitigate erosion – was planted on an eroding road embankment. Geo-Jute – a biodegradable net made of jute (vegetable fibre) – was applied over the vetiver grass because it prevents the displacement of soil & it remains wet for several days after absorption, helping the growth of vegetation. An area without the Geo-Jute application was used as the control.	To increase growth of vetiver & decrease the rate of erosion in the areas treated with Geo-Jute compared to the areas without Geo-Jute.	*Yes*: Geo-Jute prevented the erosion of soil before vetiver growth. With time, vetiver successfully grew at the sites with Geo-Jute.	 greenfix.co.uk	R	a. Not tidally-influenced b. N/A c. Road embankment, but application for tidal river embankment possible in low-flow areas	(Islam, 2013)†/‡KR, (Greenfix)*	Application of vetiver & Geo-Jute for erosion mitigation is less expensive than traditional erosion control techniques.

c. Floating rafts	Floating island rafts can be made from a variety of materials – here a recycled cable drum (approx. 2 m^2) was used. Rafts can be moored in protected locations in tidal river channels & urban waterways.	To provide a surrogate habitat for riparian plant & animal communities in urban systems.	*Yes*: Plant & animal species successfully recruited to & colonised the rafts. Also shown to function as bird habitat.	 C Cockel	R	a. Intertidal b. - c. -	(Francis et al., 2008)*^{KR} See (Hancock, 2000)* for bird habitat & (Yellin, 2014)* for fish habitat	< £1000 per raft.
d. Reviews	(Radspinner et al., 2010; Environment Agency, 2013; Dyson and Yocom, 2015; Geist and Hawkins, 2016; Natural Environment Research Council, 2017; The River Restoration Centre, 2019)							

Table 5: Ecological engineering design details for **offshore structures.** “Type” refers to the general type of eco-engineering. Within each “type”, designs are listed from small to large scale where applicable. Success of designs was based on the authors’ own interpretations. “DC or R” describes whether implementation of design can be during construction (“DC”) or added retrospectively (“R”). “Habitat” includes 3 pieces of key information about the environmental context in which the design was placed: a. intertidal or subtidal zones; b. sheltered or exposed habitats; c. type of shore where artificial structure was positioned. We include the climate where the design was tested next to the reference: *temperate, †subtropical, ‡tropical. The key reference is indicated by ^{KR}, and is the primary source of information for the design or study. The cost column includes only the cost of experiments, and costs were not scaled-up or standardised across studies. A dash (-) in any column indicates an unknown.

Type	Specific Design	Intended Outcome	Successful?	Photograph		Habitat	Ref	Cost
			Planning & Existing					
a. Tested interventions	Large pits (12 x 15 x 30 cm) were created in foundation units of wave energy structures (3 m diameter, 1 m height, 10 t) at 2 levels. Colonising biota in pits were compared to control foundations without pits & adjacent sandy bottom.	To explore the potential for enhancing the abundance of associated fish & crustaceans at the bottom of wave energy structures.	*Partially*: There was significantly higher abundance of edible crabs on the foundation units, but no noticeable differences in abundance of mobile organisms, & a negative effect on abundance of spiny starfish compared to adjacent soft bottom sediment. Presence of pits on the units had no effect on fish species.	 Source: ELSEVIER Langhamer & Wilhelmsson,		a. Subtidal b. - c. Sandy bottom	(Langhamer and Wilhelmsson, 2009)*^{KR}	-
b. Suggested interventions	No formal study to date; this is a suggested intervention. Synthetic fronds could be secured around the base of a turbine.	The primary function can be to aggregate sediment around the turbine for support, & then secondarily function as habitat that mimics seagrass for fish & invertebrate.	-	 Source: WILEY INTERSCIENCE Wilson & Elliot, 2009	-	a. Subtidal b. - c. -	(Wilson and Elliott, 2009)^{KR}	-

c. Enhance target species	One-tonne tetrapod units (4-pronged concrete units) were deployed 300 m offshore at 14 m depth on a mixed sand & gravel bottom where no seaweeds were naturally growing.	To form beds of a brown algal species where it was not naturally growing.	*Yes*: Initial densities of the algae were estimated at 200 individuals m^{-2} (approx. 6 months). Long-term measurements showed the algae were growing on the seafloor adjacent to the tetrapods (24 months), & after 48 months, standing crop was similar to natural densities in nearby areas.		-	a. Subtidal b. - c. Mixed sand & gravel	(Watanuki and Yamamoto, 1990)$^{*/\dagger KR}$	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
Planning & Existing								
d. Coastal interventions for potential offshore application	Concrete units typically used to create submerged nearshore artificial reefs (e.g., Reefballs™, www.reefball.org) have the potential to be used as scour protection around turbines. Reefballs™ (1.2-1.3 m high; 1600-2000 kg) were deployed in nearshore waters (1.6-2.0 m depth) to create a submerged breakwater.	To trial a new application for Reefballs™ as shoreline stabilisation & habitat for marine life.	*Yes*: The Reefball™ breakwater withstood hurricanes (categories 3 & 5) without a single unit moving, & created habitat for marine life. *Note*: To increase resistance to movement, Reefballs™ have been affixed to the seafloor by: (1) driving rods/pilings through the units & into the seafloor; & (2) attaching the units to an articulated mat.	 reefball.org	-	a. Intertidal & subtidal possible b. - c. Sandy bottom	(Harris, 2009)[†/‡KR], (Reef Ball Foundation Inc, 2017)[†/‡], (ARC Marine, 2019)*	-
	No formal study to date; this is a suggested intervention. Tetrapods (4-pronged concrete units), dolos units (unreinforced concrete & steel fibres) & other precast energy dissipating units have the potential to be used as scour protection around turbines.	If enhanced through addition of pits, crevices or grooves, or using eco-friendly concrete, these units could function to support a wider range of marine life.	*Note*: Tetrapods are typically constructed to be very smooth, which offers poor habitat for marine life.	 L B Firth	-	a. Intertidal & subtidal possible b. Typically used on exposed shores c. Typically used on sandy or mixed sand & gravel bottom	(Wilson and Elliott, 2009)[KR]	-

	No formal study to date; this is a suggested intervention. Artificial boulders of varying boulder sizes can be used as scour protection around turbines.	Boulder fields in nature provide habitat for marine life. If enhanced through addition of gaps, crevices or grooves, or by infilling density cores (see Firth et al., 2014b), artificial boulders could function to support a wider assemblage of marine life.	*Note*: Boulders are typically constructed to be very smooth, which offers poor habitat for marine life.	 K A O'Shaughnessy	-	a. Intertidal & subtidal possible b. Typically used on exposed shores c. -	(Pister, 2009)*, (Chapman, 2012)*/†, (Liversage et al., 2017)*/†KR	-

Type	Specific Design	Intended Outcome	Successful?	Photograph	DC or R?	Habitat	Ref	Cost
				Decommissioning				
e. Create artificial reefs	Rigs-to-reefs program in the Gulf of Mexico provides decommissioning options for oil & gas platforms that have ceased production: (1) tow to reef site, (2) topple-in-place or (3) partially remove the platform.	To provide habitat for marine organisms & preserve habitat for established marine life on the platform.	*Yes*: This method has been in effect in Louisiana & Texas waters since 1986 & 1991, respectively. As of 2006, the Louisiana Artificial Reefs Program (LARP) has utilised > 120 decommissioned oil & gas platforms to create > 83 artificial reefs. Reefs support almost all major invertebrate groups, which, in turn, support fish & other mobile species.	 Source: NATIONAL MARINE FISHERIES SERVICE—GALVESTON	DC	a. Subtidal b. - c. Typically sandy bottom	(Dauterive, 2000)†, (Kaiser, 2006a)†^{KR}, (Kaiser and Pulsipher, 2005)†^{KR}, (Louisiana Rigs to Reefs Program)†	Cost to create a reef from a platform is typically lower than commissioning transport for shore disposal.
	The concept of "renewables-to-reefs" is currently in the planning stages.	To mitigate potential negative effects of a "renewables-to-reefs" program on the deep-sea environment while providing habitat for benthic fish & invertebrates.	-	-	R	a. Subtidal b. - c. -	(Macreadie et al., 2011)^{KR}, (Smyth et al., 2015)^{KR}	-
f. Reviews	(Kaiser and Pulsipher, 2005; Ekins et al., 2006; Wilhelmsson et al., 2010; Lacroix and Pioch, 2011; Macreadie et al., 2011; Callaway et al., 2017)							

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