2016-11-25

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http://hdl.handle.net/10026.1/8025

10.1201/9781315368597
Oceanography and Marine Biology: an annual review
Aberdeen University Press

Oceanography and Marine Biology: An Annual Review, 2016, **54**, 189-262
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Taylor & Francis

OCEAN SPRAWL: CHALLENGES AND OPPORTUNITIES FOR BIODIVERSITY MANAGEMENT IN A CHANGING WORLD

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The last few decades have seen rapid proliferation of hard artificial structures (e.g., energy infrastructure, aquaculture, coastal defences) in the marine environment: ocean sprawl. The replacement of natural, often sedimentary, substrata with hard substrata has altered the distribution of species, particularly non-indigenous species, and can facilitate the assisted migration of native species at risk from climate change. This has been likened to urbanization as a driver of global biotic homogenization in the marine environment—the process by which species invasions and extinctions increase the genetic, taxonomic, or functional similarity of communities at local, regional, and global scales. Ecological engineering research showed that small-scale engineering interventions can have a significant positive effect on the biodiversity of artificial structures, promoting more diverse and resilient communities on local scales. This knowledge can be applied to the design of multifunctional structures that provide a range of ecosystem services. In coastal regions, hybrid designs can work with nature to combine hard and soft approaches to coastal defence in a more environmentally sensitive manner. The challenge now is to manage ocean sprawl with the dual goal of supporting human populations and activities, simultaneously strengthening ecosystem resilience using an ecosystem-based approach.

Introduction: Context and background

Human population growth is accelerating and is forecast to exceed 9.5 billion by 2050 (Bloom 2011, Gerland et al. 2014). Increasing demand for natural resources promotes further industrialization (Long et al. 2009) and leads to continued anthropogenic greenhouse gas emissions (Moss et al. 2010, van Vuuren & Riahi 2011). Burgeoning human populations drive the exploitation of the ocean's energy and food resources through the construction of oil and gas platforms, marine renewable energy installations, and proliferation of aquaculture (Chapman & Underwood 2011, Firth & Hawkins 2011). Furthermore, increased use of transport hubs and global shipping is increasing the connectivity of coastal cities. The burning of fossil fuels continues to raise greenhouse gas levels, driving global climate change and sea-level rise, with the prospect of more extreme climatic events, including increased storm intensity and frequency (summarized in Intergovernmental Panel on Climate Change [IPCC] 2013, 2014).

Much of the recent human population growth is in vulnerable coastal regions (Small & Nicholls 2003, Martínez et al. 2007), a trend predicted to continue. In conjunction with rising (Nicholls & Cazenave 2010) and stormier (Bader et al. 2011) seas, our coastlines have become increasingly 'hardened' (Airoldi et al. 2005a, Moschella et al. 2005, Bulleri & Chapman 2010, Chapman & Underwood 2011, Firth et al. 2013a) with the proliferation of coastal defences. This is an adaptation option (*sensu* IPCC 2014) that has been adopted worldwide to protect the growing coastal population and its property, transport infrastructure, industry and commerce, as well as valuable amenity and recreational areas (for review, see chapters in Burcharth et al. 2007, Zanuttigh et al. 2014).

In this review, we discuss current evidence and thinking on biodiversity and ecosystem responses to global drivers of change, with a focus on recent rapid climate change and its interaction with regional and local impacts due to 'ocean sprawl'—the proliferation of artificial structures in the sea. We consider how efforts to combat climate change, such as mitigation via offshore renewables ('green' energies to reduce CO_2 emissions), and adaptation via sea defences are leading to a proliferation of artificial structures, resulting in changes in the proportion of hard versus soft coastal habitats, the distribution of species, assemblage composition, and community structure. We also discuss the role of coastal development, including ports and other transport infrastructure as well as offshore structures (e.g., oil and gas platforms), in altering coastal and marine ecosystem structure and functioning. Finally, we undertake a critical review of the current 'state of the art' in the emerging field of 'green engineering', which combines environmentally conscious attitudes, values, and principles with science, technology, and engineering practice, all directed towards improving local and global environmental quality.

Our scope is the global coastline extending vertically to the uppermost extent of tidal influence, with particular emphasis on open coasts and offshore structures that have seen the most research. This is in contrast to the freshwater tidal reaches of estuaries, which have received little attention (but see Francis & Hoggart 2008, 2009, Hoggart et al. 2012). Many of the case studies and examples are drawn from temperate systems in developed countries, reflecting the experience of the authors and the distribution of published research. Two themes permeate our review: firstly, how ecosystem services are at risk from modification of the coast by artificial structures; secondly, the interaction between the provision of new 'hard' substratum as a societal adaptation response, resulting in altered habitat connectivity and changes in the distribution of species and composition of assemblages. We conclude by identifying current knowledge gaps and future research needs.

Burgeoning coastal human populations

The diversity of coastal habitats includes rocky shores, sandy and muddy beaches, barriers, spits and sand dunes, estuaries and lagoons, deltas, wetlands, and coral reefs. These individually and collectively provide a disproportionately greater number of ecosystem services (see Millennium Ecosystem Assessment [MEA] 2005 for a discussion of provisioning, regulating, supporting, and cultural services) to human health and well-being per unit area than other systems (Costanza et al. 1997, Beaumont et al. 2007, Wyles et al. 2014). Globally, coastal systems are undergoing rapid environmental change, with developing countries particularly vulnerable (Figure 1; Crain et al. 2009, Cinner et al. 2012). The drivers of change are complex, but burgeoning human populations, coastal development, and climate change are ultimately responsible (Creel 2003). Consequently, coastal regions are home to some of the most threatened ecosystems in the world (Halpern et al. 2008, Waycott et al. 2009, Knights et al. 2015).

Nearly 40% of the global population lives within 100 km of the coast (Figure 1; Martínez et al. 2007), and population densities in these areas are generally high. In fact, 44 of the 71 cities (62%) with over 5 million inhabitants are located on the coast; this is three times the global average (McGranahan et al. 2007, Seto et al. 2011, Smith 2011, IPCC 2013), and by 2030 it is estimated that 50% of the global population will live within 100 km of the coast (Small & Nicholls 2003). Consequently, many of the world's coasts are becoming increasingly urbanized. Asia has shown the greatest intensification of population, property, and infrastructure at the coast (Jongman et al. 2012); 20 of the top 30 (67%) most populated coastal cities are located in Asia, with Tokyo and Shanghai alone home to over 60 million people. Furthermore, 9 of 10 coastal cities with the highest proportional population change between 1990 and 2014 are in Asia with seven located in China (Figure 1; United Nations Environment Programme, Department of Economic and Social Affairs, Population Division [UNEP DESAP] 2014).

Threats to coastal zones: coastal processes and coastal erosion

Sea-level rise and extreme climatic events

Rates of sea-level rise have increased globally since records began (IPCC 2014) and are projected to continue to increase throughout the 2100s (Hinkel et al. 2014). Consequently, coastal habitats and their characteristic species (including those contributing to biogenic coastal defence) may experience 'coastal squeeze' wherein there is no opportunity for individuals to migrate inland or up-shore to escape rising sea levels (e.g., Doody 2004, Wolters et al. 2005, Jackson & McIlvenny 2011).

In 2012, the IPCC released a special report on risk management and extreme climatic events; IPCC noted a marked increase in frequency and intensity of tropical cyclones in the North Atlantic since the 1970s (IPCC 2012), with coastal regions becoming prone to extreme flooding (Peduzzi et al. 2012). Recent history has been punctuated by such events, which have caused catastrophic human and economic losses in coastal areas (Brown et al. 2014). For example, the 2005 Atlantic hurricane season (the most active on record) included Hurricanes Katrina and Rita, which hit the Mississippi Delta, causing about 2000 deaths, about $91 billion in damage, and 527 km^2 of eroded wetlands along the coast of Louisiana (Beven et al. 2008, Howes et al. 2010).

More recently, in the winter of 2013–2014, Western Europe experienced an unprecedented prolonged sequence of stormy conditions (Huntingford et al. 2014, Matthews et al. 2014); the south-west and north-east of England and the western coast of Wales were particularly adversely affected. Collectively, the storms led to 17 deaths and clean-up costs of approximately £1 billion (Dodds 2014). The United Kingdom, however, was relatively well prepared. Following the 1953 storms and flooding in the North Sea when over 300 people died and 40,000 were left homeless, the UK government invested heavily in coastal defence infrastructure. The comparatively lower cost of human life and livelihood of 2013–2014 has been attributed to this improvement in coastal defence infrastructure (Sayers et al. 2015).

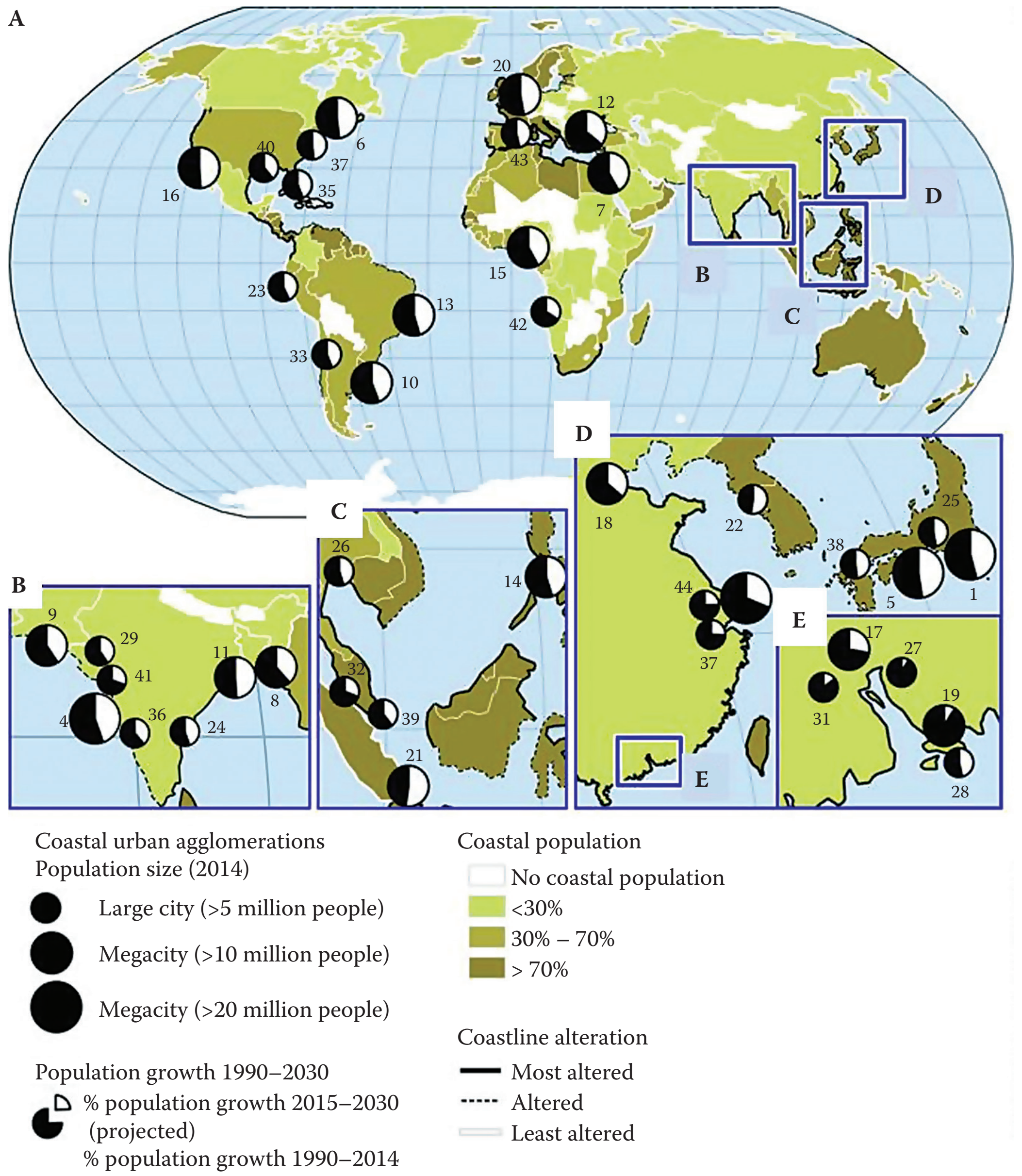


Figure 1 Large cities (>5 million people) and megacities (>10 million people), coastline alteration, and human populations living in coastal zones (within 100 km of coastline). (Coastline alteration redrawn from Rekacewicz, P. & Ahlenius, H. 2006. Coastal population and altered land cover in coastal zones (100 km of coastline). http://www.grida.no/graphicslib/detail/coastal-population-and-altered-land-cover-in-coastal-zones-100-km-of-coastline_7706, UNEP/GRID-Arendal. City population data from United Nations Environment Programme, Department of Economic and Social Affairs, Population Division [UNEP DESAP]. 2014. *World Urbanisation Prospects: The 2014 Revision, Highlights (ST/ESA/SER.A/352)*. New York: United Nations, Department of Economic and Social Affairs, Population Division. Maps created by Shaun Lewin, Plymouth University.)

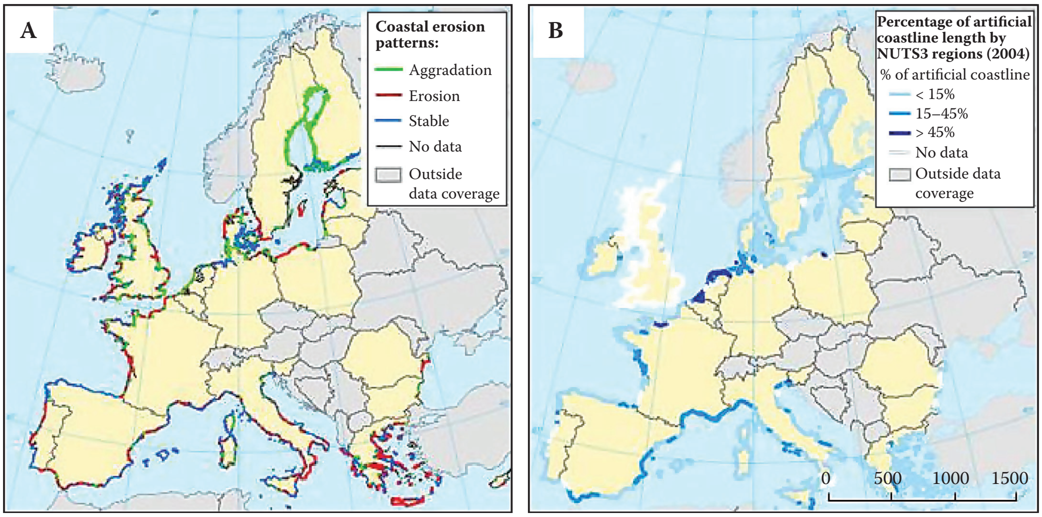


Figure 2 (A) The distribution of accreting, eroding, and stable coastlines of Europe (data from Eurosion. 2004. Living with coastal erosion in Europe: sediment and space for susceptibility. Part IV—A guide to coastal management practices in Europe: lessons learnt. http://www.eurosion.org/reports-online/part4.pdf, accessed 11 May 2015). (B) The percentage of artificial coastline. (Maps courtesy of the European Environment Agency [EEA], http://www.eea.europa.eu/legal/copyright.)

Coastal erosion

The combination of climate change, sea-level rise, and increasing storm frequency will lead to more severe coastal erosion and flooding over the next few decades (Hulme et al. 2002, Thompson et al. 2002, Hirabayashi et al. 2013, IPCC 2014). To assess the threat, two comprehensive assessments have been undertaken in Europe (Eurosion 2004) and the United States (National Oceanic and Atmospheric Administration [NOAA] 2012) to evaluate the state of the coasts and risk of erosion. Based on data collected from 22 coastal countries, Eurosion (2004) concluded that 15% of the coastline of Europe was actively eroding (Figure 2A) and that 6.4% was artificially stabilized (Figure 2B). Given recent investment, the latter figure is likely to be much higher now. More recently, the NOAA State of the Coast project (NOAA 2012) collected data from 28 coastal states and found that 36% of the coastline of the United States was highly vulnerable to erosion, and that 9% was protected using hard armouring and an estimated 350,000 structures located within 150 m of the shoreline.

In the United Kingdom, the south-eastern coast of England is characterized by soft sedimentary geology that is vulnerable to erosion. The village of Happisburgh, Norfolk, is often used as a case study to illustrate the dramatic impacts of coastal erosion on coastal communities. Although now a coastal village, Happisburgh was once some distance from the sea. Historic records indicate that over 250 m of land were lost between 1600 and 1850, prompting the use of coastal defences (groynes) to protect the shoreline. Removal of the groynes in 1991 led to the erosion of about 36,000 t of sediment, a landward retreat of about 100 m, and the creation of an obvious embayment (Figure 3; Poulton et al. 2006, Brown et al. 2014).

Coastal habitats: natural coastal defence

Coastal habitats are an important interface between the land and the sea. All coastal habitats are ultimately geological in origin (geogenic) but can be reshaped by biological processes (biogenic). Biogenic habitats can be defined as vegetated (e.g., kelp forests, seagrass beds, mangroves, and salt marshes) or

Figure 3 The eroding coastline at Happisburgh, Norfolk, United Kingdom. The removal of the groynes in 1991 led to severe coastal erosion and a landward retreat of about 100 m. (Photos copyright Mike Page.)

as 'biogenic reefs'—habitats formed by animals such as corals, bivalves (e.g., oysters and mussels), and annelids (e.g., honeycomb worms). Geogenic and biogenic habitats provide a key ecosystem service to coastal communities of protection against wave damage and erosion caused by storms (Badola & Hussain 2005, Koch et al. 2009, Barbier et al. 2011); hurricanes/typhoons (Day et al. 2007, Costanza et al. 2008); and tsunamis (Dahdouh-Guebas et al. 2005, Alongi 2008, Marois & Mitsch 2015).

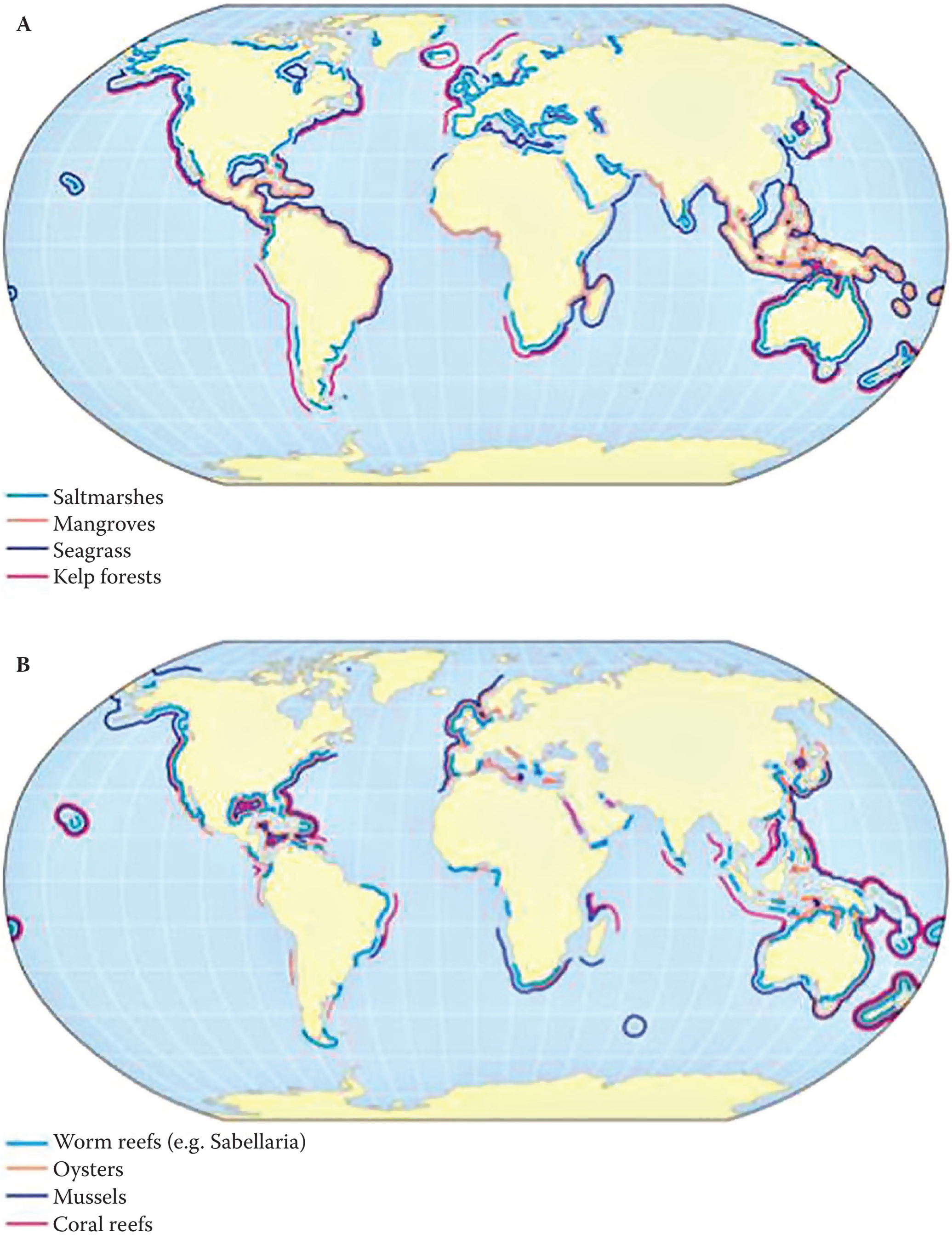
Geogenic habitats

Rocky coasts form about 80% of the world's coastline (Emery & Kuhn 1982). By their very nature, rocky coastlines offer significant coastal protection, forming a physical barrier between the land and the sea. Coastlines characterized by softer lithology are more susceptible to both physical (Naylor et al. 2010, Brooks & Spencer 2012) and biological erosion (see Naylor et al. 2012, Coombes 2014 for reviews), making them more susceptible to flooding and damage to infrastructure and assets. Soft chalk and calcareous coastlines are particularly vulnerable to erosion by bivalves (e.g., piddocks; Pinn et al. 2005a, 2008), which can be a threat to artificial limestone breakwaters (e.g., *Lithophaga lithophaga*, Devescovi & Iveša 2008).

Sandy habitats (sand bars, beaches, and dunes) have been shown to play an important role in the prevention of coastal erosion (Doody 2012, Hanley et al. 2014). These geogenic habitats are more dynamic than rocky coasts and have an important coastal protection function in many parts of the world (e.g., the North Sea coasts of Germany, Netherlands, and Belgium, see Hanson et al. 2002, Stive et al. 2013, van der Meulen et al. 2014; south-eastern Australia, see Short & Hesp 1982; the western United States, see Wiedemann & Pickart 1996). Their function as a coastal defence 'structure' is greatly enhanced by the associated vegetation (e.g., Feagin et al. 2005), such as seagrass at the seaward boundary and salt marsh and mangroves at the land-sea interface. Vegetation is not always advantageous. For example, since the introduction of the European marram grass *Ammophila arenaria* to the western coast of North America in 1868 to stabilize dunes in the San Francisco area, it has since spread along the entire western coast of North America, displacing native plant species and altering sediment dynamics (Wiedemann & Pickart 1996).

Biogenic habitats

Biogenic habitats are ubiquitous in coastal marine and estuarine systems worldwide but vary in extent and species composition across biogeographic regions (Figure 4). For example, at lower



ED: In the key at bottom right of Figure 4A, "Saltmarshes" should be "salt marshes."

PE: I don't see Saltmarshes anywhere else in this figure, so I assume the DE means this key. TS

Figure 4 Global distribution of (A) vegetated coastal habitats (kelp, seagrass, mangroves) and (B) coastal biogenic reefs (coral, mussels, oysters, worms). (Data extracted from the Global Biodiversity Information Facility, http://www.gbif.org/, and United Nations Environment Programme Ocean Viewer, http://data.unep-wcmc.org/datasets/6. Maps created by Shaun Lewin, Plymouth University.)

latitudes mangroves occupy the niche exploited by salt marshes at higher latitudes; warm-water coral reefs only occur in the shallow tropics and subtropics, whereas kelp forests and large fucoid beds are only present in shallow waters at higher latitudes or in upwelling regions (e.g., in Oman, Sheppard & Salm 1988). Biogenic habitats have the potential to provide the 'front line' of natural coastal protection and have been referred to as "biogenic coastal defences" (Mork 1996, Koch et al. 2009, Arkema et al. 2013, Bouma et al. 2014). Here, we focus on their roles in wave attenuation and coastal protection.

The value of biogenic coastal defences is dependent on the timing of natural processes such as storms, hurricanes and typhoons, and tsunamis (Koch et al. 2009). Protection will be diminished if storms occur when biomass or density of the biogenic structure is low. This may be of particular importance in temperate regions, where seasonal patterns of peak biomass (usually late summer) may be mismatched with the seasonal occurrence of storms in autumn and winter (Koch et al. 2009). In contrast, the biomass of biotic structures in tropical areas tends to be less variable over time (Tam et al. 1995), and the coastal protection service they provide may be more predictable throughout the year.

Kelp forests and large fucoid beds

Kelps (e.g., *Macrocystis, Nereocystis, Laminaria* spp.) and fucoids (e.g., *Fucus, Durvillea, Ascophyllum* spp.) are large, brown seaweeds that typically grow on subtidal and intertidal rocky reefs in temperate and polar waters (Figure 4A; Steneck et al. 2002). In comparison to other biogenic coastal defences, little is known about the role of kelps in coastal protection (Smale et al. 2013). They protect rocky coastlines and adjacent sedimentary habitats by attenuating wave energy, buffering against storm surges, and preventing the movement of sediments from adjacent beaches (Mork 1996, Rosman et al. 2007). The degree of wave attenuation is strongly influenced by the architecture of the dominant kelp species (i.e., prostate, stipitate, canopy) and the community structure of the understorey canopy (Eckman et al. 1989, Türker et al. 2006, Gaylord et al. 2007) and, as such, will vary between biogeographic regions (Smale et al. 2013). Far less attention has been given to the role of fucoids in coastal protection on rocky reefs, although Tyrrell et al. (2015) described how fucoid algae in salt marshes can attenuate wave energy and play a significant role in sediment deposition and accretion.

Seagrass beds

Seagrasses occur in shallow sedimentary habitats and have a wide geographic distribution (Figure 4A; Short et al. 2007). They are often found adjacent to salt marshes in temperate regions (e.g., Irlandi & Crawford 1997). Seagrasses can alter the environment by stabilizing sediments, reducing current velocity, and dissipating wave energy (Koch 2001, Christianen et al. 2013, Maza et al. 2013). Ondiviela et al. (2014) reviewed the role of seagrasses as coastal protection and concluded that the larger, longer-living, and slower-growing species (e.g., *Thalassia testudinum, Posidonia oceanica, Zostera marina*) provided the most effective protection, although short-leaved, low-biomass, and heavily grazed seagrasses can also significantly reduce coastal erosion (Christianen et al. 2013). The relative importance of seagrasses for wave attenuation is strongly related to both physical setting (bathymetry, hydrodynamics, sediment regime) and biological factors such as standing biomass, shoot density, and leaf length (Fonseca & Cahalan 1992, Bouma et al. 2010, Stratigaki et al. 2011, Paul et al. 2012). Despite seagrasses clearly providing some coastal protection, this service is perhaps limited compared to salt marshes (Bouma et al., 2005), on one hand due to their natural fragility and flexibility (La Nafie et al. 2012, Paul et al. 2012) and on the other due to their placement, which tends to be in the shallow subtidal zone with therefore less potential to attenuate wave energy (Paul et al. 2012).

Mangroves

Mangroves typically occur in tropical regions, but they also occur on the temperate northern coast of New Zealand and southern coast of Australia (Figure 4A), where they occupy sedimentary estuarine and low-energy marine environments (Spalding 2010). It has long been known that the complex architecture provided by mangroves is important for buffering wave energy (Othman 1994, Mazda et al. 2006, Aziz et al. 2013). The importance of mangroves as coastal protection received much attention following the Asian tsunami in 2004 (Dahdouh-Guebas et al. 2005, Danielsen et al. 2005), but subsequent studies have argued that their protection against extreme events such as tsunamis may in fact be limited (Alongi 2008, Cochard et al. 2008). More research is required on the role of mangroves in protection from tsunamis, cyclones, and hurricanes.

Salt marshes

Salt marshes occupy the coastal fringes in temperate regions (Figure 4A; Deegan et al. 2012), where they form a natural physical barrier to tidal and storm activity (Koch et al. 2009, Gedan et al. 2011, Temmerman et al. 2013). Bouma et al. (2014) discussed how the degree of wave attenuation varies in relation to a combination of physical (e.g., hydrodynamics and sediment dynamics; Möller et al. 2011, Shepard et al. 2011, Ysebaert et al. 2011, Yang et al. 2012) and biological (e.g., vegetation biomass and stiffness; Bouma et al. 2005, 2010) factors. Less is known about the role of salt marshes in response to extreme weather events and rising sea levels. Recent studies of storm surges found that the presence of saltmarsh vegetation was linked to considerably enhanced wave attenuation even when water level and wave height were greatest (Möller et al. 2014). Thus, salt marshes are a valuable component for sediment stabilization and coastal protection under predicted global change scenarios.

The erosion of salt marsh and ‘coastal squeeze’ are common in estuarine regions such as the south-eastern coast of England (Cooper et al. 2001, Foster et al. 2013). Here, management practices include managed coastal retreat and realignment, by which traditional hard coastal defences are moved inland to restore intertidal wetlands and create natural defences in the form of mudflat-saltmarsh systems. Restoring salt marshes through coastal realignment (Mossman et al. 2012) in Essex, England, not only provided enhanced tidal defences but also protected biodiversity and its associated ecosystem services.

Saltmarsh pioneers in the genus *Spartina* were extensively transplanted in the nineteenth and early twentieth century to stabilize coastlines worldwide (Strong & Ayres 2009, Pratolongo 2013). This had many unintended consequences, including hybridization with local species to produce *Spartina anglica* (Ainouche et al. 2004, Salmon et al. 2005) that outcompeted native species (Callaway and Josselyn 1992, Gedan et al. 2009, Silliman et al. 2009). In many places there are now major attempts to control proliferation of *Spartina* due to the loss of mudflats and valuable bird-feeding grounds (Wang et al. 2006, An et al. 2007, Patten & O’Casey 2007). Thus care is needed in assessing potential trade-offs between ecosystem services and desired end points if salt marshes are being deliberately enhanced for coastal defence.

Linkages between habitats and systems

There is increasing recognition of the importance of facilitative interactions and the role of organismal ecosystem engineering in establishing the structure of communities (e.g., Altieri et al. 2010, Passarelli et al. 2014). By combining field measurements of wave attenuation in salt marshes, oyster reefs, and mussel beds with modelled data from seagrasses, van Belzen et al. (unpublished) investigated the up-shore facilitation between different coastal habitats under different tidal regimes and landscapes. They found that in small tidal ranges, habitats reside within each other’s wake zone, creating an up-shore facilitative cascade across the tidal gradient and maximal wave dissipation in the most 'connected' systems. However, continuity among habitats can diminish at greater tidal ranges, jeopardizing ecosystem stability with potential consequences for coastal safety.

Dislodged macroalgae and other plants that have been exported from rocky shores and seagrass beds following disturbance are a distinctive feature of many depositing shores, and this export has been shown to indirectly contribute to coastal stabilization by providing nutrients to the flora of beach and dune systems (Colombini et al. 2003, Orr et al. 2005, Williams & Feagin 2010, Doody 2013). Similarly, human-mediated removal of macroalgal debris and its use as fertilizer has led to soil formation and stabilization of dune systems, creating the characteristic 'machair' systems of the western coast of Ireland and the Scottish Outer Hebrides (Owen et al. 2001, Kent et al. 2003, Doody 2013). Conversely, there is also some evidence that deposited seaweed can have an impact on salt marshes, leading to mortality of some species (Davies et al. 2011, 2012), perhaps compromising their role in attenuation of waves and stabilization of sediments.

Biogenic reefs

In comparison to vegetated habitats, far less is known about the role of biogenic reefs in coastal protection (Bouma et al. 2014). Biogenic reefs in tropical regions are typically formed by the calcium carbonate secreted by reef-building corals and algae and are found in shallow-water settings (Figure 4B; Huang & Roy 2015). Wave attenuation by coral reefs is a function of the water depth above the reef, but these relationships are non-linear (Kench & Brander 2006, Barbier et al. 2008). In a global meta-analysis, Ferrario et al. (2014) found that coral reefs provide substantial protection against natural hazards by reducing wave energy by an average of 97%, and that reef crests alone dissipate 86% of this energy.

Biogenic reefs in temperate regions are created by organisms such as oysters, mussels, or honeycomb worms (e.g., *Gunnarea* spp., *Phragmatopoma* spp., *Sabellaria* spp.) (Figure 4B; Barbier et al. 2008, Dubois et al. 2009). While it is widely accepted that coral and oyster reefs provide an important coastal protection service (Piazza et al. 2005, Beck et al. 2009, Scyphers et al. 2011), far less is known about the role of mussel reefs (but see Borsje et al. 2011, Donker et al. 2013). In a study comparing the relative importance of the two habitats in the Netherlands, Borsje et al. (2011) concluded that oyster beds were more effective in wave attenuation compared to mussel beds. Interestingly, the oyster investigated was *Crassostrea gigas*—a species not native to the region. This is an intriguing example of an ecosystem service delivered by a non-indigenous species. Honeycomb worms can form sizable structures and cover large areas in some parts of their range (e.g., *Sabellaria alveolata* in north-western Europe; Dubois et al. 2002, 2006, Desroy et al. 2011, Firth et al. 2015a) and may play a significant role in wave attenuation and coastal protection. However, no data currently exist on this potentially important ecosystem service (Bouma et al. 2014).

Global loss of natural coastal defences

Degradation and loss has been observed for all habitats with the potential to act as biogenic coastal defences. For example, 85% of oyster reefs (Beck et al. 2011), 65% of seagrasses (Lotze et al. 2006), 50% of salt marshes (Gedan et al. 2009), 35% of mangroves (Valiela et al. 2001), and 30% of coral reefs (Valiela et al. 2001) have been lost or are in a degraded state, and the rate of loss is expected to increase in the future (Lotze et al. 2006, Waycott et al. 2009, Barbier et al. 2011). There are currently no reports in the literature of global loss or decline for kelp forests, other macroalgal beds, mussel beds, or worm reefs, but there is considerable evidence for regional losses. Examples include kelp forests in the United States (Byrnes et al. 2011), canopy algae in Australia (Connell & Irving 2008, Wernberg et al. 2011) and the Mediterranean (Bulleri et al. 2010, Perkol-Finkel & Airoldi 2010), and mussel reefs in Northern Ireland (Strain et al. 2012, Cook et al. 2013). The drivers of this change are complex, but burgeoning human populations, coastal development, and climate change play a significant role (Creel 2003).

‘Ocean sprawl’: the proliferation of artificial structures in offshore and coastal waters

Ocean sprawl implies the proliferation of coastal and offshore artificial structures (Thompson et al. 2002, Airoldi et al. 2005a, Villareal et al. 2007, Inger et al. 2009, Firth & Hawkins 2011). These structures are built for a variety of functions, including coastal defence, oil and gas extraction, aquaculture, and more recently, marine renewable energy (Figure 5; Bacchiocchi & Airoldi 2003, Witt

Figure 5 Examples of ocean sprawl—the proliferation of artificial structures in the sea. (A) Oil and gas platforms: Seaventure, Borneo, Malaysia. (B) Offshore renewable energy installations: Liverpool Bay, United Kingdom. (C) Shellfish aquaculture: oyster trestles, Galway Bay, Ireland. (D) Ports, harbours, and marinas: Essaouira, Morocco. (E) Artificial reefs: HMAS Swan, Dunsborough, Australia. (F) Coastal defence structures: Robben Island, South Africa.

et al. 2012). The impacts of these structures on the environment have been the subject of several reviews (Airoldi & Beck 2007, Govaerts & Lauwaert 2009, Bulleri & Chapman 2010, Dugan et al. 2011), and we do not discuss these impacts here. Instead we review the variety and scope of these structures to provide habitat for benthic organisms.

Artificial structures associated with energy production

The generation of energy from renewable resources continues to move up the political agenda for many countries due to the link between non-renewable fossil fuels and global climate change (Dincer 1999, Chow et al. 2003). Countries with coastlines have plentiful and predictable renewable energy resources in the form of offshore wind, tides, waves, and currents. Considerable attention is therefore being directed towards coastal waters as a source of offshore renewable energy (Figure 6; Pelc & Fujita 2002, Gill 2005).

Marine renewable energy installations

AU: Should this be "all global offshore wind power"?

The location of wind turbines offshore on pylons was first suggested in the 1930s, but it was not until 1991 that the first offshore turbines ('World Wind') were installed 250 m off the coast of Sweden (Nikolaos 2004, Bilgili et al. 2011). After more than 30 years of development, Europe has become the front runner in the commercialization and utilization of offshore wind power technology (Figures 5B, 6B), with 74 installations (2488 turbines) spanning 11 countries and comprising more than 91% of all global offshore wind (Global Wind Energy Council [GWEC] 2014). Until recently, this was the only region in the world with operational capacity. While governments outside Europe have been slower to use this technology, many countries, including China, Japan, India, South Korea, Taiwan, and the United States, have begun to set ambitious targets (Figures 6C, 6D; Lewis 2011, GWEC 2014, Yang et al. 2015).

Large amounts of energy can also be harnessed in coastal areas using tide or wave action. Traditionally, tidal projects have involved extensive barrage systems, which are used to block estuaries. Their energy-harnessing turbines are driven by tidal flow and are particularly effective in areas of large tidal range (e.g., Brittany, France, and the Bay of Fundy, Canada) (Pelc & Fujita 2002). In the United Kingdom, the large-scale Tidal Lagoon Swansea Bay represents a large-scale project that, once built, will combine energy generation technology and green engineering with recreation and amenity facilities. Wave energy is considered to be one of the most promising renewable technologies (Pelc & Fujita 2002), with pilot projects including Limpet 500 off Islay, Scotland (Westwood 2004), and Wave Hub, Cornwall, England (Witt et al. 2012).

Oil and gas platforms

Despite the shift towards offshore renewable energy solutions, there are still thousands of offshore oil and gas platforms operating worldwide (Figure 5A). These are among the largest artificial structures in the marine environment (Patin 1999, Hamzah 2003). Globally, there are more than 7500 offshore platforms (Parente et al. 2006) located on the continental shelves of 53 countries, predominantly in the Gulf of Mexico (4500 current installations), with 950 in East Asia, 550 in West Africa, and 490 in the North Atlantic and North Sea (reviewed in Doyle & Havlick 2009). A 40- to 60-m platform has approximately 8–12 km^2 of surface area that can be colonized by fouling communities (Bull 1989) and can serve as habitat for 10,000–20,000 fish (Stanley & Wilson 1997). Offshore platforms have a production lifespan of about 17.5 years (Pulsipher et al. 2001) before they are decommissioned and removed or converted to artificial reefs, for example, through the Rigs-to-Reefs (RTR) programme (Kaiser & Pulsipher 2005).

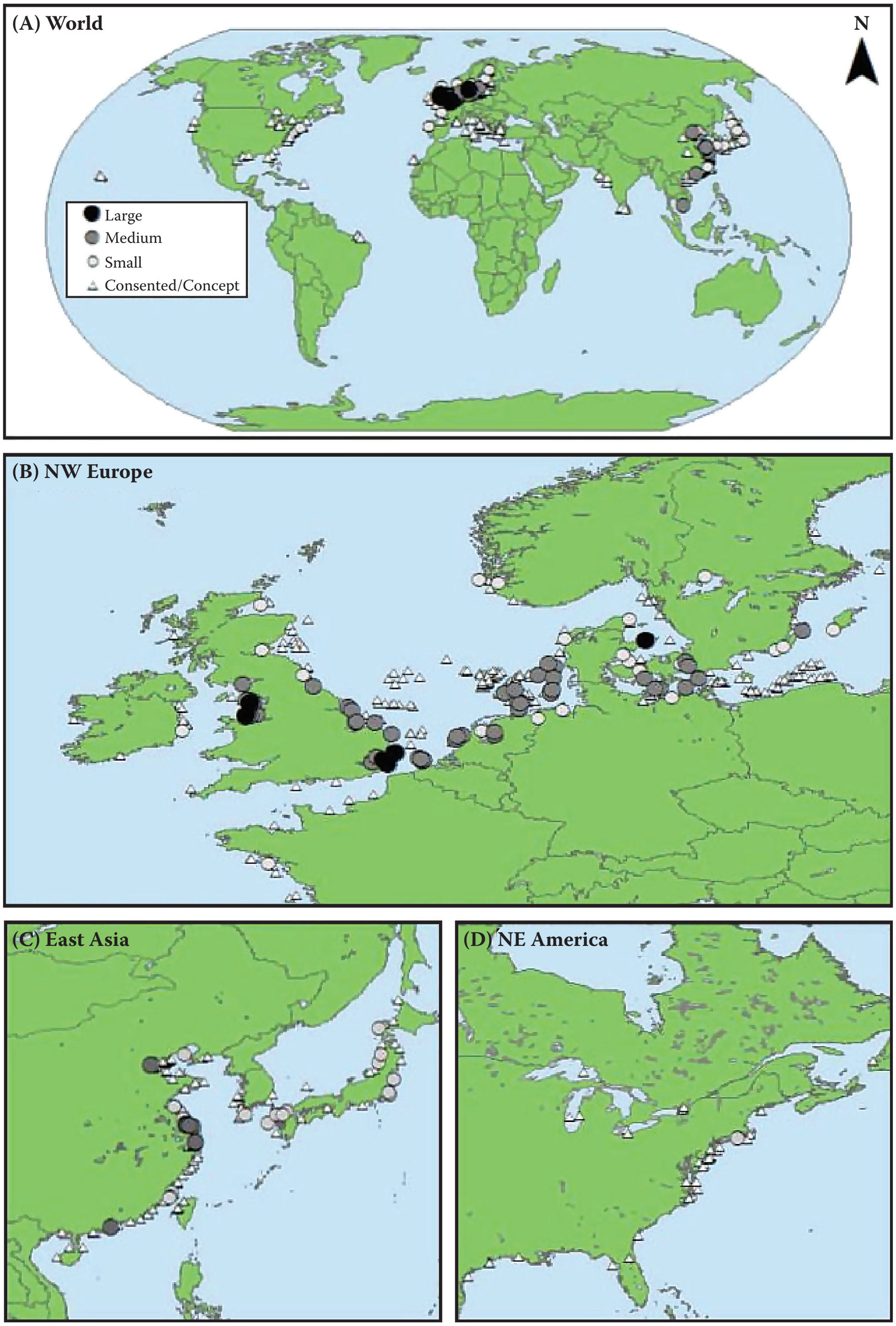


Figure 6 (A) Global distribution of operational and planned offshore wind farms. Note that the major hubs are located in (B) north-western Europe (2480 existing and 812 planned turbines), (C) East Asia (27 existing and 295 planned turbines), and (D) the north-eastern United States (5 turbines under construction, no data on numbers planned). (Data obtained from 4C Offshore; maps created by Danielle Bridger, Plymouth University.)

Artificial structures associated with food production

Artificial reefs

An artificial reef is a submerged structure intentionally placed on the seabed that mimics characteristics of natural reefs (Carr & Hixon 1997, Jensen 1998). Uses of artificial reefs include habitat rehabilitation (Baine 2001) and fisheries enhancement (Collins et al. 1994, Pickering & Whitmarsh 1997, Jensen et al. 2000), but they can also be used to enhance recreation and tourism, for example, angling, surfing, and recreational diving (Figure 5D; Stolk et al. 2007). Increasingly, artificial reefs are being constructed with a primary function of wave energy dissipation and a secondary function of habitat rehabilitation (Hirose et al. 2002, Scyphers et al. 2015).

Structures associated with finfish and shellfish aquaculture

There is increasing concern about the impacts of the placement of semi-permanent fishing equipment (Nugues et al. 1996). One example of this is crab-tiling: Bait collectors lay hard structures (e.g., car tyres and roof tiles) on estuarine mudflats and sand flats to provide shelter for crabs (Sheehan et al. 2010a). While the structures may have a positive effect on crabs on a small spatial scale (Sheehan et al. 2008), the practice has wider negative impacts on infaunal and bird communities (Johnson et al. 2007, Sheehan et al. 2010b, 2012).

At intermediate spatial scales, lobster shelters ('casitas'; Gutzler et al. 2015), oyster trestles (Figure 5C), and crab and lobster pots are contributing to the proliferation of hard structures in the sea and can attract considerable coverage of ephemeral fouling organisms such as barnacles and tube-forming polychaetes (Southward 1995). On a larger scale, the structures associated with finfish aquaculture can add a substantial amount of artificial material and, given the location of this industry, can lead to hardening in both nearshore and offshore waters. While the impacts of these structures on the receiving environment has received much attention (e.g., Ruiz et al. 2001, Callier et al. 2013), relatively little is known about the epibenthic communities that foul these structures or their role in facilitating the spread of both native and non-indigenous species (but see Naylor et al. 2001).

Artificial structures associated with urbanization and climate change

Ports, harbours, and marinas

Ports and harbours (hereafter ports) are required for the transport of people and cargo between countries. World Port Source (http://www.worldportsource.com) lists over 4700 ports within 295 countries globally. The five countries with the highest number of ports are the United States (532), United Kingdom (389), Italy (311), Japan (292), and Canada (239). A further six countries have over 100 ports: China, Denmark, France, Indonesia, Australia, and Greece. The construction of ports generally leads to land reclamation and the linearization of the coastline due to the construction of straight-sided docks, piers, and mooring seawalls (Figure 7). In addition to the creation of thousands of kilometres of artificial habitat, marine shipping activities connecting these ports on local, regional, and global scales are responsible for the spread of a wide range of invasive species (Floerl & Inglis 2005, Floerl et al. 2009), a process recognized as a key anthropogenic driver of global biotic homogenization.

As the size of vessels has increased, there has been a switch from traditional hold storage of cargo to containers, leading to many traditional port installations becoming redundant (Russell et al. 1983, Allen et al. 1992, 1995, Conlan et al. 1992, Hawkins et al. 1992a,b). As ports became increasingly obsolete from the 1970s onward, many were modified for alternative uses, including fish farms, housing, and tourist attractions (Russell et al. 1983, Hawkins et al. 1992a).

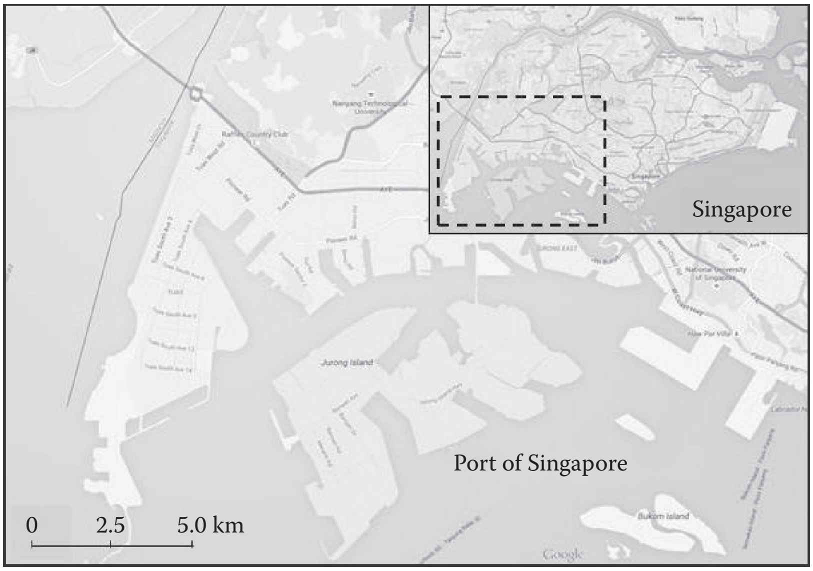


Figure 7 The Port of Singapore (inset), the second-largest port in the world (Esri 2013), which handled 32.2 million TEU (20-foot equivalent units) in 2013 (http://www.worldshipping.org). Note the linearization of the coastline. (Images from Google Earth.)

Artificial coastal defence structures

Coastlines are increasingly defended by engineered 'armouring' structures (Airoldi et al. 2005a, Charlier et al. 2005, Moschella et al. 2005, Chapman & Underwood 2011), including shore-parallel (e.g., seawalls, bulkheads, revetments) and shore-perpendicular structures (e.g., groynes, jetties, and breakwaters; Figure 5F) (Chapman & Bulleri 2003, Dugan et al. 2011). The primary goal of hard-armoured coastal defences is to protect property, infrastructure, and other landward assets from flooding and erosion (Salman et al. 2004, Charlier et al. 2005). These structures can be very large (e.g., La Spezia Breakwater, Italy, and Plymouth Breakwater, England) or can be placed in close proximity to one another, thus creating a network of artificial structures that can span extensive stretches of coastline (e.g., Cesenatico, Italy; Airoldi et al. 2005a, Dafforn et al. 2015a).

In some regions coastlines have become extensively artificial (Stancheva et al. 2011). For example, coastal armouring is reported to cover more than 89% of the natural shoreline in Monaco (http://www.medam.org); 85% of Belgium (Gregory 2010); 63% of Singapore (Lai et al. 2015); and 60% of the Netherlands and China (Eurosion 2004, Guan 2013). There is increasing concern that artificial structures are acting as 'stepping stones' between regions that facilitate the spread of invasive species (e.g., Airoldi et al. 2015), although the extent to which they are acting in this manner remains poorly understood and an important knowledge gap within the field of coastal ecology.

Artificial islands

In some places, the construction of artificial islands and associated coastal armouring has dramatically increased the linear extent of shoreline. An extreme example of this can be seen in Dubai (Figure 8A), where initially there were plans to increase the 45-km coastline to more than 1500 km (>3300%) through the construction of The Palms, The World, The Universe, and Waterfront City developments, amongst others (Velegrinis & Katodrytis 2015). Many of the plans were never realized, but the construction of The Palms alone (Figure 8A) has increased the linear extent of the

Figure 8 Examples of extreme cases of coastal development: (A) The Palm Islands and The World, Dubai; (B) the Pearl-Qatar, Doha. (Images from Google Earth.)

AU: Please update 2015 information for Pearl-Qatar.

shoreline by 130% (Burt et al. 2009, 2013). Doha and Bahrain have also constructed elaborate artificial islands; the Pearl-Qatar in Doha spans nearly 4 million m^2 (Figure 8B), and the Durrat Al Bahrain, due for completion in 2015, is made up of an array of crescent-shaped islands (Velegrinis & Katodrytis 2015). The construction of artificial islands to support infrastructure and people is not a new concept, but there is increasing concern about the environmental and political implications of these developments. At the time of writing, there was much media interest in construction of artificial islands by China in the Spratly Archipelago—a disputed group of more than 750 reefs, atolls, cays, and islands that straddles the maritime borders of China, Brunei, Malaysia, Taiwan, Philippines, and Vietnam—in the South China Sea. Other large-scale contentious projects were also in the planning for Penang and Johor, Malaysia, and Copenhagen, Denmark.

Artificial structures as habitats: the diversity deficit and non-indigenous and pest species

The diversity deficit

Artificial habitats have previously been considered as surrogates (albeit simplified) for natural habitats (Hawkins et al. 1983, Thompson et al. 2002, Bulleri & Chapman 2004), although the recent surge of comparative studies repeatedly showed distinct differences in community structure and functioning between artificial structures and natural rocky reefs. These differences can be perceived as either positive or negative. On one hand, artificial structures have been reported to support increased diversity and abundance (Chou & Lim 1986, Connell & Glasby 1999, Wehkamp & Fischer 2013, Munsch et al. 2014), provide habitat for unique taxa that are not found on natural rocky reefs (Chapman 2003, Bulleri & Chapman 2004, Andersson et al. 2009), or support larger adult individuals (Kirk et al. 2007). On the other hand, artificial structures are more commonly considered to support a comparatively lower diversity (Moschella et al. 2005, Wilhelmsson & Malm 2008, Pister 2009, Firth et al. 2013b, Aguilera et al. 2014, Munsch et al. 2014), particularly of rare and mobile species (Chapman 2003, 2006, Pister 2009), than adjacent natural hard substrata, resulting in a more homogeneous landscape (Lam et al. 2009). Associated organisms have also been shown to have lower genetic diversity (Fauvelot et al. 2009, Sammarco et al. 2012) or reduced reproductive output (Moreira 2006) or to be smaller in individual size (Moreira 2006, Diaz-Agras et al. 2010).

The influence of habitat complexity

In natural environments, microhabitats (pits, crevices, and rock pools) are widely known to be important for biodiversity through the provision of refuges from abiotic and biotic stress (Fairweather 1988, Metaxas & Scheibling 1993, Johnson et al. 1998, Firth et al. 2013b). The diversity deficit in artificial habitats may largely be explained by lower habitat complexity compared with natural habitats (e.g., Chapman 2003, Moschella et al. 2005, Loke et al. 2015). For example, engineered materials (e.g., quarried granite, concrete, steel) often have smoother surface texture than rocky-reef substrata, and structures tend to lack important microhabitats, such as rock pools, pits, and crevices.

Construction material and habitat complexity are repeatedly shown to be important determinants of community composition on artificial structures (e.g., Potts & Hulbert 1995, Andersson et al. 2009, Bracewell et al. 2013, Coombes et al. 2015). For example, Connell & Glasby (1999) found that urban structures in Sydney Harbour made from a range of materials supported very different epibiotic assemblages both between structural types and in comparison to natural reefs. Rilov & Benayahu (1998) found that fish abundance and diversity around oil platform pillars were correlated with habitat complexity. Hunter & Sayer (2009) reported up to three times higher abundances of fish and crustacean species using complex artificial reef modules, compared with simple modules and natural reefs.

The influence of surface orientation and inclination

The proliferation of artificial structures is leading to an increase in the proportion of steep and vertical-facing artificial substrata (Andersson et al. 2009, Chapman & Underwood 2011, Firth et al. 2015b), and it is considered that the relative importance of orientation (i.e., north-south directionality) will increase with increasing substratum inclination (Firth et al. 2015b). Surface orientation, inclination, and shading may influence biodiversity on vertical or floating structures such as seawalls, pontoons, and pilings (Connell 1999, Glasby 1999, Knott et al. 2004, Perkol-Finkel et al. 2006, Langhamer et al. 2009, Chapman & Underwood 2011, Firth et al. 2015b), leading to different emergent communities compared with natural reef habitats. On intertidal structures, a steeper shore profile can also lead to a reduction in habitat extent compared to natural shores, which may limit species diversity and abundance as a simple product of species-area relationships (Hawkins & Hartnoll 1980).

The influence of wave exposure

Pister (2009) suggested that wave exposure might also contribute to differences in diversity between intertidal artificial and natural habitats in California (see also Davis et al. 2002). Indeed, where structures are introduced to high-energy environments (as coastal defences often are), conditions may favour colonization by certain species (e.g., filter-feeders and limpets: Moschella et al. 2005, Jonsson et al. 2006, Vaselli et al. 2008) but hinder settlement and post-settlement survival of others (e.g., some macroalgae: Jonsson et al. 2006; see also Mullineaux & Garland 1993). Structures with both exposed and leeward sides may present ‘unnatural’ sheltered habitat along exposed open coasts, which may favour algal-dominated communities (Southward & Orton 1954, Jenkins et al. 1999, Jonsson et al. 2006, Burt et al. 2013). Further, high-disturbance regimes caused by wave energy and sand scouring around structures (Moschella et al. 2005, Burcharth et al. 2007, Firth et al. 2014b) may prevent communities from developing beyond early successional stages. Artificial structures often support assemblages more typical of rocky reefs jutting out from high-energy sandy beaches (Bally et al. 1984) that tend to be dominated by ephemeral early successional species.

The influence of structure age

Finally, the age of structures at the time of assessment may be an important determinant of how similar colonizing communities are to natural mature reef communities. Age has been shown to explain considerable variation in community structure in artificial habitats (Knott et al. 2004, Sammarco et al. 2004, Perkol-Finkel et al. 2005, Pinn et al. 2005b, Burt et al. 2011, but see Wendt et al. 1989, Langhamer et al. 2009). Sheehan et al. (2013) recently highlighted the importance of appropriate monitoring of artificial structures over long timescales to effectively assess their ecological impact. At the Wave Hub site in the south of England, they observed recovery of opportunistic and fast-growing reef species on the cable rock armouring route within 2 years of construction. Slower-growing species were, however, still largely absent.

Non-indigenous and pest species

Non-indigenous species appear more prevalent on artificial structures than on adjacent natural habitat (see Mineur et al. 2012 for review). The introduction of novel artificial habitats in the marine environment may enable opportunistic and weedy species to take advantage of the unexploited bare substrata, particularly with increased surface inclination and shading (Chou 2006, Glasby et al. 2007, Dafforn et al. 2009, 2012, Marzinelli et al. 2009, 2011, Forrest et al. 2013, Simkanin et al. 2013).

In the Mediterranean, structures introducing ‘unnatural’ sheltered rocky habitat on the landward side of coastal defences along exposed open coasts can provide opportunities for non-indigenous algal species to colonize (e.g., *Codium fragile* ssp. *tomentosoides* and *Caulerpa racemosa*; Bulleri & Airoldi 2005, Vaselli et al. 2008, Airoldi & Bulleri 2011, Airoldi et al. 2015, but see Pister 2009), and this can be exacerbated by disturbance events such as structural maintenance or recreation (Airoldi et al. 2005b, Bulleri & Airoldi 2005, Airoldi & Bulleri 2011; see also Bracewell et al. 2013, Salomidi et al. 2013).

In Australia, the non-indigenous mussel *Mytilus galloprovincialis planulatis* frequently colonizes vertical seawalls in Sydney Harbour, where it can often occupy nearly all of the available space, overgrowing native assemblages (Chapman et al. 2005, Chapman & Underwood 2011). In Europe, the invasive Australasian barnacle *Austrominius* (formerly *Elminius*) *modestus* colonizes structures, particularly on coastlines that are more sheltered and those in proximity to estuaries (Bracewell et al. 2012, 2013).

Structures in close proximity to transport infrastructure, such as ports and harbours, are particularly susceptible to colonization by non-indigenous species, particularly encrusting invertebrates and ascidians (Lambert & Lambert 2003, Glasby et al. 2007, Dafforn et al. 2009, Griffith et al. 2009, Firth et al. 2011, Bishop et al. 2015). Non-indigenous species have also been recorded in high abundances on offshore structures such as oil and gas platforms (Fenner and Banks 2004, Sammarco et al. 2004, 2010, Page et al. 2006, Yeo et al. 2010) and wind power turbines (Wilhelmsson & Malm 2008).

Artificial structures associated with aquaculture (e.g., oyster trestles, mussel ropes) can provide substratum for the attachment of non-indigenous species (e.g., Minchin 2007, Rius et al. 2011, Morgan & Richardson 2012, Nunn 2014, Pochon et al. 2015). Negative effects include direct impacts on cultured species (e.g., smothering, competition for space and food); deterioration of farm infrastructure (immersed structures such as cages, netting, and pontoons); and effects on natural ecosystem functioning of adjacent areas (Fitridge et al. 2012, Fletcher et al. 2013).

Disentangling ‘natural’ spread and facilitation by artificial structures

It has been suggested that artificial structures may provide opportunities for assisted migration of species at risk from climate change (Hoegh-Guldberg et al. 2008). The distribution of species is continually changing as fluctuations and trends in sea and air temperatures alter the suitability of a habitat (Parmesan & Yohe 2003, Harley et al. 2006, Sunday et al. 2012, Bates et al. 2014, 2015). The velocity of climate change (*sensu* Loarie et al. 2009) is dependent on local or regional features of the environment, some of which can act as barriers to species movement (Damschen et al. 2006, Burrows et al. 2011, Poloczanska et al. 2013), as well as changes in the physiological performance of species (and in particular their free-living early life-history stages) as their environment changes (*sensu* proximate responses; Harley et al. 2006).

There is increasing evidence that artificial structures are facilitating the spread of species by allowing these barriers to be overcome (Herbert et al. 2003, Sammarco et al. 2012), increasing the rate of spread of some species (Hawkins et al. 2008, 2009) and leading to biotic homogenization. While it is becoming increasingly evident that artificial structures provide novel habitat for species (especially non-indigenous species; see Mineur et al. 2012 for review), disentangling 'natural' changes in distribution patterns associated with climate change from those associated with the proliferation of artificial structures is challenging. Next, we attempt to disentangle changes in natural spread associated with climate change from those distributional shifts facilitated by artificial structures.

It is important to point out that the very definitions of *native* and *non-indigenous* species will be challenged by both climate change and ocean sprawl. Hellmann et al. (2008) noted that taxa that were previously considered 'invasive' might diminish in impact under climate change; conversely, previously native species may become invasive. The geographic distributions of many native species will shift, moving into areas where they were previously absent. In the examples that follow, we assign native or non-indigenous status to the species, based on that identified by the relevant authors. Care must be taken, and we advise only using the term *non-indigenous species* for those taxa whose origin is another biogeographic province. Thus a species whose range is moving polewards is indigenous to that region—and might well have been present in that region before, during previous warm interglacial periods. Many species have shown polewards spread from refugia following the last glacial maximum (Maggs et al. 2008, Searle et al. 2009, McDevitt et al. 2010).

Range changes of non-indigenous species associated with artificial structures

Artificial structures have been widely reported to facilitate the spread of non-indigenous species in the marine environment (Tyrrell & Byers 2007, Ruiz et al. 2009, Sheehy & Vik 2010, Mineur et al. 2012, Airoldi et al. 2015). For example, in South Africa, the number of reported non-indigenous species has risen dramatically in recent years (see Griffiths et al. 1992, Mead et al. 2011 for reviews). Small harbours with yachts commonly support more non-indigenous fouling species than other harbours (Peters et al. 2014). In a study encompassing a range of biogeographic provinces, Rius et al. (2014) found that increases and expansions of non-indigenous species distributions were uncorrelated with levels of boat traffic but concurrent with increases in sea-surface temperature (SST), suggesting that climate change fostered the spread and abundance of non-indigenous tunicates across multiple spatial scales.

In the United States, the mussel *Perna viridis* is a recent invader to the south-eastern states, where it can be found overgrowing the native oyster *Crassostrea virginica* (Baker et al. 2007) or attached to any kind of artificial hard structure available (pier pilings, pontoons, sea walls). This species is susceptible to winter mortality events linked to extremely cold air temperatures (Firth et al. 2011, Urian et al. 2011). The invasive range of *P. viridis* is spreading eastward along the Florida Panhandle and northward towards South Carolina (Benson 2010, Crickenberger & Moran 2013, Spinuzzi et al. 2013). This region of the United States is characterized by sedimentary habitats and the spread of this species has been facilitated by artificial structures. In the case of *P. viridis*, it is considered that cold winters are limiting the northward range expansion in the short term, but it is expected that long-term warming will ultimately facilitate further spread, providing hard substrata are available (i.e., artificial structures; Firth et al. 2011).

In addition to non-indigenous species, artificial structures have been implicated in the increase and spread of pest and harmful species. Jellyfish blooms have been reported to be increasing in intensity and frequency worldwide (Condon et al. 2013, Graham et al. 2014, Pitt & Lucas 2014) and have been linked to growth in marine shipping and aquaculture and the proliferation of artificial structures providing habitat for the polyps (Lo et al. 2008, Ishii & Katsukoshi 2010, Duarte et al. 2012). In addition, the cold-water toxic dinoflagellate *Alexandrium catenella* exhibited multiple blooms along the Spanish Mediterranean coastline in the 1990s (Vila et al. 2001); this expansion was attributed to newly constructed harbours. Similarly, oil platforms in the Gulf of Mexico were considered responsible for the spread of cigatuera (human disease acquired by consuming finfish containing ciguatoxins) due to the creation of new suitable habitat for the dinoflagellate *Gambierdiscus toxicus*—the source of the ciguatoxins (Villareal et al. 2007).

Range changes of non-indigenous species associated with climate change

It has long been claimed that global climate change is linked to the increasing success of non-indigenous species (Dukes & Mooney 1999, Stachowicz et al. 2002a, Sorte et al. 2010), with associated negative impacts on native biodiversity (Vitousek et al. 1997, Sala et al. 2000; see review by Occhipinti-Ambrogi 2007). A global meta-analysis did not find a global increase in invasive species distributions following climate and land use changes (Bellard et al. 2013), but as this study combined both climate and land use changes for marine, aquatic, and terrestrial taxa, it is difficult to disentangle any specific patterns for individual groups (see Lyons et al. 2015).

Climate-driven changes may affect both local dispersal mechanisms, due to the alteration of current patterns, and competitive interactions between non-indigenous species and native species, due to the onset of new thermal optima. The effects of warming climate are primarily a cause for physiological stress, which acts more strongly on species already near their tolerance limit (Laubier 2001). Extreme climatic events such as heatwaves and cold waves can cause mass mortalities (Cerrano et al. 2000, Garrabou et al. 2001, Petes et al. 2007, Firth & Williams 2009, Firth et al. 2011), and storm events can cause dislodgement of benthic organisms (Denny et al. 2009, Airoldi & Bulleri 2011), resulting in bare space for invasion by non-indigenous species (reviewed in Diez et al. 2012).

Range changes of native species associated with artificial structures

Climate change–induced range shifts are complicated by additional non-climatic factors operating at smaller spatial scales, including habitat suitability, fragmentation, hydrodynamics, and deployment of artificial structures, which provide stepping stones in regions of unsuitable natural habitat and can bridge barriers to natural larval dispersal (Gaylord & Gaines 2000, Burrows et al. 2008, Keith et al. 2011, Sammarco et al. 2012, Firth et al. 2013a, Adams et al. 2014). Here we focus on the potential for artificial structures to potentially interact with climate change, thus exacerbating the rate of spread of species by acting as stepping stones to natural dispersal.

The proliferation of oil and gas platforms in the Gulf of Mexico has been linked with the range extensions of coral and fish species (Rooker et al. 1997, Sammarco et al. 2004, Atchison et al. 2008). Sammarco et al. (2012) investigated the genetic connectivity of corals on oil platforms in the northern Gulf of Mexico. Genetic connectivity was highest on platforms near the Flower Garden Banks (the only natural coral reef in the area) and decreased with distance away from the banks. Their study also revealed two genetically distinct populations either side of the Mississippi River, indicating that the river represents a formidable barrier to larval dispersal. Such an increase in gene flow can reduce genetic diversity by removing barriers for dispersal, with a significant negative effect on the potential adaptive capacity of a species and, ultimately, on evolutionary processes (Palumbi 2003, Airoldi et al. 2005a).

The spread of non-indigenous species is becoming increasingly linked to human-mediated transport of organisms, in particular associated with the aquaculture industry. In contrast, there are few examples of native species range expansions being facilitated by the same mechanism. One example is the northward extension of the native infaunal polychaete *Diopatra biscayensis* beyond a regional biogeographic boundary in northern France. Woodin et al. (2014) suggested that the placement of aquaculture structures provided the most likely mechanism for the bridging of a regional biogeographic boundary. It is expected that future warming will prompt the further northward extension of populations (Wethey et al. 2011), illustrating how climate change and artificial structures can act synergistically.

The proliferation of artificial breakwaters along the Belgian coastline is thought to have facilitated the range extension of the Boreal periwinkle *Littorina saxatilis* (Johannesson & Warmoes 1990). Interestingly, this species lacks a planktonic larval stage, and it is assumed that the continuous nature of the structures, rather than larval dispersal or climate change, has facilitated this particular range extension. In the United Kingdom, artificial coastal defence structures are becoming increasingly common along the southern coast of England. Historically, Portland Bill (Dorset) and St. Catherine's Point on the Isle of Wight have acted as natural barriers to dispersal (Crisp & Southward 1958), but in recent years, populations of many southern warm-adapted invertebrate species, such as *Perforatus* (formerly *Balanus*) *perforatus, Gibbula umbilicalis, Patella ulyssiponensis*, and *Melaraphe neritoides*, have managed to breach these hydrographic barriers (Herbert et al. 2003, Mieszkowska et al. 2006, Herbert et al. 2007, Keith et al. 2011). It has been suggested that artificial coastal defence structures and marinas have acted as stepping stones in this instance, 'artificially' facilitating an extension in range of these species (Moschella et al. 2005, Hawkins et al. 2008).

The construction of artificial structures can also infill the gaps in species distributions by effectively creating corridors to dispersal between previously unconnected areas. In North Wales, the reef-forming polychaete worm *Sabellaria alveolata* has successfully colonized a network of coastal defence structures, bridging a historic gap in distribution of natural rocky shore populations that were previously separated by about 35 km (Firth et al. 2015a). The same study also documented population increases within the geographic region, suggesting that the species may also be benefitting from recent warming. The authors highlighted the difficulties in disentangling the effects of the proliferation of artificial structures from climate-driven warming. This spread has most likely come from *S. alveolata* populations on the coast of north-western England, showing the importance of artificial structures in consolidation of fragmented populations at range edges.

Range changes of native species associated with climate change

Evidence for changes in the latitudinal location of one or more range limits has been recorded for many marine species across the globe since the onset of the current period of climate warming in the 1980s. The general pattern has been a shift in 'leading' range edges expanding polewards towards higher latitudes and cooler environmental temperature regimes and a contraction of the 'trailing' low-latitude range edge away from warming temperatures. These changes have been observed in global meta-analyses for pelagic fish (MacNeil et al. 2010, Sunday et al. 2012), plankton (Edwards et al. 2014), and marine species in general (Sorte et al. 2010, Poloczanska et al. 2013).

AU/PE: Is "towards" correct? Or should it be "toward" throughout? TS

Leading edges

The leading edge is the range limit that is expanding as new populations become established at locations where previously none existed. 'Hotspots' of range shifts include the biogeographic break point between Boreal and Lusitanian regions in the north-eastern Atlantic, where leading range edges of Lusitanian species from warmer, low-latitude origins are extending into higher latitudes where environmental temperatures have increased sufficiently to facilitate survival and reproduction (Burrows et al. 2011). Several range extensions have been recorded around the UK coastline, many reported by the Marine Biological Association of the UK MarClim project, which has documented range shifts for a wide range of rocky intertidal invertebrates and macroalgae since the mid-1980s (summarized in Helmuth et al. 2006, Hawkins et al. 2008, 2009, Mieszkowska et al. 2014). The leading range edges of Lusitanian gastropods (*Patella depressa*, *Phorcus lineatus*, and *Gibbula umbilicalis*); barnacles (*Chthamalus stellatus*, *C. montagui*, and *Perforatus perforatus*); and kelp (*Laminaria ochroleuca*) have shifted northward around the Atlantic coastline and north-east along the English Channel coastline (Herbert et al. 2003, Mieszkowska et al. 2006, 2007, Smale et al. 2014, Yesson et al. 2015). These shifts in range have implications for biotic interactions and community structure and functioning in the 'receiving' environment (e.g., Moore et al. 2007a,b, Blight & Thompson 2008, Poloczanska et al. 2008, Firth et al. 2009). The extent of range shifts, however, is species specific, with some species moving much less than others (e.g., *C. montagui* and *C. stellatus* in the English Channel; Herbert et al. 2007, 2009), most likely related to the duration of their free-living planktonic life-history stage (Shanks 2009). As such, the potential for a species to breach a hydrographic barrier is very much dependent on its particular early life-history characteristics.

Outside the United Kingdom, evidence of range shifts is mostly limited to recent decades, stemming from the growing awareness of the need for datasets of broad spatial and temporal coverage to track and predict impacts of global environmental change (Lima et al. 2006, 2007a,b, Blanchette et al. 2008, Broitman et al. 2008). Nevertheless, significant range shifts have been observed. For instance, polewards shifts at the leading edge are reported along the Pacific coastline of the United States for the gastropod *Kelletia kelletii* (Zacherl et al. 2003). In the temperate zone of Australia, there are many endemic species due to its geographic isolation from other climatically similar regions (Poore 2001), and range extensions have been reported for a number of species. For example, along the eastern coast, the urchin *Centrostephanus rodgersii* (Ling 2008, Ling et al. 2009) and the intertidal barnacle *Austromegabalanus nigrescens* have shifted considerable distances from the Australian mainland to Tasmania due to the intensification of the East Australia Current and resulting warmer sea temperatures (Pitt et al. 2010, Johnson et al. 2011). There have also been marked increases in abundance of the warm-water spiny lobster *Jasus edwardsii* and the abalone *Haliotis rubra* (Poloczanska et al. 2011).

Some evidence of range shifts is, however, equivocal in part due to localized warming trends or challenges in predicting the direction of shifts. For example, a study of 10 intertidal species along the Chilean coast involving the comparison of field studies to museum records did not find pervasive range shifts between the mid-1900s and 2000 (Rivadeneira & Fernández 2005). This was attributed to differential warming trends along the Chilean coast during this time. Similarly, a study of over 80 intertidal species in eastern Australia comparing data from the 1940s and 1950s with current distributions indicated little change (Poloczanska et al. 2011). In New Zealand, there have been few large-scale studies. However, those that exist suggest fragmented distributions and complex evolutionary histories, which makes the detection and prediction of climate-driven distribution changes problematic (Goldstien et al. 2006, Mieszkowska & Lundquist 2011).

Trailing edges

Far less information exists on the fate of lower-latitude range limits, even for well-studied taxa. Where assessments have been undertaken, shifts in trailing range edges have been observed. The tortoiseshell limpet *Testudinalia testudinalis* and the brown macroalga *Alaria esculenta* (Simkanin et al. 2005, Mieszkowska et al. 2006) have shown retractions in their southern extent as well as decreases in abundance in Britain and Europe during the last few decades. Some retractions have been over significant geographic distances. For example, the trailing edge of the blue mussel *Mytilus edulis* has retreated more than 350 km to higher latitudes in response to warmer summers related to climate change in the North Carolina region of the United States over the past few decades (Jones et al. 2009, 2010). In contrast, there has been an extension in range of the Boreal barnacle *Semibalanus balanoides* at the Boreal/Lusitanian breakpoint region along the Biscay coast of France following the extremely cold winter of 2009–2010 (Wethey et al. 2011, Jones et al. 2012). In marine macroalgae, fewer changes in distribution have been detected than for animals. This could be due in part to difficulties in monitoring subtidal species over large spatial scales. The lower dispersal capability of some macroalgae may also limit the ability of species to colonize new habitats (Araújo et al. 2011, Moalic et al. 2011).

Evidence of range shifts can be influenced by the phylogeographic history of the species in question. Lima et al. (2007a) showed a prevalence of shifts in 'warm-water' species (leading edge) in comparison to 'cold-water' counterparts (trailing edge). In those instances, there have been significant alterations in the range edge. Surveys of macroalgal distributions along the coast of Portugal during the 1950s, 1960s (Ardre 1970, 1971), and 2000s (Lima et al. 2007a) identified about 120 conspicuous species that have shown significant alterations in the location of a range edge. A greater number of warm-water species showed northward extensions in latitudinal range limits, with significant correlations between distributional shifts and mean annual inshore SST since 1941 (Lemos & Pires 2004). Species classified as cold water in origin displayed both northward and southward shifts with no significant change when considered as a group.

Mechanisms affecting distribution patterns: climate-driven changes in dispersal capacity and enhanced connectivity

Climate envelope models can be used to forecast where a species could potentially survive (Berry et al. 2002, Araújo et al. 2004, Thuiller 2004) as temperature is often the ultimate factor setting species distributions (e.g., Tomanek & Somero 1999, Perry et al. 2005). Direct limitation of dispersal capacity by coastal topographic features such as headlands or islands, coupled with the hydrodynamics of nearshore waters, such as residual currents, tidal streams, and frontal systems, is often the proximate factor setting distributional limits (Crisp & Southward 1958, Gaylord & Gaines 2000, Keith et al. 2011). Interannual variability in climate conditions (e.g., extreme weather events) may lead to changes in dispersal or survivorship in a given year (Occhipinti-Ambrogi 2007, Cheung et al. 2009, Aprahamian et al. 2010, Firth et al. 2011), and species are likely to 'track' suitable conditions for survival (Burrows et al. 2011). Depending on larval 'fitness' under those conditions, the absence of suitable habitat, which could include artificial structures, may make the distance between patches of suitable habitat too great for successful recruitment or establishment of a viable population. Alternatively, their introduction could play a role in providing stepping stones for dispersal (Bulleri & Airoldi 2005, Glasby et al. 2007, Miller et al. 2013), leading to biotic homogenization.

Disentangling the relative importance of climate change as an ultimate driver from the proximate role of artificial structures in enabling range extensions is challenging. Many species display a biphasic life history, in which they utilize a free-living (planktonic) larval life-history stage as a means of dispersal prior to metamorphosis to an often-sessile adult form. This larval life-history stage can last from minutes (e.g., Thorson 1946) to days (e.g., Ryland et al. 2000), to weeks (e.g., Ayata et al. 2009), or to months (e.g., Shanks 2009), the duration of which—referred to as the planktonic larval duration—greatly influences the dispersive capacity of a species.

Larval development can be broadly classified into one of three strategies: direct development, lecithotrophy, or planktotrophy, with dispersal capability being least in direct developers and greatest in planktic developers (Thorson 1950, Shanks 2009). Despite marked differences in strategies, there is evidence of increased fragmentation of natural habitats and reduced connectivity between populations, especially for species with short planktonic durations (Hughes et al. 2005b, Trakhtenbrot et al. 2005). Under current climate change scenarios, connectivity is predicted to further decrease as increased sea temperatures and ocean acidification negatively affect reproductive success, development, and growth (Petes et al. 2007, Lika et al. 2011).

For many species, increased temperature leads to faster rates of development of larval, juvenile, and adult forms (Manush et al. 2006, Aprahamian et al. 2010, Mueller et al. 2015), reducing their exposure to ocean currents for transport (Shanks 2009). A meta-analysis by O'Connor et al. (2007) highlighted the general reduction in development times as temperatures increase for a range of phyla. While useful, this analysis was perhaps overly simplistic, in that it inferred a linear relationship between planktonic larval duration and dispersal distance, predicting an average increase in dispersal distance of about 3.1 km with each additional day in the plankton. However, as highlighted by Shanks (2009), while in many instances larval duration is significantly correlated with dispersal distance, there are many exceptions, with individuals travelling much shorter distances than predicted (Siegel et al. 2003).

Artificial structures offsetting reduced dispersal potential

Predicting dispersal is challenging, and the use of 1-dimensional estimates of spread (e.g., km y^{-1}) may not capture range shifts effectively (Mineur et al. 2010). Certainly, there appears to be an increase in rates of species spread associated with human vectors in recent years (Mineur et al. 2010, 2012), perhaps related to the proliferation of artificial structures (both onshore and offshore) that has altered the connectivity of marine populations (Saura et al. 2013, Adams et al. 2014). In most instances, structures are built in areas that would otherwise be sedimentary, on one hand causing the fragmentation and loss of existing natural sedimentary habitats and on the other creating stepping stones or corridors for hard-bottom species (Dethier et al. 2003, Airoldi et al. 2005a, 2015, Bulleri & Airoldi 2005, Bulleri & Chapman 2010, Miller et al. 2013).

To date, the potential interactions between climate change and ocean sprawl on the connectivity of marine populations are poorly understood. Any increase in connectivity arising from the introduction of artificial structures could be a cost-effective way of enhancing the conservation of threatened species and habitats, for example, by providing new dispersal routes that facilitate migrations in response to climate change (Thomas 2011). There could be severe drawbacks, however, as these novel habitats can act as barriers or partial filters to the regional-scale dispersal of coastal species, disproportionately favouring non-indigenous over native species (Tyrrell & Byers 2007, Airoldi & Bulleri 2011, Airoldi et al. 2015).

The increased prevalence of artificial structures may therefore not be desirable in terms of increased risk of spread of potentially harmful non-indigenous species. Certainly, artificial structures have been implicated in the increase and spread of pest species (see previous discussion). Understanding the factors that facilitate or prevent the migration of species through networks of structures would allow improved decision-making about the size and spacing of artificial structures in marine seascapes to simultaneously preserve fundamental ecological processes, enhance conservation of native biodiversity, and achieve economic and social goals. To that end, accurate descriptions of dispersal distance both today and forecast for the future are needed to underpin the management and use of marine space.

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Understanding the mechanisms of range extension: a modelling approach

Biophysical modelling has become an increasingly widely used tool for predicting dispersal and evaluating mechanisms used by species to facilitate their dispersal. In brief, the approach simulates the dispersal of planktonic species by coupling a physical (hydrodynamic) description of the environment with a description or mimicry of biological traits or behaviours (e.g., vertical swimming) in response to a specific cue or cues, such as temperature, halocline, or pycnocline (e.g., North et al.

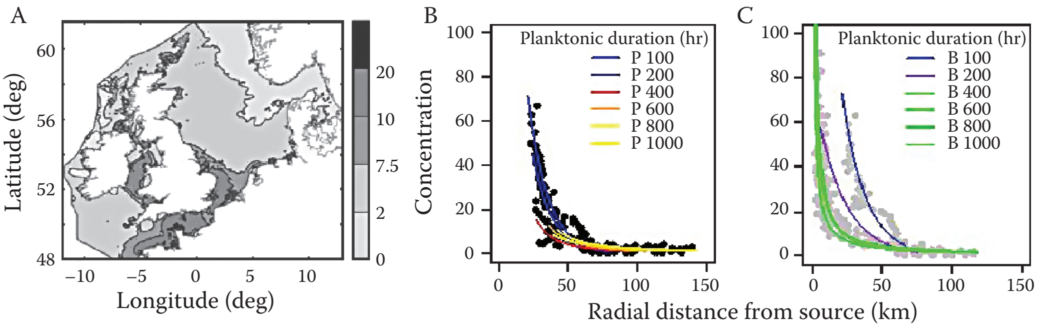

Figure 9 (A) The average tidal excursion distance (km) per semi-diurnal tidal cycle (M2) and generalized dispersal kernel estimates (larval concentration km^{-2}) for a range of planktonic larval durations (h) from a source population predicted by (B) physical forcing only and (C) physical forcing plus biological traits. In (B) and (C), the same colour regression line indicates no significant difference (at $P = .05$) in the dispersal kernel estimate within or between (B) physical and (C) biophysical models. (Figure 9A was redrawn from Polton et al. 2014 with permission from Taylor & Francis Ltd., http://www.tandfonline.com/toc/ggaf20/current.)

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2008, Lloyd et al. 2012). Simulations can be run to examine the effects of climate change on performance of individuals of a species (i.e., planktonic larval duration) in a spatially resolved context. When coupled with data on the location of artificial structures, the interactions between these structures and climate change in facilitating species range extensions can be investigated.

The output of biophysical models is particularly useful to stakeholders, as the maps that are generated can be used to indicate areas of high or low connectivity (e.g., Figure 9). This information can support decision-making by managers to meet environmental objectives by identifying areas where dispersal potential is high, supporting natural spread, or conversely areas where dispersal potential is low, reducing the likelihood of invasive species spread. Predictions of larval retention can also aid forecasts of whether sites are likely to exhibit high or low recruitment rates (Gaines & Bertness 1992, Swearer et al. 1999, Morgan et al. 2009, Morgan et al. 2014).

In a recent study, Adams et al. (2014) used a biophysical model to examine how changes in population connectivity may arise following the introduction of artificial structures in the marine environment. They showed that dispersal was driven by advection by wind forcing and boundary layer hydrodynamic processes, with propagules remaining close to the coast during dispersal. New habitat (i.e., the artificial structures) increased the theoretical population size, increased the likelihood of settlement, and facilitated access to previously inaccessible areas, particularly for short planktonic duration species (Adams et al. 2014). This type of analysis has the potential to shed light on sources of species as well as indicate possible locations for colonization.

Alternatively, the use of a physical model excluding any biological trait information may also provide valuable insights into areas of high and low connectivity (Largier 2003). For example, Polton (2014) characterized tidal excursion distances in and around the United Kingdom and Ireland (Figure 9A). This analysis revealed water retention time varied by an order of magnitude at local or subregional scales. If the physical environment alone can act as a suitable proxy for dispersal (Figure 9B), then this type of output could feasibly be used to highlight areas of larval retention (self-recruitment) or dispersal (connectivity) and support decision-making related, for example, to the placement of artificial structures to minimize connectivity. This approach, however, may not be suitable for species with longer planktonic larval durations. Certainly, a number of studies have highlighted the potential of larval behaviour to decouple dispersal predictions from estimates generated by physical (hydrodynamic) forcing alone (e.g., Shanks et al. 2003, Shanks 2009, Phelps et al. 2015), particularly for species with planktonic larval durations exceeding 10–100 hours (Shanks 2009, Knights et al. unpublished data; Figures 9B, 9C). Certainly, larval behaviour is often cited as playing a crucial role in determining dispersal distance and may well be responsible for the general failure of biophysical models to replicate patterns in nature (Jenkins 2005, Marshall et al. 2010).

The problem: biotic homogenization

Ocean sprawl—the proliferation of artificial structures—can be likened to urbanization (McKinney 2006) and is one of the most homogenizing human activities in the marine environment. Artificial structures are built to meet the relatively narrow needs of humans. They have traditionally been built with little consideration for the habitats that they replace and the communities that they inevitably support. In comparison to analogous hard-bottom natural habitats, these structures are more physically homogeneous at a range of spatial scales (Moschella et al. 2005, Burcharth et al. 2007). It is ultimately this physical homogenization of the environment that drives biotic homogenization—the process by which species invasions and extinctions increase the genetic, taxonomic, or functional similarity among locations at regional and global scales (see review by Streftaris et al. 2005). Biotic homogenization is now considered a discrete component of the broader biodiversity crisis, with significant ecological, evolutionary, and social consequences.

The diversity resistance hypothesis states that diverse communities are highly competitive and therefore more resistant to invasion (Elton 1958, Levine & D'Antonio 1999, Stachowicz et al. 2002b). This hypothesis has been tested and supported by many experimental studies in marine systems (Stachowicz et al. 1999, Stachowicz et al. 2002b, Arenas et al. 2006). Artificial structures are often characterized by lower species diversity and density than natural habitats (Bulleri & Chapman 2004, Moschella et al. 2005, Moreira et al. 2007, Vaselli et al. 2008), and the establishment of invasive species on artificial structures could therefore be enhanced by the lower diversity and weaker competitive interactions. This might also be exacerbated by artificial structures often being subject to high levels of disturbance, which facilitate colonization by opportunistic species.

Predation (including grazing) is an important element of biotic resistance (Simkanin et al. 2013). Predator abundance can differ between natural and artificial habitats (Dumont et al. 2011, Forrest et al. 2013). Artificial structures, especially those that lack structural complexity or are separated from natural substrata, may have a lower abundance of mobile predators (Chapman 2003, Chapman & Blockley 2009, Dumont et al. 2011) and therefore may act as refuges for the establishment of non-indigenous species. In natural habitats, where generalist predator numbers are greater, there may be increased resistance to invasion by newly arriving propagules (Forrest et al. 2013).

Understanding the factors and processes sustaining the biodiversity of artificial habitats and assessing their influences on establishment of non-indigenous species is therefore of key importance for our ability to predict and manage future pathways of invasion in coastal areas. Furthermore, the design of artificial structures in such a way that they enhance biodiversity is one management option that not only will increase the biotic value of the structure but also will increase the resilience of the assemblages on these structures to biotic invasion (Elton 1958, Stachowicz et al. 1999, Stachowicz et al. 2002b, Arenas et al. 2006). We discuss possible options for biodiversity management and enhancement in the following section.

Managing artificial structures

In the previous sections we illustrated how ocean sprawl or the global proliferation of artificial structures is occurring at an increasing rate along coastlines and in nearshore waters. There are significant environmental impacts associated with their construction, operation, and decommissioning (Dafforn et al. 2015b). Without planning and long-term management any structure that is placed in the sea can become a pollutant or hazard that contributes to the further degradation of the marine environment (Chou 1997). Here we consider options for managing marine development and provide recommendations for existing and future developments (Table 1). Our primary focus

Table 1 Management options for existing structures, with selected examples from the published literature

Approach	Description	Summary of major findings	Location	References
Manipulating species				
Transplantation	Corals and sponges transplanted on to intertidal seawalls	Higher survival of massive and encrusting species	Singapore	Ng et al. (2015)
	Corals transplanted on to natural and artificial reefs	Higher survival and growth on artificial reef	Israel	Perkol-Finkel & Benayahu (2009)
	Kelp transplanted on to subtidal pilings	Showed that kelp can be transplanted successfully onto artificial structures	Australia	Marzinelli et al. (2009)
	Canopy algae transplanted on to subtidal rock breakwaters	75% survival after 6 months, indicating this is a viable rehabilitation option	Italy	Susini et al. (2007)
	Mussel cultivation in disused docks	Significant improvement in water quality, elimination of harmful algae	United Kingdom	Conlan et al. (1992), Hawkins et al. (1992a,b, 1999), Allen & Hawkins (1993), Russell et al. (1983), Allen et al. (1995), Wilkinson et al. (1996)
Augmentative biocontrol	Use of native species to prevent establishment and spread of non-natives on subtidal artificial structures	Settlement of non-natives reduced by native species predation and space occupancy	New Zealand	Atalah et al. (2013a,b, 2014, 2015), Forrest et al. (2013)
Removal	Chemical or physical removal of non-native species	Results vary according to location, method, and species	Various	Farnham & Gareth-Jones (1974), Critchley et al. (1986), Carver et al. (2003), Hewitt et al. (2005), Coutts & Forrest (2007), Forrest & Hopkins (2013), McCann et al. (2013), Aldred & Clare (2014)
Ecoengineering				
Tiles	Concrete ‘artificial units of habitat’ (AUHs) affixed to natural intertidal rocky reef	Deployed for research purposes but demonstrate habitat provision by artificial surfaces	Australia	Chapman et al. (2008)
	Pitted tiles affixed to intertidal rock armour	Many, smaller (14-mm) pits supported more species than fewer, larger (32-mm) pits	United Kingdom	Moschella et al. (2005), Witt et al. (2012)

Continued

Table 1 (Continued) Management options for existing structures, with selected examples from the published literature

Approach	Description	Summary of major findings	Location	References
	Textured slabs (±grooves and pits) affixed to intertidal rock armour	Mussel and periwinkle abundance higher on pitted/grooved slabs	Netherlands	Borsje et al. (2011)
	Concrete tiles of varying complexity affixed to intertidal rock armour (Figure 11B)	Higher species richness on more complex tiles	Singapore	Loke et al. (2014)
	Textured concrete tiles affixed to intertidal rock	Higher barnacle cover on grooved compared to smooth tiles	United Kingdom	Coombes et al. (2015)
Drilling	Pits drilled into intertidal seawall	Higher limpet abundance in areas with experimentally drilled pits	Azores	Martins et al. (2010)
	Pits and grooves drilled into intertidal seawall	Smaller pits generally supported more limpets and chitons than larger pits and grooves	Australia	Chapman & Underwood (2011)
	Pits of different diameters drilled into intertidal concrete wave-breaker units (Figure 10A)	Higher species richness in pitted than control areas; no pit diameter effect	United Kingdom	Firth et al. (2014)
	Shallow (5-cm) and deep (12-cm) rock pools drilled into intertidal rock armour (Figure 10B)	After 6 months, higher taxon richness in shallow pools; no difference after 18 months	United Kingdom	Firth et al. (2014), Evans et al. (2015)
Manipulate concrete	Rock pools created in poured concrete on intertidal causeway (Figure 10D)	Lower pools supported greater diversity than upper pools; lower-shore kelp found in upper pools; sheltered pools filled up with sediment	Ireland	Firth (unpublished)
	Pools created in concrete on intertidal groyne (Figure 10C)	Important habitat-forming coralline algal germlings found in pools	United Kingdom	Firth et al. (2014)
	Pits, grooves, and recesses in concrete between blocks of intertidal seawall (Figure 11A)	Recesses supported greater species richness than other treatments	United Kingdom	Firth et al. (2014)

Continued

Table 1 (Continued) Management options for existing structures, with selected examples from the published literature

Approach	Description	Summary of major findings	Location	References
	Water-retaining depressions created between blocks on intertidal seawall	Depressions rapidly colonized by rock pool fauna	Australia	Chapman & Underwood (2011)
	Indentations created in concrete between blocks on intertidal seawall	Indentations supported greater richness of algae and sessile invertebrates	Australia	Dugan et al. (2011)
Precast concrete units	Prototype BIOBLOCK with multiple habitats (pits, ledges, pools) replace boulder in intertidal rock armour breakwater (Figure 10E)	Diversity of habitats rather than any particular one drove greater diversity on BIOBLOCK compared to surrounding boulders	United Kingdom	Firth et al. (2014)
	Precast Econcrete® rock pools deployed in intertidal rock armour revetment (Figure 10F)	Pools supported high epibiotic cover and a range of fauna typical of rock pools	USA	Perkol-Finkel & Sella (2015)
	Precast Econcrete piling jackets deployed on subtidal pier pilings	Concrete jackets supported higher epibiotic cover than control fibreglass jackets	USA	Perkol-Finkel & Sella (2014)
	Precast modified flowerpots attached to intertidal seawalls (Figure 11E)	Epibiotic diversity and abundance higher in pots than on seawall	Australia	Browne & Chapman (2011), Browne & Chapman (2014), Morris (unpublished)
	Large-scale precast concrete faciae of various designs attached to subtidal and intertidal seawalls (Figures 11C, 11D)	Results varied among treatments but diversity and abundance generally higher than on existing seawalls	USA	Toft et al. (2013)
	Artificial reefs for restoration and rehabilitation of target species	Econcrete armouring units, Oyster Castles®, Reef Balls, Tecnoreef®, WABCORE units	Various	Harris (2009), Kingsley-Smith et al. (2012), Dafforn et al. (2015), Ponti et al. (2015), Perkol-Finkel (unpublished)
Other	Novel habitats (rock pools, shaded substrata) created on intertidal seawall by replacing blocks with a lip	Novel habitats increased diversity of epibiota, particularly higher on the shore	Australia	Chapman & Blockley (2009)

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Table 1 (Continued) Management options for existing structures, with selected examples from the published literature

Approach	Description	Summary of major findings	Location	References
	Rock piles (habitat benches) constructed adjacent to seawalls to create shallow water	Habitat benches generally supported greater abundance of larval and juvenile fish than control sites, also diverse macroalgae	USA	Toft et al. (2013)
	Construction of rock pools on top of intertidal seawall	Reports of debris accumulation despite large openings for tidal flow	Australia	Chapman & Underwood (2011)
	Gabion baskets containing rocks of different sizes	No significant difference in species richness but total abundance greater in small rock treatments	United Kingdom	Firth et al. (2014)
	Changing slope of seawalls	Abundance of mobile organisms and percentage cover of sessile organisms higher on vertical than horizontal surfaces	Australia	Chapman & Underwood (2011)
	Treating surfaces with chemical cues to promote recruitment	Enhanced recruitment around treated surfaces	Tunisia	Rivera-Ingraham et al. (2011)
Site or structure designation				
Site of Special Scientific Interest (SSSI)	Protected areas designated for biological, geological, or physiographic interest	Network of intertidal coastal defence structures at Elmer (United Kingdom) proposed in 2007 as a candidate SSSI due to vegetated shingle and organisms colonizing the breakwaters; no update since	United Kingdom	Burcharth et al. (2007)
Rigs-to-Reefs	Conversion of decommissioned offshore oil/gas rigs into artificial reefs	Applied widely in Gulf of Mexico, but few data to assess 'success' of the practice or for comparison of different techniques	Gulf of Mexico	Kaiser & Pulsipher (2005), Macreadie et al. (2009), Sammarco et al. (2014)
Renewables-to-Reefs	Proposed conversion of decommissioned wind farms into artificial reefs	Recently suggested but not yet implemented	Europe	Smyth et al. (2015)

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Continued

Table 1 (Continued) Management options for existing structures, with selected examples from the published literature

Approach	Description	Summary of major findings	Location	References
Artificial Marine Micro Reserve (AMMR)	Proposed designation of artificial structures as refuges for endangered species	Network of AMMRs proposed for the western Mediterranean	Western Mediterranean	García-Gómez et al. (2011, 2014)
Marine reserves	Areas designated to protect natural or cultural resources; levels of human activity (e.g., fishing, diving) will be site specific	Oil/gas platforms and wind farms described as de facto marine reserves due to the 'artificial reef effect' and exclusion of fishing; official designation could be applied to these locations during operation	Gulf of Mexico, North Sea	Wilhelmsson et al. (2006), Wilhelmsson & Malm (2008), Inger et al. (2009), Wilson & Elliott (2009), Feary et al. (2011), Reubens et al. (2011, 2013), Witt et al. (2012), Ashley et al. (2014), Pearce et al. (2014)

is the protection and promotion of native biodiversity with the ultimate goal of limiting undesirable biological homogenization. We identify management strategies for the cultivation of biodiverse communities through manipulations of target species, simple engineering interventions to create novel habitats, and designation of protective status. We also identify potential management strategies for future developments that offer opportunities to undertake an ecosystem approach to coastal defence by rehabilitating degraded natural habitats or working with stakeholders to create multifunctional structures. We outline how marine spatial planning can inform management decisions and briefly discuss how stakeholder engagement and perceptions may be used to inform future development plans.

Management of existing structures

Any hard structure placed in the marine environment will ultimately become fouled by sessile species (Wahl 1989, Dürr & Watson 2010, Bracewell et al. 2013) and attract mobile organisms such as fish and crustaceans (Collins et al. 1994, Jensen 2002, Langhamer & Wilhelmsson 2009). Occasionally, these colonizing communities can provide valuable ecosystem goods and services such as fisheries, carbon sequestration, and water purification, amongst others (Table 2; e.g., Langhamer & Wilhelmsson 2009, Gkoumas et al. 2013, Layman et al. 2014), or be of conservation importance (Table 3; e.g., Gass and Roberts 2006, Martins et al. 2010, García-Gómez et al. 2014, Pearce et al. 2014, Firth et al. 2015a). In contrast, they can also support non-indigenous, pest, and harmful species (e.g., Bulleri & Airoldi 2005, Villareal et al. 2007, Lo et al. 2008, Firth et al. 2011, Mineur et al. 2012). Of course, there are many situations where the desirable end point is no fouling community (e.g., ships, aquaculture), and an increasing number of antifouling technologies are being developed to prevent settlement of marine organisms (Whelan & Regan 2006, Grozea & Walker 2009, Chapman & Regan 2012). With accumulating knowledge from best practice, simple and cost-effective measures can be used to achieve multiple ecosystem services, such as local biodiversity maintenance, provision of harvestable species, and protection of rare or endangered species.

Species manipulations: removals and transplantations

In comparison to terrestrial systems, the manipulation of organisms for purposes other than human consumption (aquaculture) is not well developed in marine systems. Here we outline some examples

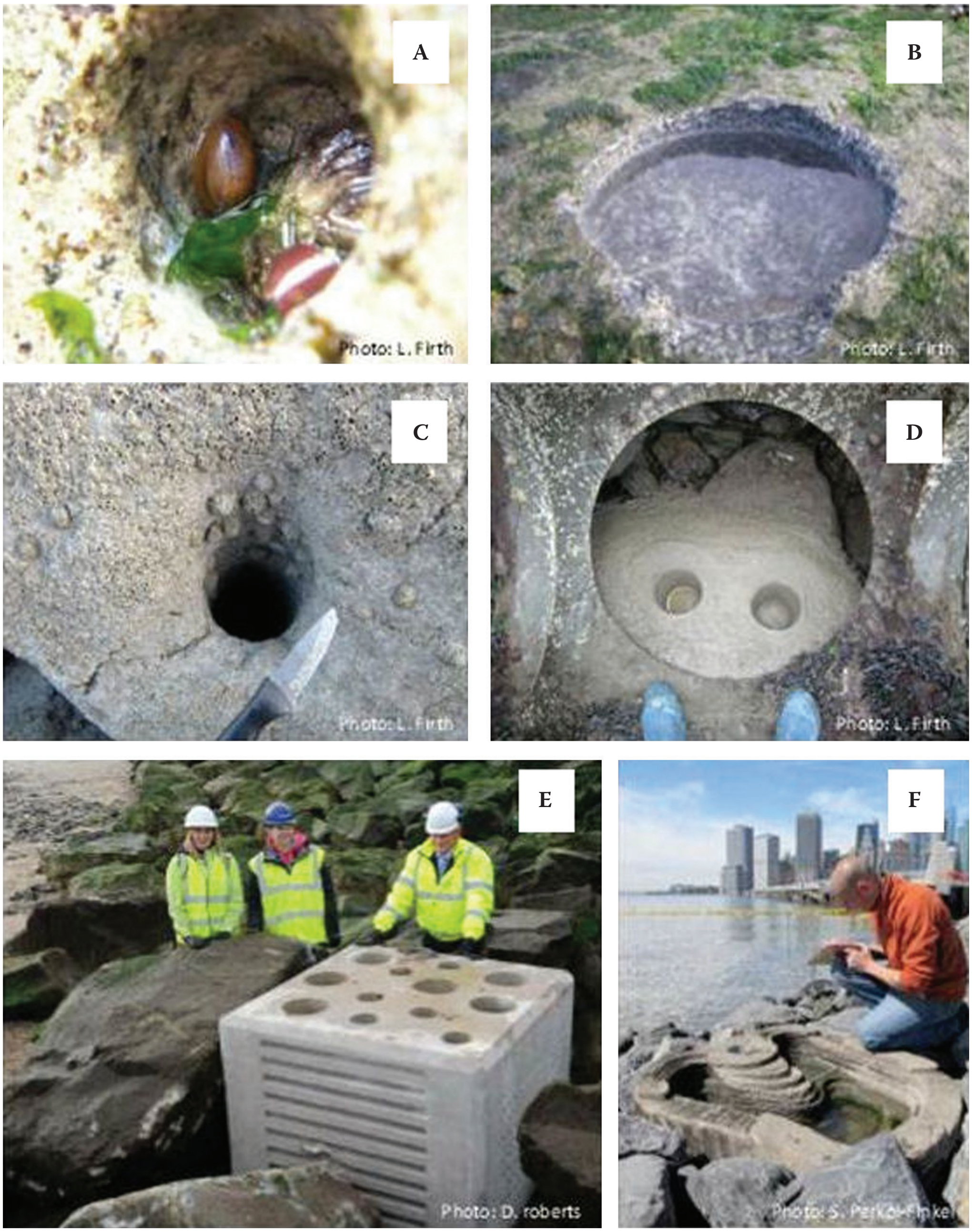

Figure 10 Variety of different ecological engineering techniques that can be incorporated into rock revetment or riprap. (A) Pits drilled into wave-breaker units on Plymouth Breakwater, United Kingdom (Firth et al. 2014). (B) Rock pools drilled directly into boulders on Tywyn Breakwater, United Kingdom (Firth et al. 2014, Evans et al. 2015). (C) Drill-cored hollows infilled with concrete to retain water at Penrhyn Bay, United Kingdom (Firth et al. 2014). (D) Concrete poured at base of SHED units in Galway Bay, Ireland (Firth unpublished). (E) Precast concrete BIOBLOCK with multiple habitat types at Colwyn Bay, United Kingdom (Firth et al. 2014). (F) Precast concrete rock pools in Brooklyn Bridge Park, United States (Perkol-Finkel & Sella 2015).

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AU: Indicate whether Firth et al. 2014a or 2014b (NOTE: a and b designations reversed from your original) four times this caption. Also, indicate if the figures were taken from their source given and if permission needed/in hand.

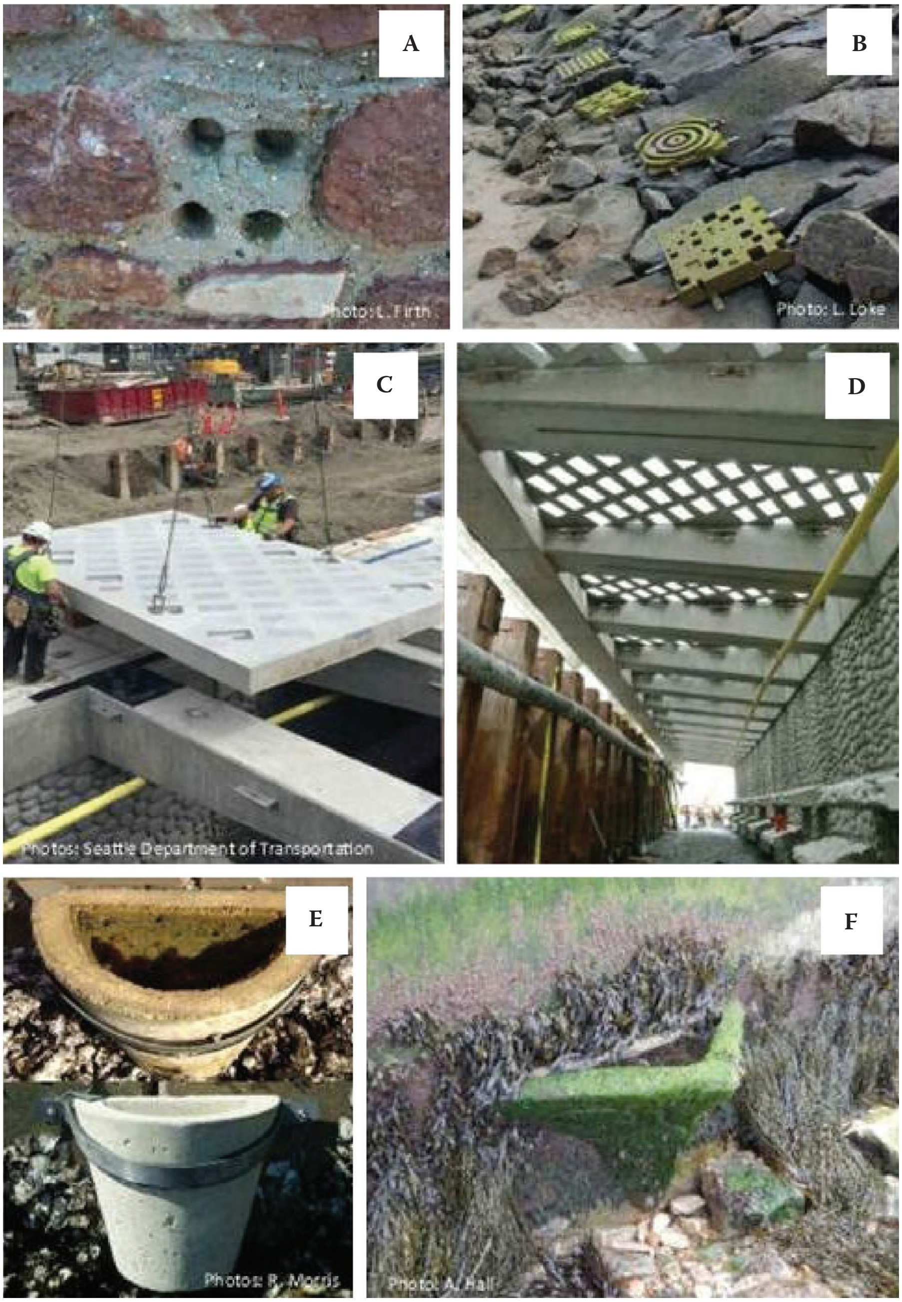

Figure 11 Variety of different ecological engineering techniques that can be incorporated onto seawalls. (A) Pits created by manipulating the concrete between bricks on a seawall, Shaldon, United Kingdom (Firth et al. 2014). (B) Precast habitat enhancement plates/tiles with different levels of complexity affixed to a seawall in Pulau Hantu, Singapore (Loke et al. 2014, 2015). (C, D) Large-scale precast facia fronting urban seawalls in Seattle, Washington, USA (Toft et al. 2010, 2013). (E) Modified precast concrete flowerpots affixed to seawalls in Sydney, Australia (Browne & Chapman 2011, 2014, Morris unpublished). (F) Precast concrete Vertipool affixed to seawall on the Isle of Wight, United Kingdom (http://www.ecclestongeorge.co.uk).

AU: Indicate whether Firth et al. 2014a or 2014b (NOTE: a and b designations reversed from your original). Also, indicate if the figures were taken from their source given and if permission needed/in hand.

Table 2 Summary of organisms providing important ecosystem services associated with artificial structures

AU: Verify that revised heads for Table 2 are OK.

Service	Descriptor	Type of structure	References
Provisioning	Commercially important shellfish	Coastal defences	Bacchiocchi & Airoldi (2003), Devescovi & Iveša (2008), Jackson et al. (2008), Martins et al. (2010), Dafforn et al. (2012)
	Commercially important finfish	Oil and gas platforms, coastal defence structures	Page et al. (1999), Toft et al. (2007, 2013), García-Gómez et al. (2014)
	Commercially important crustaceans	Renewable energy installations, coastal defence structures	Langhamer & Wilhelmsson (2009), Langhamer et al. (2009), Wehkamp & Fischer (2013), Ashley et al. (2014), García-Gómez et al. (2014)
	Nursery habitat for fish and crustaceans	Renewable energy installations, coastal defence structures	Caine (1987), Able et al. (1998), Martin et al. (2005), Langhamer & Wilhelmsson (2009), Langhamer et al. (2009), Scyphers et al. (2015)
	Overexploited species	Coastal defences	Guerra-García et al. (2004), Devescovi & Iveša (2008), Martins et al. (2010)
Regulating	Carbon sequestration	Potentially all structures	Chung et al. (2011), Gkoumas et al. (2013)
	Water purification	Potentially all structures	Allen et al. (1992, 1995), Allen & Hawkins (1993), Wilkinson et al. (1996), Kohata et al. (2003), Hughes et al. (2005a), Layman et al. (2014)
	Wave attenuation	Coastal defences	Borsje et al. (2011), Firth et al. (2015a)
Cultural	Protection of bathing beaches	Coastal defences	Lamberti & Zanuttigh (2005)
	Scuba diving	Artificial reefs, oil rigs, coastal defences	Stolk et al. (2007), Wilhelmsson et al. (1998)
	Bait digging, shellfish gathering	Coastal defences	Airoldi et al. (2005)
	Recreational fishing	Artificial reefs, harbours, coastal defences	Fayram & de Risi (2007)
	Education (e.g., rock pooling)	Coastal defences	Burcharth et al. (2007), Herbert et al. (2011, 2013), Firth et al. (2013)
	Scientific research	Artificial reefs	Wilding & Sayer (2002), Wilding (2014)
	Surfing	Artificial surf reefs, multipurpose reefs	Black (2001), Fletcher et al. (2011)
Supporting	Primary production by algae and corals	Potentially all structures	Southward & Orton (1954), Sammarco et al. (2004), Firth et al. (2014)
	Habitat provision for other species	Potentially all structures	Borsje et al. (2011), Perkol-Finkel et al. (2012), Pearce et al. (2014), Firth et al. (2015)

AU: Indicate whether Airoldi et al. 2005a or 2005b

AU: Provide Herbert et al. 2011. Or, do you mean Herbert 2011 as provided?

AU: For all Firth et al. 2013, 2014, 2015 entries in the table indicate whether you mean the a or b entry (i.e., 2013a, 2013b, 2014a, 2014b, 2015a, 2015b).

Table 3 Summary of organisms of conservation importance associated with artificial structures

AU: Verify that revised heads for Table 3 are OK.

Taxa	Relevant legislation	Type of structure, location	References
Algae			
Cystoseira amentacea var. *stricta, C. barbata, C. compressa*	Bern	Coastal defences, northern Adriatic	Susini et al. (2007), Perkol-Finkel et al. (2012), Firth et al. (2014), Ferrario et al. (unpublished)
Lithophyllum byssoides	Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)

Continued

Table 3 (Continued) Summary of organisms of conservation importance associated with artificial structures

Taxa	Relevant legislation	Type of structure, location	References
Porifera			
Spongia agaricina	Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Tethya aurantium	Barcelona	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Anthozoa			
Astroides calycularis	CITES, Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Corralium rubrum	Bern	Artificial reefs, Monaco	Allemand et al. (2000)
Lophelia pertusa	CITES, Habitats	Oil platforms, North Sea	Gass & Roberts (2006)
Polychaeta			
Sabellaria alveolata	Habitats	Coastal defences, western United Kingdom	Firth et al. (2013, 2015), Evans et al. (2015)
Sabellaria spinulosa	Habitats, Bern	Renewable energy installations, southern North Sea, United Kingdom	Pearce et al. (2014)
Mollusca			
Charonia lampas, Dendropoma petraeum, Lurida lurida	Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Cymbula nigra	Bern, Barcelona	Coastal defences, western Mediterranean	Rivera-Ingraham et al. (2011), García-Gómez et al. (2014)
Lithophaga lithophaga	CITES, Bern, Habitats	Coastal defences and harbours, western Mediterranean and Adriatic	Devescovi & Iveša (2008), García-Gómez et al. (2014)
Patella ferruginea	Bern, Habitats	Coastal defences, western Mediterranean	Guerra-García et al. (2004), Espinosa et al. (2006, 2008), Rivera-Ingraham et al. (2011), García-Gómez et al. (2014)
Patella candei	Bern	Seawalls, Azores, Portugal	Martins et al. (2010)
Pinna nobilis	Bern, Barcelona, Habitats	Sediments near coastal defences, western Mediterranean	García-Gómez et al. (2014)
Pinna rudis	Bern	Sediments near coastal defences, western Mediterranean	García-Gómez et al. (2014)
Crustacea			
Homarus gammarus	Bern	Coastal defences and marine renewable energy installations, western Mediterranean	Langhamer & Wilhelmsson (2009), Garcia-Gomez et al. (2014)
Maja squinado	Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Palinurus elephas	IUCN (VU), Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)

AU: Indicate whether Espinosa et al. 2006a or 2006b.

AU: Rivera-Ingraham et al. 2011 OK as provided?

Continued

Table 3 (Continued) Summary of organisms of conservation importance associated with artificial structures

Taxa	Relevant legislation	Type of structure, location	References
Scyllarus arctus	IUCN (LC), Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Echinodermata			
Centrostephanus longispinus	Bern, Barcelona	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Echinus esculentus	IUCN (LR/NT)	Coastal defences, Isle of Man	Moore (1934)
Paracentrotus lividus, Ophidiaster ophidianus	Bern	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Osteichthyes			
Caranx crysos	CITES, IUCN (LC), Bern	Oil platforms, northern Gulf of Mexico	Keenan (2002)
Hippocampus brevirostris	CITES, IUCN (data deficient), OSPAR, Bern, Barcelona	Coastal defences, western Mediterranean	García-Gómez et al. (2014)
Hippocampus abdominalis, H. whitei	CITES, IUCN (data deficient)	Swimming nets, Sydney harbour, Australia	Clynick (2008), Hellyer et al. (2011)
Epinephelus coioides	IUCN (NT)	Artificial reefs, Arabian Gulf	Feary et al. (2011)
Epinephelus marginatus	IUCN (EN), Bern	Coastal defences and artificial reefs, western Mediterranean	Charbonnel et al. (2002), García-Gómez et al. (2014)
Oncorhynchus tshawytscha	ESA	Coastal defences, Puget Sound, USA	Toft et al. (2010, 2013)
Sciaena umbra	CITES, Bern	Coastal defences and artificial reefs, western Mediterranean	Charbonnel et al. (2002), García-Gómez et al. (2014)
Chondrichthyes			
Pristis pectinata	IUCN (CR), CITES, ESA	Seawall-lined canals, Florida	Poulakis et al. (2013)
Rhincodon typus	CITES, IUCN (VU), UNCLOS, CMS	Oil platforms, Arabian Gulf	Robinson et al. (2013)

Note: Species were selected if protected under international or national legislation. Barcelona, Convention for the Protection of the Mediterranean Sea Against Pollution; Bern, Bern Convention on the Conservation of European Wildlife and Natural Habitats; CITES, Convention on International Trade in Endangered Species of Wild Fauna and Flora; CMS, Convention on the Conservation of Migratory Species of Wild Animals; ESA, Endangered Species Act, USA; Habitats, EU Habitats Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora; IUCN, International Union for Conservation of Nature Red List (categories: LC, Least Concern; LR, Lower Risk; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered); UNCLOS, United Nations Convention on the Law of the Sea.

of pioneering research on methods of removal of non-indigenous species and the transplantation of desirable species on to artificial structures. All of the examples that follow are from relatively recent studies, and it must be noted that this form of marine wildlife management is very much in its infancy. Much more research is required before removals or transplants can be advocated as generic management strategies for artificial structures.

Removal of non-indigenous species

Regarding removal of non-indigenous species, there are several examples where traditional methods (e.g., physical and chemical control) have been used in unsuccessful attempts to control or eradicate marine pests such as the colonial ascidian *Didemnum vexillum* (Coutts & Forrest 2007, Forrest & Hopkins 2013, McCann et al. 2013); the solitary ascidian *Ciona intestinalis* (Carver et al. 2003, Aldred & Clare 2014); and the brown macroalgae *Sargassum muticum* (Farnham & Gareth-Jones 1974, Critchley et al. 1986) and *Undaria pinnatifida* (Hewitt et al. 2005). There are many challenges and limitations with traditional control methods for target marine pests, especially those that rely on chemical treatment or repeated diver detection, maintenance, and removal of visible organisms (Caffrey et al. 2010, 2011, Atalah et al. 2013a). Atalah et al. (2014) advocated that many of the limitations could be overcome with biocontrol (i.e., control by natural predators, either native or non-indigenous) as effective control agents will have a sustained effect on all life stages of target species or multispecies assemblages. This method of control of non-indigenous species is relatively well established in terrestrial and freshwater aquatic systems (e.g., Newman et al. 1996, Baars et al. 2010, Mangan & Baars 2013). Despite the promising preliminary results to date, this field is very much in its infancy in the marine environment (but see Atalah et al. 2013a,b, 2014, 2015), and further research is needed in this area.

Transplanting of desirable species

The growth of ecologically valuable benthic communities can be promoted through direct transplanting of desirable target species. The transplanting of corals on to artificial reefs has long been common practice in coral-reef rehabilitation and fisheries enhancement on artificial reefs (e.g., Clark & Edwards 1994, Perkol-Finkel & Benayahu 2009). In a recent study Ng et al. (2015) investigated the feasibility of transplanting corals and sponges to the intertidal zone of seawalls. After only 18 months, species with massive and encrusting growth forms were most successful at establishing on the seawall and were even observed to provide food and shelter for reef fish and gastropods. Despite the short-term nature of this study, the results indicated that the transplantation of nursery-reared reef biota is a viable strategy that enhances the ecological value of seawalls. Habitat-forming algae (e.g., *Cystoseira barbata*) can be successfully transplanted on to artificial structures (Falace et al. 2006, Susini et al. 2007, Perkol-Finkel & Airoldi 2010, Perkol-Finkel et al. 2012), but care should be taken to protect younger individuals from biotic disturbance from grazers (Ferrario et al. unpublished data).

Mussels are important filter-feeders and provide an important biofiltration service by removing toxins and particulates and preventing unsightly and potentially toxic phytoplankton blooms, contributing to improved water quality in both natural and artificial settings (e.g., Wilkinson et al. 1996). One example from the United Kingdom describes how mussels settled on to ropes in an experimental fish farm (Russell et al. 1983, Hawkins et al. 1992a,b) and were transplanted into experimental docks in Liverpool, leading to recovery of these enclosed artificial ecosystems (Allen et al. 1992, Allen & Hawkins 1993, Allen et al. 1995, Wilkinson et al. 1996).

Eco-engineering: creating novel habitats for biodiversity enhancement

The field of eco-engineering (the integration of ecological, economic, and societal needs in the design of artificial habitats) has received much attention in recent years (for reviews, see Dugan et al. 2011, Dafforn et al. 2015a,b, Dyson & Yocom 2015). A major output of this surge of research has been a wide range of studies that have implemented small-scale modifications on artificial structures that can be widely applied in a range of different situations. Due to access and cost implications, the vast majority of this work has focused on intertidal seawalls and coastal defence structures. A number of recent reviews provided excellent summaries of the different management approaches to coastal development (see Dyson & Yocom (2015) for a comprehensive review of ecological design for urban waterfronts and Dafforn et al. (2015a) for a broader approach to restoration and hard and soft engineering).

Here we specifically cover the various ecological engineering techniques that have been tested on hard artificial structures (Figures 10 and 11; Table 1). On artificial structures in the marine environment eco-engineering is largely implemented to increase heterogeneity and complexity of otherwise topographically simple and featureless substrata. Ideally, engineering modifications should be implemented during construction (see the discussion that follows). A range of options is also available for retrofitting enhancements on to existing structures. Microhabitats such as pits, crevices, and rock pools are important refuges from abiotic and biotic stress and disturbance on natural rocky shores, thus supporting diverse communities (Moschella et al. 2005, O'Connor & Crowe 2005, Firth et al. 2009, Firth & Crowe 2010). These microhabitats are largely absent from artificial structures (Moschella et al. 2005, Firth et al. 2013b).

Texturing and the addition of pits and ledges (millimetre-centimetre scale)

The incorporation of surface roughness, pits, grooves, and ledges can facilitate the persistence of species that would not normally be able to live on a featureless surface (Firth et al. 2014b). They can also promote species of conservation and commercial importance (Martins et al. 2010). Surface roughness and pits and crevices can be incorporated directly on to artificial structures by drilling directly into the substratum (Figure 10A; Martins et al. 2010, Firth et al. 2014b); by manipulating the concrete between the blocks on seawalls (Figure 11A; Chapman & Underwood 2011, Firth et al. 2014b); or by affixing precast or predrilled habitat enhancement tiles or plates (Figure 11B–11D; Moschella et al. 2005, Chapman et al. 2008, Borsje et al. 2011, Witt et al. 2012, Toft et al. 2013, Loke et al. 2014, Coombes et al. 2015). Recently, 3-dimensional printing has been used to create artificial enhancement units (Talia Sherrard personal communication).

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Water-retaining features (centimetre-metre scale)

Water-retaining features (i.e., rock pools) are particularly important in artificial habitats (Moschella et al. 2005, Firth et al. 2013a). A wide range of techniques has been tested on seawalls and coastal defences, all of which had similar results, increasing taxon richness and functional diversity (Table 1; Figures 10 and 11). Deep and shallow pools drilled directly into the boulders of rock armour at Tywyn in Wales showed no significant differences in colonizing diversity but did show differences in community structure (Figure 10B; Firth et al. 2014b, Evans et al. 2015). Even after 18 months, the cumulative number of taxa colonizing the pools had not levelled off (Evans et al. 2015), indicating that a greater diversity of transient and ephemeral taxa were utilizing the novel habitats at different times of year. This intervention requires horizontal or near-horizontal substrata but can be implemented in locations of all exposures, ranging from sheltered to very exposed. The drilled pools remained undamaged following the extreme storms of 2013–2014 (Evans personal observations), indicating that drilling pools may represent a long-term option that will be resilient to storm and wave damage.

AU: Provide first initial for Evans.

AU: Provide country for Sydney if not Australia.

Pools were incorporated into Sydney, Australia, seawalls during repair works by replacing sandstone blocks with a lip that retained water, thus functioning as a shaded rock pool supporting significantly greater diversity and abundance of epibiota than the existing seawall (Chapman & Blockley 2009). This option can only be implemented during construction work and in relatively sheltered environments due to danger of damage to the seawall from wave action. Depending on the size of the blocks used for constructing the seawall, the size of cavities can be varied to offer a range of different habitat types along the same stretch of seawall.

Manipulating concrete can also create rock pools. Taking advantage of cores drilled through boulders on a groyne in North Wales (Figure 10C), Firth et al. (2014) in-filled these cores with concrete to a depth of 10 cm, resulting in the creation of small pools that supported important habitat-forming crustose coralline algae after only 6 months. A potentially universal method of creating rock pools on rock armour is by pouring concrete among the boulders or concrete units. Buckets were placed in wet concrete that was poured at the base of concrete units in Galway Bay, Ireland (Figure 10D). Once the concrete had set, the buckets were removed, yielding water-retaining

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features that supported a wide variety of organisms that were not otherwise present on the structure (Firth unpublished data). These manipulations were unaffected by the severe storms of 2013–2014, which caused severe damage in Galway Bay, indicating that this option may also be a long-term solution that will be resilient to storm and wave damage.

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Precast concrete units (beyond metre scale)

A wide variety of materials has been used in artificial reef construction, including used tyres, old vehicles, boats, pipes, fibreglass, metal, building materials, and waste products from industry (Collins et al. 1994, Chou 1997, Jensen et al. 2000, Collins et al. 2002, Loh et al. 2006). The Reef Ball is perhaps one of the most famous and successful examples of a purpose-built precast habitat enhancement unit (Harris 2009) that can be used for a variety of purposes, ranging from coral and oyster reef rehabilitation to mangrove planting. This concept has been applied to artificial structures deployed in the intertidal zone with the development of a range of different precast concrete habitat enhancement units. The BIOBLOCK is a large unit that has multiple habitats in a single unit (pits, ledges, rock pools; Figure 10E) that can replace rock armouring boulders and can be retrofitted or deployed during construction (Firth et al. 2014b). The BIOBLOCK is another potentially universal method of habitat creation in rock armouring that can be implemented in a range of different exposures, ranging from sheltered to very exposed. At 5.4 t, it is unlikely to be moved during a storm and represents a potential long-term option that will be resilient to storm and wave action.

A clever way of incorporating water-retaining features on existing seawalls is the attachment of modified concrete flowerpots (Figure 11E; Browne & Chapman 2011, 2014), a concept that captured a lot of media attention in Sydney and has now been applied elsewhere (e.g., Vertipools on the Isle of Wight, UK; Figure 11F). Dyson & Yocom (2015) described seawall stairs as precast concrete steps designed to increase nearshore habitat area. These add both horizontal surfaces and microhabitat to the urban waterfront by incorporating exposed aggregate (surface texture) and depressions designed to mimic tide pools and may provide habitat, enhance food production, and improve migration corridors for juvenile salmon and other organisms (Enabling the Business of Agriculture [EBA] 2011).

Interdisciplinary research among ecologists, engineers, and materials scientists is rapidly advancing the field with the design of environmentally friendly concrete (e.g., Econcrete®) and other materials for the production of artificial reef units (Loh et al. 2006, Ponti et al. 2015); armouring units (Perkol-Finkel unpublished data); pile encapsulation (Perkol-Finkel & Sella 2014, 2015); rock pools (Figure 10F; Perkol-Finkel & Sella 2015); and seawalls (Figure 11B; Toft et al. 2013). All of this can be retrofitted to existing structures or indeed considered at the planning stage and incorporated during construction.

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Other novel approaches to habitat enhancement

Rock-filled gabion baskets and mattresses are also widely used in more sheltered locations. Preliminary work carried out by Firth et al. (2014b) revealed that by careful selection of the stone sizes it is possible to enhance diversity and abundance of epibiota, and these habitats undoubtedly provide refuge from predation as well as wave action and adverse thermal conditions for mobile fish and crustaceans. Further research is required to fully test the potential for this feature to be incorporated into design of new structures as a management option.

Habitat benches can be constructed on top of and adjacent to seawalls to create areas of shallow water. The addition of novel shallow-water habitat may provide habitat for benthic flora and fauna and mobile fish and crustaceans (Toft et al. 2010, 2013, Chapman & Underwood 2011). Finally, baskets can be attached to seawalls to support both submergent and emergent vegetation, which in turn may provide habitat and nursery grounds for other shallow-water species (Holloway & Connell 2002, Perkol-Finkel et al. 2008; see Dyson & Yocom 2015).

Designation of sites as reefs or de facto reserves

All artificial structures have the capacity to act as both artificial reefs and fish aggregation devices through the 'artificial reef effect' (e.g., Rilov & Benayahu 1998, Love et al. 1999, Helvey 2002, Reubens et al. 2011, 2013). Owing to the potential for collision between vessels and marine renewable energy installations or fishing gear entanglement, it is not possible to undertake many forms of commercial fishing within the immediate vicinity of marine renewable energy installations. Providing a refuge from intense fishing pressure, artificial structures have the potential to protect and enhance exploited stocks (Wilhelmsson et al. 2006, Wilhelmsson & Malm 2008, Langhamer et al. 2009). In recent years various authors have discussed the potential for marine renewable energy installations to act as *de facto* marine protected areas (MPAs) (Inger et al. 2009, Witt et al. 2012, Ashley et al. 2014). Ultimately, the implementation of such MPAs will also enrich benthic biota by locally eliminating the damage caused by fishing gear towed along the seabed (e.g., Pearce et al. 2014).

Artificial marine microreserves

Occasionally, endangered and threatened species can be found in high densities on artificial structures (Guerra-García et al. 2014). In the Mediterranean, overexploited molluscs have been found on coastal defence structures in harbours. The limpet *Patella ferruginea* is the most endangered invertebrate in the Mediterranean but can be found in abundance in the Port of Ceuta, Tunisia (Guerra-García et al. 2004, Espinosa et al. 2006a,b, 2008, Rivera-Ingraham et al. 2011). Similarly, the overexploited date mussel *Lithophaga lithophaga* is found in abundance on the soft limestone breakwaters in Rovinj, Croatia (Devescovi & Iveša 2008). In a similar way to marine renewable energy installations functioning as *de facto* reserves from the impacts of fishing pressure, artificial coastal constructions like breakwaters, docks, and harbours may be closed to the public and ultimately prevent harvesting and fishing (García-Gómezet al. 2011). Following the discovery of abundant populations of *Patella ferruginea* in the Port of Ceuta, there have been proposals for the establishment of artificial sites termed artificial marine microreserves (AMMRs), where some endangered species experience a refuge from human disturbance (García-Gómez et al. 2011, 2014).

AU: Provide Guerra-García et al. 2014.

Other protection status for artificial structures

Artificial structures can be considered important for other reasons, such as heritage or scientific value. Harbours, ports, and piers are often designated for their historic value, and many even have UNESCO World Heritage status. For example, the disused docks of Liverpool, England, fall within the Liverpool Maritime Mercantile City UNESCO site and represent an important example of an urban 'lagoonoid' system supporting high biodiversity in clean waters (Allen et al. 1995, Hawkins et al. 2002). Furthermore, the conservation value of the Elmer network of artificial coastal defence structures on the southern coast of England has been recognized by the proposed designation as a Site of Special Scientific Interest (SSSI). This is largely because of the vegetated shingle but also because of the animals and plants colonizing the breakwaters (Burcharth et al. 2007).

Should it stay or should it go? Applications of the Rigs-to-Reefs concept

The removal of existing structures has significant environmental and financial costs (Dafforn et al. 2015b). The typical lifespan of oil platforms and wind farms is 17.5 and 20–30 years, respectively (Pulsipher et al. 2001, Ortegon et al. 2012). Macreadie et al. (2011) estimated that 6500 oil and gas platforms are due for decommissioning by 2025, with an estimated cost of $8 billion for the Gulf of Mexico alone (Kolian and Sammarco 2005). The Rigs-to-Reefs programme was developed in the United States to convert decommissioned offshore oil and gas platforms into artificial reefs (Kaiser & Pulsipher 2005). This initiative operates under a 'win-win' premise (Rosenzweig 2003), whereby obsolete rigs are recycled as artificial reefs with the primary goal to provide substantial cost savings

Should this be US$8 billion?

for the oil and gas industry while providing secondary benefits through benthic habitat conservation and fisheries management. Macreadie et al. (2011) discussed how this perception is widely recognized despite little evidence supporting the ‘production hypothesis’ over the ‘attraction hypothesis’ (Pickering & Whitmarsh 1997). Since the implementation of the programme in the United States, similar schemes have been implemented throughout South-East Asia and Mexico. There was interest in implementing the programme in Europe, but following much debate, environmental opposition has prevented the implementation of Rigs-to-Reefs in the North Sea (Picken & McIntyre 1989, Picken et al. 2000, Baine 2002, Sayer & Baine 2002).

The Rigs-to-Reefs concept has been proposed recently as a potential management strategy, termed *renewables-to-reefs*, for the large number of European wind farms that will be decommissioned in the future (Smyth et al. 2015). This new technology means few baseline data are currently available (Ashley et al. 2014). Much of the focus of the construction of marine offshore renewable energy installations has focused on the impact on marine megafauna, birds, and the receiving environment (Carstensen et al. 2006, Drewitt & Langston 2008, Bailey et al. 2010), with little consideration of the fouling communities.

Sammarco et al. (2014) provided one of the few studies that has conducted a quantitative assessment of different options for Rigs-to-Reefs. They found no significant difference in coral density between standing and toppled oil platforms and recorded that the invasive coral *Tubastraea coccinea* was more abundant on the toppled compared to standing rigs. While Rigs-to-Reefs may potentially represent a popular and viable option by reducing access to towed fishing gear, with little existing data, careful consideration will be required in relation to the management goals, and each installation should be considered on a case-by-case basis (Smyth et al. 2015).

Planning future developments

Some of the greatest advances can potentially be made as a result of broader consideration, at the design stage, of the ecological consequences of new structures. In particular there is a need to recognize that the overarching drivers for construction in the marine environment (sea-level rise, global trade infrastructure, tourism) often operate at a much broader scale than the ‘impacts’ on society (flooding in a particular part of a town) and the associated societal responses (construction of a seawall to protect that location) (Smyth et al. 2015). Equally important in the context of this review, the ecological consequences of coastal structures can have far-reaching effects on species and habitats away from the structures themselves. Hence there is a clear need for marine spatial planning to consider synergistic and antagonistic consequences at broad spatial and temporal resolution (Kidd 2007; Fischer et al. 2009, Jay et al. 2012). Such consideration needs to be incorporated at the design and planning stage to maximize opportunities and minimize threats. For example, in large arrays of structures there could be potential to enhance stocks of commercially important species by green engineering. Similarly, it may be possible to achieve synergistic benefits by designing multifunctional structures for a range of different purposes. Overall it is important to work with nature using an ecosystem-based approach.

Ecological engineering

At present the evidence base for ecological benefits from engineering modifications comes from relatively small-scale interventions. Few studies describe eco-engineering that has been incorporated into the planning stage of a new development. In the previous section, we reviewed the range of different methods that have been retrofitted on to existing structures (Table 1). All of the examples could be considered at the design phase. Whenever and wherever possible, eco-engineering should be incorporated into a project during construction rather than retrospectively. Any manipulations will be cheaper, can be implemented on a much larger scale, can take advantage of heavy-lifting machinery on site, and can be covered by the existing licence for the construction work. They can also be considered in any environmental assessment at the design stage.

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Langhamer & Wilhelmsson (2009) conducted one of the few eco-engineering studies implemented at the design phase. They showed that small holes cast into the concrete base of wave energy converters had a significant positive effect on the abundance of the commercially important crab *Cancer pagurus*. Furthermore, the European lobster (*Homarus gammarus*) was also found to occupy these holes (Table 1). Hence, there could be real opportunities here, for example, to create local potting fisheries in areas where arrays of wind turbines now preclude fishing by trawling. Further research is essential to determine the long-term effects and in particular whether these manipulations represent new 'production' as opposed to 'attraction' of mobile organisms from elsewhere (Pickering & Whitmarsh 1997, Baine 2001, Spanier et al. 2011). Whichever applies, concentrating shellfish in defined areas makes pot and creel fisheries more productive.

Multifunctional structures

In light of the potential negative impacts of introducing additional novel habitats to the marine environment, multifunctional structures may provide a better option for fisheries enhancement and spatial efficiency. For example, secondary fisheries benefits may be designed-in to multifunctional coastal structures (e.g., Wilhelmsson et al. 2010, Zanuttigh et al. 2015) alongside their primary function as coastal defence that has been deemed essential or appropriate for shoreline management (e.g., Scyphers et al. 2015). Albertelli et al. (1995) suggested that using artificial structures for aquaculture of *Lithophaga lithophaga* might help to divert pressure from the very damaging harvesting techniques on natural reefs (Fanelli et al. 1994). However, care is needed to ensure destructive harvesting methods are still compatible with the primary function of structures. Alternatively, collocation of aquaculture with offshore industries may be viable, thereby increasing food or biofuel provision while minimizing additive impacts that would result from multiple and more dispersed developments resulting from single-use constructions (e.g., Buck et al. 2008, Zanuttigh et al. 2015). However, multifunctional usage needs to be considered from multiple perspectives (engineering, ecological, societal) to ensure synergies rather than conflicts of interest (Scyphers et al. 2015).

Water filtration by diverse rocky-reef assemblages has been linked to societal benefits of a coastal breakwater in an integrated approach to beach management in Italy (Lamberti & Zanuttigh 2005). Consequently, there is growing interest in artificial reefs (including coastal protection reefs) that are constructed from, seeded by, or are naturally colonized by oysters and other filter-feeding organisms (Piazza et al. 2005, Gao et al. 2008, Borsje et al. 2011, Reckenbeil & Ozbay 2014, Scyphers et al. 2015). It is important to consider the outcomes holistically. Wilhelmsson & Malm (2008) pointed out the risk associated with a lack of understanding of the potential for dense aggregations of filtrating animals (on wind farm pilings) to profoundly affect ecosystem dynamics (e.g., see Maar et al. 2010).

Artificial reefs used for coastal protection can also enhance recreational amenities, such as surfing, and are known as multifunctional artificial reefs (MFARs). For example, artificial surf reefs (ASRs) have been successfully developed in Australia, New Zealand, the United Kingdom, and the United States (Fletcher et al. 2011, Mead et al. 2011), with others planned for the Azores (Ng et al. 2015). Not all such constructions have functioned well for surfing activities. Constructed in 2008, Boscombe Surf Reef is a multifunctional artificial reef on the southern coast of England that has been criticized for failing as an ASR, yet its value as habitat for a wide range of organisms has been widely recognized, with it now being a popular snorkelling site as part of a larger 'coastal activity park' (Fletcher et al. 2011, Herbert et al. 2013).

Hybrid engineering and the ecosystem approach: building with nature

In addition to the potential environmental impacts and poor habitat quality of artificial structures described previously, 'hard' coastal defence approaches are often extremely expensive. In the absence of adequate coastal zone management and marine and maritime spatial planning, they can lead to inappropriate coastal development along eroding or low-lying coasts. They can also exacerbate coastal erosion through 'coastal squeeze' of natural intertidal habitats (Turner et al. 2007, Govaerts & Lauwaert 2009). Consequently, 'soft' engineering approaches, such as beach replenishment, sand dune stabilization, and managed realignment, are widely considered to be more sustainable options for flood and coastal erosion risk management (Turner et al. 2007, Govaerts & Lauwaert 2009). Nevertheless, in scenarios where no alternative options are viable for protecting people and assets, many shoreline management plans continue to recommend a strategy of 'hold the line'. This means that local authorities are required to maintain existing defences and potentially augment these with additional hard protection measures. Where hard defence structures are considered necessary for flood and coastal erosion risk management, it is essential that they be implemented with ecologically sensitive design to minimize impacts on the natural environment (Firth et al. 2014b, Hoggart et al. 2014).

Some locations are already implementing the ecosystem and hybrid approaches to coastal defence (e.g., Bilkovic & Mitchell 2013, Temmerman et al. 2013). For example, in Selangor, Malaysia, breakwaters and geotextile tubing were deployed in front of degraded mangroves at two locations, reducing wave energy and protecting seedlings of transplanted mangroves (Hashim et al. 2010, Kamali et al. 2010, Kamali & Hashim 2011, Tamin et al. 2011). Such rehabilitation practices are not currently widely used in conjunction with coastal protection (but see Perkol-Finkel et al. 2012, Firth et al. 2014b). These preliminary studies showed the potential for cost-effective habitat rehabilitation. Any rehabilitation technique, however, must take into consideration ecological principles, including detailed knowledge of the species concerned (Dafforn et al. 2015b). It is also important to have clear restoration targets against which to measure success (Hawkins et al. 2002, Knights et al. 2014) and where possible to work by 'nudging nature' (Hawkins et al. 1999) to achieve maximum leverage from natural capital. We can build on these early successes and develop a more robust and widespread use of hybrid structures viewed using an ecosystem approach. To echo the plea by Sutton-Grier et al. (2015), now is the time to design, test, research, develop, and apply hybrid structures and the ecosystem approach to protect human populations and infrastructure and strengthen coastal resilience (Spalding et al. 2014).

Managing artificial structures and infrastructure and the need for marine spatial planning

Structures placed in the sea can have impacts ranging from the local-scale (1- to 10-m) loss or modification of habitat to much larger scales (over hundreds of kilometres) by influencing networks of connectivity. Widespread habitat modification, particularly of fringing coast, modification of sediment transport across large areas of seabed by structure placement, or crossing of the seabed by power cables and pipelines can lead to modification at the 1000-km scale (Dafforn et al. 2015a, Goodsir et al. 2015). The extent and type of impact will be determined partly by the attributes of the structures themselves, for example, in the manner and extent to which they modify not only sediment transport (Wilhelmsson et al. 2010) but also their its arrangement (Dafforn et al. 2015a, Huang et al. 2015), hence the need for marine (or maritime) spatial planning.

AU: Change to Goodsir et al. 2015 correct as provided? If not, provide Goodsir 2015 and mention Goodsir et al. 2015 in text.

Many structures are built in response to local needs, often by locally focused businesses (such as holiday resorts or hotels) or authorities (ports, local municipal councils). These can then scale up over extensive stretches of coastline. Perhaps the best-documented example is in the northern Adriatic, where over 80% of the coastline is now defended, often with one defence starving an adjacent location of sediment and exacerbating erosion (Airoldi et al. 2005a, Burcharth et al. 2007). Isolated patches ('islands') of artificial, mainly hard and modified, habitats surrounded by natural, usually soft sediment, habitat can also occur. The scope for colonization of such islands (e.g., an isolated offshore rig or a single breakwater or jetty on a sandy coast) will be restricted by suitability of the receiving habitat and hydrodynamics influencing larval supply, settlement, and recruitment to adult populations as well as food supply (Floerl & Inglis 2005). For example, Airoldi et al. (2015) found non-indigenous species were two or three times more abundant on infrastructure built along sedimentary coastlines than on natural rocky reefs or infrastructure built close to rocky coastlines in the northern Adriatic. Dafforn et al. (2015b) suggested that the designs and placements of different structures could restrict (breakwaters enclosing marinas) or enhance (dense configuration of pilings, pontoons, breakwaters) larval exchange and hence connectivity (Thomas 2011). On the Adriatic coast of Italy connectivity has been increased, facilitating the spread of non-indigenous species (Airoldi & Bulleri 2011, Airoldi et al. 2015). These examples emphasize the importance of spatial planning for urban development; this is as important in the sea as on land (Dafforn et al. 2015b).

Limitations

Research focusing on the ecological consequences of coastal construction is now fairly extensive, and there are data indicating the potential for modification of engineering design to influence ecological outcomes. Our ability to achieve specific ecological objectives, such as boosting stocks of commercially important species or minimizing the spread of non-indigenous species, is still limited. One of the key drivers behind coastal construction is societal need, yet we know little about human perceptions of these constructions, in particular perceptions relating to different designs and differing ecological outcomes (but see van Loon-Steensma & Slim 2013). For example, the availability of alternative designs with known and predictable different outcomes may be valuable in gaining public engagement during the consenting process. In addition to debate about whether a structure should be built (i.e., managed retreat or soft defences), there should be discussion about what type of structure should be built (Wilson et al. 2015), including secondary outcomes. There is a growing body of work on perception of the natural world (e.g., Wyles et al. 2014, 2015) and in particular use of visualizations to help understand perceptions about future scenarios relating, for example, to flooding and climate change (e.g., Sheppard 2012, Tebboth 2014). Such approaches need to be incorporated within the planning and consenting process for coastal structures.

There is also limited understanding of the interactive effects between structures, and the underlying drivers for their construction, and other environmental challenges, such as proliferation of pest species (e.g., jellyfish) and non-indigenous species, and interactive effects with climate change. Despite this gap in our knowledge, it is important to consider construction within the context of the multiple stressors that now challenge our environment.

Future directions

Looking to the future, it is essential to consider all of the relevant concerns and benefits in a wider perspective of marine spatial planning. The deployment of artificial structures in the marine environment has the potential to cause conflict among interest groups, including the public, energy companies, the fishing sector, and environmental groups. Conflicts should be minimized by integrating key stakeholders from the outset into the design, siting, construction, and operational phases of the installations and by providing clear evidence of both positive and negative potential environmental consequences (Scyphers et al. 2015, Wilson et al. 2015). It is also important to consider this in a framework of global change so that planning considers temporal as well as spatial elements.

Concluding remarks

Often, we have considered structures either in isolation or as part of a network of similar structures, for example, windfarms (Adams et al. 2014), oil and gas platforms (Sammarco et al. 2010, 2012), coastal defences (Airoldi et al. 2015), or ports and harbours (Peters et al. 2014, Rius et al. 2014). With the increasing human population, continued ocean sprawl, the increase in global shipping, and biotic homogenization, these structures could begin to function as super ‘artificial networks’. For example, there are already some 4000 structures in the Gulf of Mexico, referred to as the ‘steel archipelago’ (Villareal et al. 2007). The challenge is therefore to take a holistic view of this bigger picture in terms of spatial scale and at the same time to consider the challenges in terms of multiple stressors (e.g., pollution, see Dafforn et al. 2009, Crooks et al. 2011; climate change, see Occhipinti-Ambrogi 2007; pest species [e.g., jellyfish], see Lo et al. 2008, Ishii & Katsukoshi 2010, Duarte et al. 2012; toxic algae, see Vila et al. 2001, Villareal et al. 2007; extreme climatic events, see Firth et al. 2011, Diez et al. 2012, 2015a, Wernberg et al. 2013, Smale & Vance 2015), both now and in the future. The potential rewards from such a holistic approach are considerable, with real opportunities for 'win-win ecology' (Rosenzweig 2003).

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