



Monograph

Effects of ocean sprawl on ecological connectivity: impacts and solutions



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ABSTRACT

The growing number of artificial structures in estuarine, coastal and marine environments is causing “ocean sprawl”. Artificial structures do not only modify marine and coastal ecosystems at the sites of their placement, but may also produce larger-scale impacts through their alteration of ecological connectivity - the movement of organisms, materials and energy between habitat units within seascapes. Despite the growing awareness of the capacity of ocean sprawl to influence ecological connectivity, we lack a comprehensive understanding of how artificial structures modify ecological connectivity in near- and off-shore environments, and when and where their effects on connectivity are greatest. We review the mechanisms by which ocean sprawl may modify ecological connectivity, including trophic connectivity associated with the flow of nutrients and resources. We also review demonstrated, inferred and likely ecological impacts of such changes to connectivity, at scales from genes to ecosystems, and potential strategies of management for mitigating these effects. Ocean sprawl may alter connectivity by: (1) creating barriers to the movement of some organisms and resources - by adding physical barriers or by modifying and fragmenting habitats; (2) introducing new structural material that acts as a conduit for the movement of other organisms or resources across the landscape; and (3) altering trophic connectivity. Changes to connectivity may, in turn, influence the genetic structure and size of populations, the distribution of species, and community structure and ecological functioning. Two main approaches to the assessment of ecological connectivity have been taken: (1) measurement of structural connectivity - the configuration of the landscape and habitat patches and their dynamics; and (2) measurement of functional connectivity - the response of organisms or particles to the landscape. Our review reveals the paucity of studies directly addressing the effects of artificial structures on ecological connectivity in the marine environment, particularly at large spatial and temporal scales. With the ongoing development of estuarine and marine environments, there is a pressing need for additional studies that quantify the effects of ocean sprawl on ecological connectivity. Understanding the mechanisms by which structures modify connectivity is essential if marine spatial planning and eco-engineering are to be effectively utilised to minimise impacts.

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1. Introduction

Continued human population growth and associated development of coasts and offshore waters have led to marine and coastal environments that are increasingly dominated by artificial (engineered) structures, termed “ocean sprawl” (Duarte et al., 2012; Firth et al., 2016a). More than 40% of the world's population and 60% of the world's largest cities are within 100 km of the coast (Tibbetts, 2002) and the proportion of the world's population living in the coastal zone is projected to further increase (Nicholls et al., 2007). This population growth has led to construction of residential and commercial developments (e.g. waterfront housing, canal estates, bridges and crossings), coastal roads, railways and transport infrastructure for shipping (e.g. berths, moorings, dolphins, shipping canals), tourism and recreational infrastructure (e.g. marinas, pilings, pontoons, mooring buoys, boat ramps and swimming enclosures), as well as structures for offshore resource extraction (wind farms, oil and gas platforms) and for intensive fisheries and aquaculture industries (see Dafforn et al., 2015a,b). Many of these developments involve land reclamation and often have to be defended (e.g. by seawalls, groynes and breakwaters) against rising and stormier seas (Titus et al., 1991; Nicholls and Cazenave, 2010; Hinkel et al., 2014).

In estuarine and coastal environments, the desire for a waterfront lifestyle has led to the construction of over 4000 linear km of residential canal estates globally, covering 270 km² of intertidal wetland habitats (Waltham and Connolly, 2011). The construction of marinas, boat ramps, wharves and docks to support recreational boating and commercial passenger services has also extensively modified urban foreshores and coastal habitats (see Dafforn et al., 2015a). International shipping accounts for >90% of global trade (IOC-UNESCO et al., 2011) and an extensive network of global port infrastructure has been developed to support these movements. Port facilities and other commercial and residential assets are protected by armouring, such as seawalls, which in some parts of Asia, America and Europe now account for >50% of shoreline (Bacchiocchi and Airoldi, 2003; Bulleri and Chapman, 2010; Dugan et al., 2011; Lee and Li, 2013).

This extensive, human-mediated, habitat modification is not just limited to coastal waters, with sprawl of infrastructure into offshore environments also recognised as an increasingly important source of

environmental and ecological change (Duarte et al., 2012). As the world's coastal population has grown, so too has demand for food and energy production. Fisheries and aquaculture assure the livelihoods of 10–12% of the world's population (FAO, 2014). While offshore mariculture remains in its infancy, the potential for large areas of the oceans to be utilised for this purpose is increasingly considered (Kapetsky et al., 2013). In 2009, offshore oil fields accounted for 32% of worldwide crude oil production with expectations that this will increase to 34% by 2025 (IOC-UNESCO et al., 2011). Infrastructure associated with offshore renewable sources of energy, such as marine tides, waves, currents and temperature and salinity gradients, are gaining momentum and construction is expected to increase around the globe (IOC-UNESCO et al., 2011; Firth et al., 2016a). Overall, the construction of artificial structures in coastal areas is growing at rates ranging from 3.7% year⁻¹ to support merchant shipping requiring harbor space, up to 28.3% year⁻¹ for the development of offshore wind energy installations (Duarte, 2014).

Urban, coastal and offshore infrastructure has a myriad of impacts on biodiversity and ecosystem functioning (e.g. Airoldi and Beck, 2007; Bulleri and Chapman, 2010; Dugan et al., 2011; Dafforn et al., 2015b). Early studies on the effects of artificial structures focused on the extent to which they modify ecological communities at the site of construction (Bacchiocchi and Airoldi, 2003; Martin et al., 2005; Moschella et al., 2005), and the extent to which they can act as surrogates for the microhabitats provided by natural rocky shores and reefs (Moschella et al., 2005; Bulleri and Chapman, 2010). Artificial structures differ physically from natural habitats with respect to substratum composition, complexity, surface area, age, orientation, movement and disturbance regimes (Bulleri and Chapman, 2010; Airoldi and Bulleri, 2011; Chapman and Underwood, 2011). Increasingly, the novel habitat they provide is shown to support very different ecological communities to natural habitats (Connell and Glasby, 1999; Connell, 2001; Firth et al., 2013a), often characterised by greater abundances of opportunistic and non-native species (Glasby et al., 2007; Dafforn et al., 2009; Firth et al., 2011, 2015; Bracewell et al., 2013; Airoldi et al., 2015). Additionally, they may modify the communities of adjacent habitats by affecting light availability, flow, wave energy, sediment and resource transport, by leaching chemicals, modifying predator-prey interactions and/or by

producing noise during their construction (reviewed by Dugan et al., 2011; Dafforn et al., 2015b; Heery et al., 2017-in this issue).

More recently, there has been a growing realisation that the effects of ocean sprawl may propagate far beyond the sites of the structures themselves (Airoldi et al., 2005), through effects of artificial structures on ecological connectivity (*sensu* Taylor et al., 1993). Ocean sprawl may modify the movement of organisms and their resources among patches, across the seascape, by acting as barriers or conduits to the movement of organisms and their resources, and/or by altering ecological processes such as trophic transfer that act across habitat boundaries (Adams et al., 2014; Airoldi et al., 2010; Moss, 2017-in this issue). Ocean sprawl may also lead to shifts in the spatial extent, configuration and dynamics of natural habitats by altering sediment dynamics and geomorphic connectivity (Lee et al., 2006). Despite the growing awareness of the capacity of artificial structures to influence ecological connectivity, we lack a comprehensive understanding of the mechanisms by which connectivity is modified, when and where effects on connectivity occur and are greatest, and how the design of structures can take into consideration their effect on connectivity, particularly in the marine environment (LaPoint et al., 2015).

Here we provide the first review of how ecological connectivity is modified by ocean sprawl, defined here as artificial structures introduced to estuarine, coastal and marine waters. We start by reviewing the types and scales of ecological connectivity in estuarine, coastal and ocean environments, including trophic connectivity of nutrients and resources. We then discuss the ways in which ocean sprawl may modify connectivity and the resulting ecological consequences. Our consideration thereby goes beyond the more normal consideration of local-scale impacts of artificial structures on population processes and community structure to consider impacts on ecological processes that operate across habitat and ecosystem boundaries. Where impacts are identified, we suggest potential management solutions to address impacts of ocean sprawl on connectivity and identify key research gaps that need to be filled if these are to be successfully applied.

2. Definitions: corridors, barriers and types and scales of ecological connectivity in coastal and marine environments

Ecological connectivity refers to the way in which the landscape facilitates or impedes the movement of organisms, materials and energy between habitat units (Taylor et al., 1993). In this context, a corridor or barrier is defined as any structure, distinct from neighbouring ones, that facilitates or limits relatively more transfers per unit area and unit time between contributing habitat units than predicted from the surrounding habitat (Dennis et al., 2013). This concept is clearly a relative one, as whether a structure serves as a barrier or corridor is sensitive to landscape structure (Ewers and Didham, 2006), the spatial and temporal scale of consideration (Viles et al., 2008), as well as the organisms and ecological processes being considered (Powney et al., 2011; Vergara, 2011). Corridors and barriers can be ranked in importance based on the comparative numbers of individuals/resources undergoing successful transmission.

Connectivity influences ecological systems at levels of organisation ranging from genes to ecosystems (Sheaves, 2009). The dispersal and/or movement of organisms influences gene flow and the survival of individuals (e.g. Kinlan and Gaines, 2003; Epps et al., 2005), affecting population dynamics (e.g. Roughgarden et al., 1988), species interactions (Gaines and Lafferty, 1995; McIntyre and Wiens, 1999), patterns of distributions (Reed et al., 2000) and, ultimately, the functioning of systems (Jeltsch et al., 2013). Similarly, the transport of materials and energy from areas of high to low availability influences the types and numbers of organisms the recipient environment can support, as well as their biological interactions and, more broadly, the functioning of the ecosystem (Polis et al., 1997). In aquatic environments, connectivity can be a particularly important determinant of community structure and ecosystem functioning because many organisms display multiple life history

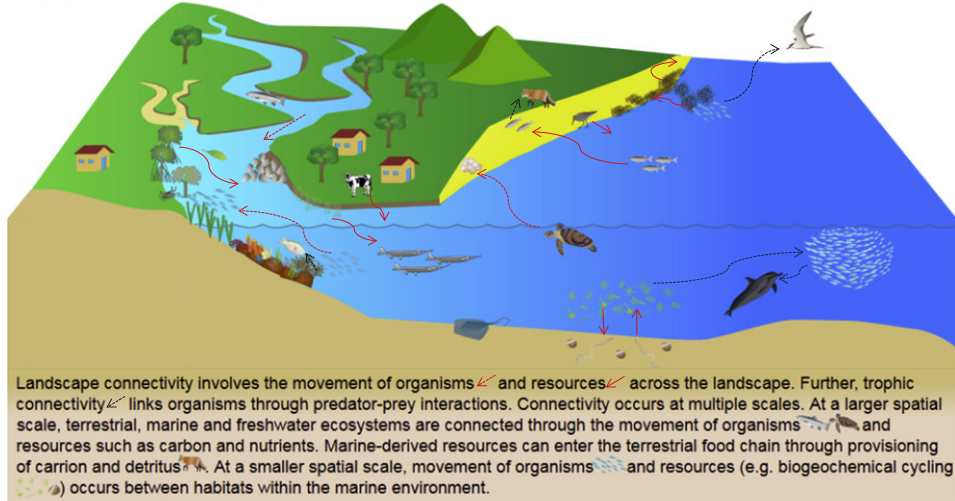
stages that utilise different habitats (Giller et al., 2004; Sheaves, 2009), and display positive and negative interactions with other organisms that operate across habitat boundaries (van de Koppel et al., 2015). Many populations or communities are spatially fragmented, and are linked solely by dispersal of early life-history stages (i.e. meta-populations or communities; Fagan, 2002; Shima et al., 2010). Also, productivity is highly variable within and among habitats, with some ecosystems entirely dependent on cross-habitat subsidies of food and nutrients, from resource-rich 'donor' to resource-poor 'recipient' sites (Polis et al., 1997; Bishop et al., 2010; Moss, 2017-in this issue).

As in terrestrial systems, connectivity in aquatic ecosystems operates at a number of spatial and temporal scales, ranging from microns to 1000s of kilometres and/or from tidal migrations to once in a life-time spawning events (Fig. 1a; Sheaves, 2009; LaPoint et al., 2015). At smaller spatial scales (e.g. centimetres to meters), organisms may move between habitat patches within a landscape to forage, in order to minimise risk from physico-chemical stressors or predation, to colonise new habitats or to facilitate ontogenetic shifts in diet (Fig. 1a; Lancaster, 1999; Lucas et al., 2001; Noël et al., 2009; Ng et al., 2017-in this issue). These movements may be as small as centimetres in the case of rotifers (Ignoffo et al., 2005). At intermediate scales (e.g. 10s and 100s of meters), copepods and other planktonic species may display diurnal vertical migration to facilitate dispersal (e.g. Tankersley et al., 1998; Knights et al., 2006) and/or to minimise abiotic stressors and predation risk (Ohman et al., 1983; Forward, 1988; Lampert, 1989), surf clams may migrate up and down beaches with the tides (Turner and Belding, 1957; McLachlan and Brown, 2006), and fish and crustaceans may move onto rocky shores (Silva et al., 2009, 2010, 2014), sandy beaches (Lasiak, 1983; Robertson and Lenanton, 1984) or tidal wetlands (Kneib, 1997, 2003; Sheaves, 2009; Simith et al., 2017-in this issue) to forage at high tide (Fig. 1a). At larger spatial scales (e.g. kilometres), several species of fish, such as lamprey, salmon and eels, display large-scale migrations from freshwater to marine environments, or vice versa, to spawn (Fig. 1a; McDowall, 1998; Almeida et al., 2002; Wright et al., 2014, 2015). Additionally, some species of shorebirds and marine mammals display global patterns of migration for the purposes of feeding and reproduction (e.g. Morrison, 1984; Stone et al., 1990; Holbrook and Schmitt, 1988; Luschi et al., 2003; Sims et al., 2009).

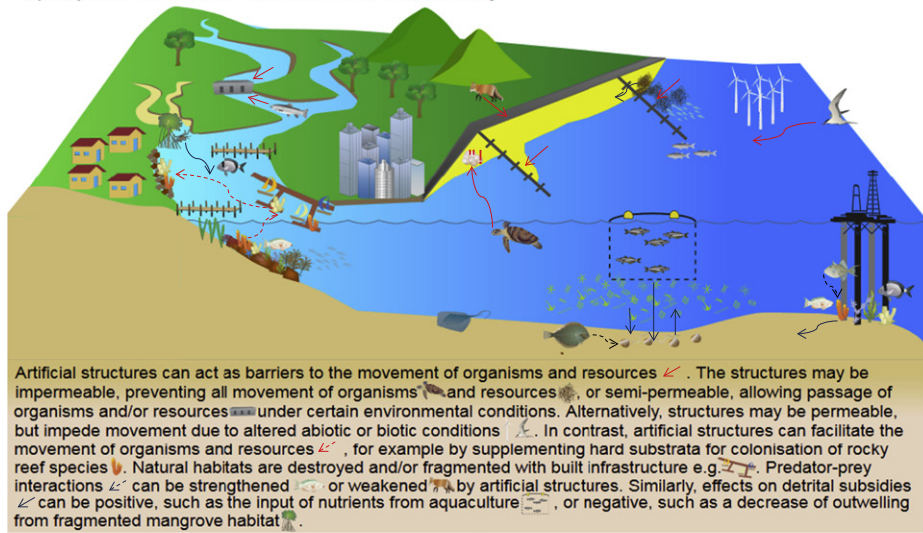
The active or passive (i.e. transport by waves and currents) movement of reproductive propagules, early life-history stages or adult organisms from source populations (net exporters of recruits) to sink populations (net importers of recruits) can prevent demographic decline and extinction of sink populations (Brown and Kodric-Brown, 1977; Gotelli, 1991; Pulliam, 1988). Such movements are not only important in determining the growth, survival and distribution of species and their interactions (Underwood and Fairweather, 1989), but can also redistribute resources (Polis et al., 1997). For example, the nitrogenous waste of birds and marine mammals has been demonstrated to have a fertilisation effect on primary producers in environments in which it is excreted (e.g. Bosman et al., 1986; Roman and McCarthy, 2010). Similarly, macrophytic detritus (Polis et al., 1997; Polis and Hurd, 1996; Mellbrand et al., 2011) and carrion (e.g. Schlacher et al., 2013) that washes up on beaches can move carbon from ocean to terrestrial food webs. These effects may be particularly important where sites of resource uptake by organisms are spatially separated from sites of release (Polis et al., 1997).

Although organism movement is the most researched aspect of ecological connectivity, many other forms of connectivity - such as the physical dynamics and translocation of habitats, abiotic resources (e.g. nutrients, sediments), contaminants, and freshwater through time and space, and predator-prey and organism-sediment interactions - can also be important determinants of ecological structure and function, particularly at ecosystem scales (Fig. 1a; Sheaves, 2009). For example, movement of sediments by long-shore drift and tidal currents can determine the availability and grain size of sedimentary habitat (Bishop et al., 2006a). Similarly, within estuaries patterns of sediment

a) Types of connectivity



b) Impacts of artificial structures on connectivity



c) Management solutions

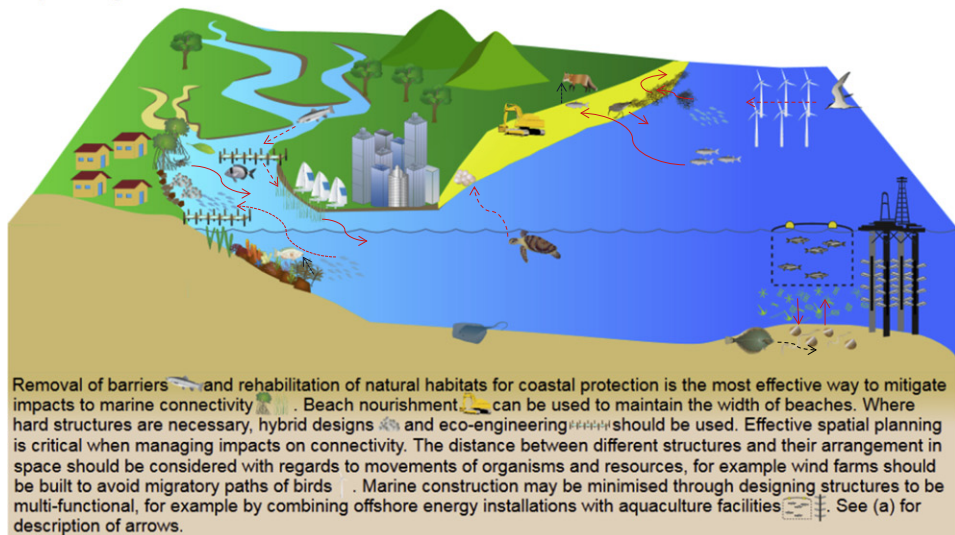


Fig. 1. Conceptual diagram, providing examples of (a) the types of ecological connectivity that sustain near- and off-shore environments, (b) the way in which ocean sprawl modifies connectivity and (c) potential management solutions for reducing the effects of ocean sprawl on ecological connectivity.

movement across habitat boundaries can influence whether salt marshes erode or accrete at a particular location or point in time (Viles et al., 2008). Patterns of freshwater flow into estuarine and coastal environments can trigger reproduction and movement of organisms, and dictate, via effects on salinity and dissolved nutrient concentrations, environmental suitability for particular organisms (Gillanders et al., 2003; Knights et al., 2012). Additionally, movement of anthropogenically-sourced nitrogen from terrestrial to estuarine and coastal environments can influence productivity and patterns of species dominance (Gorman et al., 2009). Predation (in its broader sense, which also includes herbivory) determines connectivity between lower and higher trophic levels and varies spatially and temporally according to landscape features (Lubchenco, 1978; Sheaves, 2009; Firth et al., 2017-in this issue). In operating across habitat boundaries, predation can lead to movement of resources from nearshore to offshore through trophic relays (Kneib, 1997).

There have been two main approaches to the assessment of ecological connectivity: (1) measurement of structural connectivity - the configuration of the landscape and habitat patches; and (2) measurement of functional connectivity - the response of organisms or particles to the landscape (LaPoint et al., 2015). Structural connectivity is typically quantified using landscape metrics such as patch size, isolation, and fragmentation that are thought to act as conduits or barriers to movement (LaPoint et al., 2015). Functional connectivity, on the other hand, is typically assessed using techniques such as genetics, tracking and modelling (LaPoint et al., 2015). In this review, we include studies that have taken both structural and functional approaches to assessing effects of ocean sprawl to connectivity. We identify few studies that have directly measured connectivity, presumably due to the large temporal and spatial scales of sampling needed to assess it. Hence, we also discuss studies that argue implications of ocean sprawl for connectivity, without directly investigating it.

3. Mechanisms by which ecological connectivity is modified by artificial structures

The introduction of artificial structures (typically made of rock, wood, metal or concrete) to estuarine and marine environments may alter connectivity by: (1) creating barriers to the movement of some organisms and resources; (2) introducing new structural material that acts as a conduit for the movement of other organisms or resources across the landscape; and (3) altering trophic connectivity (Table 1; Fig. 1b). In this section, we review the demonstrated and potential mechanisms by which ocean sprawl influences ecological connectivity at spatial scales ranging from centimetres to 1000s of kilometres, and at temporal scales of tidal cycles to years. We then discuss the ecological ramifications of altered connectivity in the following section.

3.1. Creation of barriers to the movement of organisms, materials and energy

Artificial structures can reduce ecological connectivity by acting as physical barriers to the movement of organisms, materials and/or energy within and among habitats, or by altering environmental conditions in a way that deters species migrations or movement of resources (Table 1; Fig. 1b). They may not only impede connectivity by introducing physical or environmental barriers to species and resource dispersal, but may also do so by destroying, fragmenting or modifying natural habitats (Boström et al., 2011).

The permeability of artificial structures to organisms is variable, depending on the mobility of organisms, the size of organisms or resources relative to any pores in the structure, the design and size of the structure, its orientation relative to vectors of dispersal, and the characteristics of the landscape matrix. For example, the permeability of coastal defence structures can vary from low to fairly high depending on the construction material (e.g. use of rock boulders vs geotextiles), size of

materials (e.g. whether there is a core of fine materials or not), number of construction layers, size, position, depth and height of the structure, and even within the same structure, there can be areas of different permeability (Burcharth et al., 2007). Similarly, the extent to which structures serve as barriers can vary depending on whether they are built within a sedimentary or a rocky environmental context (Airoldi et al., 2005; Bulleri, 2005). Organisms with high capacity for active movement may be able to swim around artificial structures, such as groynes, but movement of passively dispersed resources and organisms may be more restricted (Lechner et al., 2013). Sediments, water and organisms of small body size can move through shark-proof swimming enclosures that trap larger organisms such as sharks and litter (NSW DPI, 2015).

3.1.1. Physical barriers

Many hard structures aimed at stabilising shorelines or protecting infrastructure are specifically designed to create physical barriers to the movement of water and sediments (Burcharth et al., 2007). Structures, such as groynes, that are constructed perpendicular to shorelines primarily interfere with long-shore transport (Bush et al., 2001; Charlier et al., 2005) while structures, such as revetments and breakwaters, constructed parallel to shorelines intercept tidal-currents and may reduce wave action on their landward side (Thomalla and Vincent, 2003; Cuadrado et al., 2005). In interfering with tidal currents, these structures can accumulate sediments and materials on their up-current side, reducing supply to down-current locations (Thomalla and Vincent, 2003; Cuadrado et al., 2005; Moschella et al., 2005; Oldham et al., 2010; Pattiaratchi et al., 2011). The magnitude of these effects varies with the design, location and tidal elevation at which structures are built, but in general, the effects increase with their length and height (e.g. Tait and Griggs, 1990; Engelhardt et al., 2004; Burcharth et al., 2007; Uijtewaal, 2005), as well as with the strength of tidal currents and the degree of wave action at the site of their placement (Martin et al., 2005). As a side effect, these coastal defence structures can trap or impede transport of other resources and organisms, changing the structural landscape through time. For example, wrack (dead macrophytic matter) has been observed to accumulate on the up-current side of groynes, resulting in starvation of down-drift beaches of wrack (Oldham et al., 2010; Pattiaratchi et al., 2011) and forming unsightly and odorous banks of decaying algae, that are colonised by flies and other invertebrates, which local authorities have to remove on tourist beaches (De Falco et al., 2008). In a mark-recapture study of larval fish, longitudinal dispersal was disrupted by groynes, forcing larvae to enter the main channel (Lechner et al., 2013). A recruitment survey in a marina enclosed by breakwaters revealed that short-lived larvae of invertebrates such as bryozoans, spirorhids and sponges were more abundant on the inside surface of the breakwater (i.e. landward side) than on the outside (i.e. seaward side; Rivero et al., 2013), possibly due to the retention of larvae following spawning. Unfortunately, the extent to which these processes directly or indirectly affect the movement of organisms or resources is rarely studied, and the ultimate effects on ecosystem functioning are mostly unknown.

Hardening of the coast, by construction of seawalls and revetments along the intertidal and/or supratidal zones, can also act as a physical barrier to the tidal movement of organisms and resources between terrestrial and marine environments. Many organisms regularly move between marine and terrestrial coastal systems. For example, daily tidal migration up and down beaches has been observed for many sandy beach invertebrates (McLachlan and Brown, 2006), and the high intertidal and supratidal zones of sandy beaches can be important nesting or haul-out sites for otherwise aquatic species such as sea turtles, terrapins or seals (Godsell, 1988; Witherington et al., 2011; Winters et al., 2015). Although breakwaters constructed on subtidal sediments may, in some instances, add new haul out sites for seals (Firth et al., 2016a), vertical seawalls can prevent movement of these organisms onto land (Witherington et al., 2011; Winters et al., 2015). When and where these migrations are constrained by extensive coastal armouring,

Table 1

Aspects of ecological connectivity that could be modified by coastal infrastructure, and the mechanisms by which this might occur.

Aspect of connectivity	Recreational infrastructure	Coastal and foreshore defence	Offshore energy installation	Fisheries/aquaculture infrastructure	Residential infrastructure	Port/commercial infrastructures
Population level – dispersal of gametes	<ul style="list-style-type: none"> - Provide hard substrates that serve as stepping-stones for dispersal of fouling organisms - Modify currents and flow and can serve as a physical barrier to movement of propagules/reproductive material (e.g. structures may accumulate particles on their up-drift side). 		<ul style="list-style-type: none"> - Where spawning stock biomass of mobile organisms is enhanced, either through reduction of trawling around offshore energy installations or artificial reefs, or attraction to structures, there can be spill-over of larvae into adjacent habitat 			<ul style="list-style-type: none"> - Shipping canals connect isolated waterways and allow dispersal.
Population level – adult migrations	<ul style="list-style-type: none"> - By providing food and habitat, structures act as attractants for mobile species, in some instances influencing migration between habitats. - Shark nets impede migration of larger animals between deeper waters, and shallower waters where feeding may otherwise occur, and trap drift algae 	<ul style="list-style-type: none"> - Can impede migration of organisms between estuaries and coastal environments (e.g. some breakwaters), between on-shore and offshore habitats (e.g. tidal barrages), or along the shore (e.g. groyne). 	<ul style="list-style-type: none"> - Production of noise and electromagnetic fields can deter birds, fish and marine mammals, altering migration paths 		<ul style="list-style-type: none"> - Culverts and weirs impede migration of fish between habitats 	<ul style="list-style-type: none"> - Shipping canals serve as corridors for migration of some mobile species between naturally isolated water bodies
Population level – daily tidal excursions		<ul style="list-style-type: none"> - Seawalls and revetments that restrict or modify the profile of the intertidal zone via placement loss and/or active and passive loss can: (1) modify tidal swash behaviour of sandy beach invertebrates and (2) prevent high tide utilisation of intertidal wetlands by fish and invertebrates and low tide utilisation by shorebirds. 			<ul style="list-style-type: none"> - Culverts and weirs impede tidal migrations into wetlands - Where canal estates replace wetlands, high tide migration of fishes and invertebrates into marshes is prevented 	
Population level – ontogenetic movement		<ul style="list-style-type: none"> - Where seawalls or revetments impede tidal inundation of coastal vegetation, drowned nursery and feeding habitats may be lost. - Seawalls and revetments can serve as barriers to movement of sea turtles and terrapins from sea to land to lay eggs on sandy beaches - Tidal barrages can interfere with onshore/offshore ontogenetic migration 			<ul style="list-style-type: none"> - Culverts and weirs impede migration of fish between freshwater and marine habitats – Culverts and weirs can impede tidal inundation of coastal vegetation - Canal estates that replace wetlands result in loss of nursery and feeding habitats 	

Community level – predator-prey	<ul style="list-style-type: none"> - Enhance trophic linkages by facilitating hard-substrate fouling communities in environments in which they are not usually found and which serve as a prey resource for fish and invertebrates. This can be while still attached or following detachment. - Shark nets prevent top predators from foraging on near-shore bait-fish, weakening trophic relays. <ul style="list-style-type: none"> - Homogenous surfaces of seawalls can enhance trophic linkages, as compared to rocky shores, by rendering organisms more susceptible to predation - Where seawalls replace rocky shores, their comparatively small surface area for growth of algae and invertebrates may reduce consumer-prey interactions. - Structures that narrow intertidal habitats such as sandy beaches, mangroves and saltmarshes can weaken the land-sea trophic subsidy by reducing foraging grounds for shorebirds at low tide and surf fishes at high tide. - Artificial reefs provide refuge to meso-predators and grazers, potentially leading to adjacent grazing halos. - Culverts and weirs impede movement of predators - Locks impede movement of predators, but canals could facilitate novel predator-prey interactions by facilitating species invasions
Ecosystem level – detrital subsidies	<ul style="list-style-type: none"> - Structures that facilitate growth of macroalgae and invertebrates can enhance detrital subsidy to adjacent sediments. - Structures built over vegetation may shade and kill macrophytes, reducing/eliminating carbon subsidy to adjacent ecosystems. - Structures that attenuate flow/wave energy may result in deposition of POM. <ul style="list-style-type: none"> - Structures that reduce intertidal and shallow subtidal habitats (through placement, passive and active loss) may reduce the area of suitable habitat for growth of wrack-producing macrophytes, may eliminate the high intertidal zone of wrack accumulation, and may influence the physico-chemical environment for decomposition. - The loss of high and mid intertidal habitats through coastal armoring can increase proximity of terrestrial and aquatic communities and hence vegetation land-sea subsidies (e.g. mangrove trees overhanging seawalls, to deposit leaf-litter on their landward side) - Bird strikes by wind turbines can enhance carrion subsidies to offshore habitats - artificially high densities of animals on farms can enhance resource subsidies to the benthos. For, example, in extreme cases, organic enrichment of sediments by food and animal waste can induce hypoxia

important sites for species could be lost (e.g. Dugan et al., 2008; Jaramillo et al., 2012). These effects can extend beyond the species themselves, altering land-sea connectivity, although these effects have received little to no attention to date. For example, terrapins, turtles, seals and other organisms can be important transporters of nutrients and energy between terrestrial and marine ecosystems (e.g. Bouchard and Bjorndal, 2000). Seawalls may also impede transport by tidal currents of aquatically-sourced organic matter onto the high intertidal shore (Dugan et al., 2013), where it can subsidise terrestrial communities (Polis and Hurd, 1995; Mellbrand et al., 2011) and promote incipient dune formation (Hemminga and Nieuwenhuize, 1990; Nordstrom et al., 2011).

Water-retaining structures such as dams, weirs, flood-gates and barrages can disrupt the flow of water from catchments to coasts, along with the biota, sediments, pollutants and nutrients transported in the flow (Apitz, 2012). For example, these structures can directly affect the passage of diadromous fish, between both marine and freshwater environments used at different life-history stages (Sheer and Steel, 2006; Aprahamian et al., 2010), and also the movement of fish and invertebrates among estuarine breeding and nursery grounds, and between estuarine and marine habitats (Gillanders et al., 2003). Indeed, marina locks have been deliberately used to control the spread and eradicate an incursion of the invasive black striped mussel, *Mytilopsis sallei*, in Darwin, Australia (Willan et al., 2000). Additionally, water-retaining structures may indirectly influence the passage of organisms by inducing other chemical or physical barriers to migration, or affecting the strength and circulation of residual currents in estuaries and coastal regions that are strongly influenced by river discharge (Drinkwater and Frank, 1994). Many species of zooplankton, invertebrate, and fish spawn near the head of estuaries, their eggs and larvae drifting seaward, eventually returning back up the estuary to spawn (e.g. Bousfield, 1955; Tyler and Seliger, 1978; Tankersley et al., 1998). Other species are known to use outflowing surface currents from estuaries to transport larvae (e.g. the blue crab, *Callinectes sapidus*: Johnson and Hester, 1989; Tankersley et al., 1998; *Mytilus* sp. bivalves: Knights et al., 2006). In some instances, reduced freshwater flushing of estuaries can lead to sedimentation and closure of the estuarine entrance (Potter et al., 2010; Lloyd et al., 2012), inhibiting movement of organisms and resources between the estuarine and coastal environment (Garside et al., 2014). Where flow reduction is not accompanied by estuarine entrance closure, an increase in salinity may favour marine over estuarine species. By contrast, where the construction of dams, barrages and weirs cause large pulses of freshwater runoff, estuarine species may be favoured.

The permeability of water-retaining structures to organisms and resources varies not only with design but also with operational use - in particular, the frequency of water release. Whereas water may only be released from dams during major rainfall events, tidal barrages and floodgates can be made more or less permeable to movement of organisms and resources. Barrages used for harvesting tidal energy have sluices that open on flood tides, allowing water to move into the bay or river, and close on ebb tides so that water can instead be routed through turbines. Conversely, floodgates used to prevent flooding of land, seal to prevent tidal inundation on the incoming tide, and open to drain water out on the ebb tide. Structures, such as the Thames Barrier, which is designed to protect the people and infrastructure of London from major storm surges and extreme high tides, are predominantly open and only constrict movement of water, and associated organisms and resources during extreme events. Barrages and tide gates physically prevent fish migration when closed (Giannico and Souder, 2005; Tonnes, 2007; Aprahamian et al., 2010). When open, they enable passage, although associated conditions such as high flow velocities (Haro et al., 1998; Russon and Kemp, 2011), abrupt changes in salinity (Zaug et al., 1985), sudden temperature gradients (Berggren and Filardo, 1993; Boyd and Tucker, 1998; Jonsson, 1991) and overhead cover from the structure itself (Kemp et al., 2005) can deter migration.

There is also a rise in the use of much smaller, manually operated tidal-regulation devices (e.g. 50–75 cm diameter pipes connecting the ocean to a saltmarsh), which allow managed realignments, such as saltmarshes, to be controlled like locks during extreme flood events. The effects of these systems on ecological connectivity are largely unknown.

The timing of water release is potentially important in determining the impact of water-retaining structures on connectivity. Structures used for flood control or hydroelectric power production change the pattern of seasonal discharge of water, nutrients and sediments to estuaries and coastal environments (Milliman and Farnsworth, 2013). Where variations in river run-off induce upstream spawning migrations of anadromous fish (Fraser, 1972; Northcote, 1982), a temporal shift in discharge patterns could alter migration cues (McCarthy et al., 2008). The construction of dams is thought to have reduced upstream migrations of shad (*Hilsa ilisha*) in several rivers in southern India by reducing high freshwater flow rates (Ganapati, 1973). Many marine fish species spawn in estuaries or flood plains, generally at times near peak run-off. Significant shifts in the timing of flood waters may result in asynchrony between peak run-off and spawning time (Drinkwater and Frank, 1994).

3.1.2. Modification of environmental conditions

Instead of serving as physical barriers, some artificial structures create environmental conditions that deter organisms, or modify transport of resources. For example, piers allow movement of water and sediments, but it has been hypothesised that the large number of piers constructed along urbanised shorelines, such as that of Puget Sound, USA, could delay the out-migration of juvenile salmon from estuarine to marine habitats because the fishes avoid crossing the shaded areas under piers (Munsch et al., 2014). In many instances the salmon do not simply swim around piers, which typically extend to deeper depths than those traversed by juvenile salmon, but instead accumulate adjacent to the piers in lit areas (Simenstad et al., 2011).

Even relatively small structures such as wind turbines and offshore oil platforms, which have cross sectional areas that allow passage of organisms and resources through their matrix, can modify connectivity by altering currents and sediment distribution, and by creating

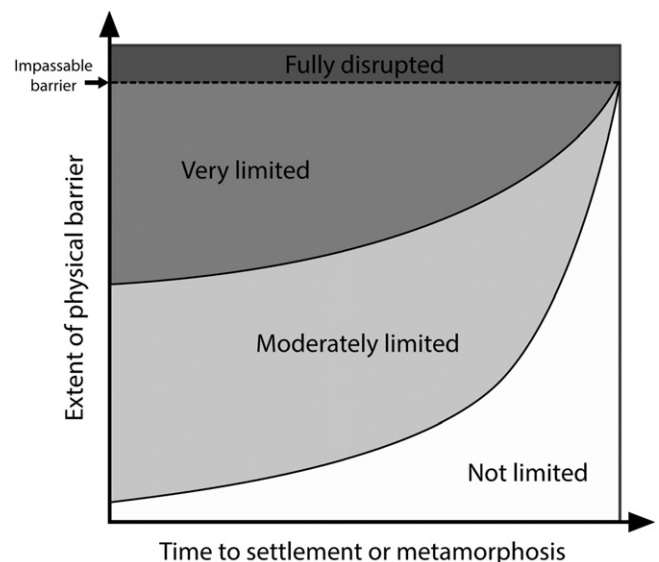


Fig. 2. The dispersal ability of marine invertebrate larvae depends on both the time to settlement or metamorphosis (X-axis) and the extent of the physical barrier (Y-axis). For example, dispersal of species with short larval stages (i.e. very quick to settle or metamorphose) is likely to be more severely impacted by ocean sprawl compared to those with longer larval durations. Extensive physical barriers (or at the extreme, impassable barriers such as causeways) are likely to interfere with (or fully disrupt) connectivity regardless of the length of their larval duration.

noise either during construction and/or operation (e.g. Millar et al., 2007; Desholm and Kahlert, 2005; Snyder and Kaiser, 2009). Modelling analysis has indicated that arrays of offshore wind turbines can alter mean wave height and wave period (Millar et al., 2007; Palha et al., 2010) and wave energy converters may extract between 3 and 15% of incident wave energy (Largier et al., 2008). Consequently, large-scale offshore energy developments could alter sediment transport and deposition, affecting beach erosion and accretion (Millar et al., 2007; Largier et al., 2008). Electric and magnetic fields caused by buried underwater cables connected to wind farms and other offshore energy generating devices may deter fish migrations by disrupting their electric and magnetic fields used for orientation and prey detection (Snyder and Kaiser, 2009). Noise and vibrations from construction-related pile driving have been linked to increased mortality of fish eggs and embryos (Banner and Hyatt, 1973), avoidance of construction sites by porpoises (Carstensen et al., 2006) and may also deter fish (Snyder and Kaiser, 2009), although there is currently limited evidence. Birds may alter migration paths to reduce risk of collision with wind turbines, or be displaced from formerly important feeding grounds (Drewitt and Langston, 2006). Such effects are of concern because longer flight paths may, by increasing energy expenditure, decrease energy available for reproduction and disrupt connectivity between feeding, roosting, moulting and breeding areas (Drewitt and Langston, 2006). The percentage of flocks of long-lived geese and ducks that entered the Nysted offshore wind farm in Denmark decreased by a factor of 4.5 from pre to post construction (Desholm and Kahlert, 2005).

3.1.3. Habitat loss and fragmentation

The construction of near- and off-shore infrastructure necessarily results in the loss of natural habitat. At best this loss is confined to the footprint of the structure. For example, when accompanied by back-filling of land, the construction of a seawall in the mid-intertidal zone of a sandy beach causes placement loss (*sensu* Griggs et al., 2005) of high intertidal habitat. Similarly, pontoons and jetties built over seagrass can cause habitat loss below them as a result of shading (Fitzpatrick and Kirkman, 1995). In some instances, however, damage to natural habitat occurs at a scale that exceeds the area of the structure itself. For example, the area of seagrass denuded by a swing mooring buoy can extend beyond the area of the concrete block to which the mooring is anchored (Walker et al., 1989). Similarly, grazers attracted to artificial reefs might produce denuded halos around structures, just as urchins reduce macrophytes to nearly bare sand around natural reefs (Ogden et al., 1973).

The loss of habitat interferes with connectivity by modifying habitat configuration and by reducing resource availability. Fragmentation of suitable habitat can also impede gene flow and connectivity among metapopulations, especially for species with low dispersal potentials (Fig. 2; Kritzer and Sale, 2004; Jones et al., 2007). Even for species with high dispersal potential (e.g. relatively long larval durations), large gaps between patches of suitable habitat can, in theory, result in low dispersal and connectivity (Fig. 2; Jones et al., 2007). In the extreme case of impassable physical barriers (see Section 3.1) such as causeways, populations on either side of the barrier can be completely disconnected and the resulting genetic structure could diverge overtime (Palumbi, 1994). In most cases, however, man-made coastal structures are not complete physical barriers to dispersal. For example, in highly urbanised locations such as Singapore, where man-made seawalls comprise approximately 63% of the coastline (Lai et al., 2015), coral (broadcast spawner, *Platygyra sinensis*) populations within the Singapore Straits were found to be panmictic with relatively high genetic diversity (Tay et al., 2015). This suggests that the scale of fragmentation for species with high dispersal potentials (e.g. *P. sinensis* larvae can take up to six days to settle and disperse over 100 s of kilometres; Tay et al., 2011, 2015) have to be relatively large (beyond 100s of kilometres).

3.2. Conduits to the movement of organisms and resources

Whereas some artificial structures limit the movement of organisms and resource by introducing barriers, others can enhance movement by weakening or removing existing barriers or by acting as stepping stones across unfavourable stretches of habitat such as extensive sandy areas (Table 1; Fig. 1b). Enhancement of dispersal may be seen where they allow organisms or resources that previously only rarely transgressed a barrier to do so more regularly.

For the many marine organisms with a life history phase that is dependent on hard substrate, the large areas of ocean or even coastal areas that lack or have low densities of hard substrates can be a natural barrier to dispersal. Artificial structures provide new hard substrate, which may be used by some species in addition to their natural substrates and enable them to transgress existing barriers, or provide new dispersal pathways by serving as destinations and sources of larvae (Rooker et al., 1997; Adams et al., 2014). Additionally, coastal structures may provide habitat for species dispersed by shipping and other vectors (Sheehy and Vik, 2010; Knights et al., 2016). In the northern Gulf of Mexico, c. 4000 oil and gas platforms have extended the distribution of coral populations into offshore areas where they were previously absent (e.g. Sammarco et al., 2004). Similarly, the extensive coastal defence structures built along 100s of kilometers of sedimentary coastal areas along the Italian side of the North Adriatic sea or along the Yangtze River estuary in China are creating corridors for numerous hard-bottom species (Bacchiocchi and Airoldi, 2003; Airoldi et al., 2005; Huang et al., 2015). Dispersal of species with short pelagic larval durations may particularly benefit from structures that serve as 'stepping stones', with species with longer pelagic larval durations less affected (Adams et al., 2014).

The quality of the emergent novel habitats created by the artificial structures for hard bottom species can be extremely variable, and dependent on several aspects of seascape as well as on structural, environmental and biological factors (Bulleri and Airoldi, 2005; Moschella et al., 2005; Dugan et al., 2011; Perkol-Finkel et al., 2012; Firth et al., 2014a; Airoldi et al., 2015; Ferrario et al., 2016). There is growing evidence that early colonists/opportunists/invasive species, in particular, might be able to take advantage of the new artificial spaces (Bulleri and Airoldi, 2005; Farrell and Fletcher, 2006; Glasby et al., 2007; Vaselli et al., 2008; Dafforn et al., 2012; Duarte et al., 2012; Mineur et al., 2012). For example, extensive sampling along artificial structures built along 300 km of sedimentary coasts in Italy have shown that, in this region, artificial structures have acted as regional corridors for non-indigenous invertebrates and seaweeds (Bulleri and Airoldi, 2005; Airoldi et al., 2015), while not representing adequate substrata for equivalent native species (Airoldi et al., 2015; Ferrario et al., 2016), disproportionately affecting their spread at regional scales.

The construction of canals for shipping across narrow land bridges is another example of how ocean infrastructure can remove barriers to the movement of organisms and resources (Galil, 2000). In connecting watersheds or seas, canals remove land barriers, enabling new opportunities for both natural and ship-mediated dispersal. Primary examples include the Suez Canal, which has allowed exchange of organisms between the Mediterranean Sea and the Indo-Pacific Ocean, and the Panama Canal, which has facilitated connectivity between the Atlantic and Eastern Pacific oceans. Since the opening of the Suez Canal in 1869, >300 species of macro flora and fauna have dispersed from the Red Sea to the Mediterranean generating dramatic modifications in the local communities (Por, 1978; Galil, 2000), and this number is set to increase with the Canal's expansion (Galil et al., 2015). Similarly, in connecting previously isolated estuaries, the Atlantic Intracoastal Waterway, a 4800 km navigable channel along the Gulf and Atlantic coasts of the USA, can serve as a conduit for spread of pathogens and introduced species between coastal waterways (Bishop et al., 2006b). In an analogous freshwater example, the New York State Canal and Hudson River systems, that allow navigation between the Great Lakes, have

facilitated at least 162 species invasions, including the much publicised zebra mussel, *Dreissena polymorpha* (Griffiths et al., 1991; Mills et al., 1994; Pimentel, 2005).

3.3. Alteration of trophic connectivity

Amongst the key mechanisms by which ocean sprawl modifies connectivity is the alteration of the strength and nature of trophic interactions that transfer energy and nutrients across habitat boundaries (Table 1; Fig. 1b). This topic was briefly mentioned above (Section 3.1), but is examined more comprehensively here. In some instances, artificial structures strengthen trophic interactions by enhancing prey resources for predators and herbivorous fishes, by making prey more accessible to predators, by locally enhancing predator populations, or by enhancing detritus. In other instances, artificial structures can weaken trophic interactions by reducing abundances of prey or by restricting predator movement between habitats or foraging grounds.

3.3.1. Predator-prey interactions

Communities of algae and sessile invertebrates that establish on permanently or tidally submerged artificial structures are an important food resource for mobile grazers and predators (Jonsson et al., 2006; Jackson et al., 2008; Munsch et al., 2014; Ferrario et al., 2016; Teagle et al., 2017-in this issue), particularly on artificial structures that lack the protective microhabitats of topographically complex natural substrates, such as seawalls, pontoons and pilings (Chapman and Blockley, 2009). These predators include not only residents of the artificial structures (Jackson et al., 2008), but also transient predators, such as fish and crustaceans, that forage on submerged structures (Munsch et al., 2014). Presumably, this also includes shorebirds that forage on intertidal structures at low tide, although this has not explicitly been studied. Greater rates of foraging have been observed among fish at seawalls than at adjacent shorelines (Munsch et al., 2014), and seawalls have, in some instances, been observed to support greater numbers of juvenile fish than natural habitats, raising the possibility that they may, in some contexts, serve as nurseries (Pastor et al., 2013). Fish and mobile invertebrates may be attracted to artificial structures as a result of the high prey densities inhabiting these structures, as well as the structural habitat they provide (Pickering and Whitmarsh, 1997; Wilhelmsson et al., 2006; Reubens et al., 2011, 2013; Krone et al., 2013; Ferrario et al., 2016). The novel configurations of species that arises on artificial structures can alter biological interactions, as compared to natural habitats (Klein et al., 2011).

In some instances, the effects of grazing and predation may spill over from artificial structures into adjacent sedimentary environments, resulting in grazing 'halos' (Posey and Ambrose, 1994; Kurz, 1995; Einbinder et al., 2006). This is shown by the use of caging experiments and videoin, which indicate greater predation on soft-sediment invertebrates close to than away from offshore rocky ledges (Posey and Ambrose, 1994). In the Red Sea, intense grazing on algae extended up to 20 m from artificial reefs, into adjacent sedimentary environments, and was considerably greater than at control sites, without reefs (Einbinder et al., 2006). In the Gulf of Mexico, triggerfish predation upon sea urchins extended to 20 m around aggregated artificial reefs, and a 30 m around individual, dispersed, reefs (Kurz, 1995). Reef configuration is hypothesised to have affected triggerfish foraging strategy by influencing the surface area for growth of fouling organisms, which may provide a more proximal source of food than the urchins (Kurz, 1995).

In other instances, artificial structures may in fact weaken predator-prey interactions that transfer carbon and other nutrients across habitat boundaries. When ocean sprawl results in significant habitat loss, either directly or indirectly through coastal squeeze, the resource base provided to predators and grazers by the artificial structure may be insufficient to offset the loss of foraging area. This is particularly apparent when intertidal foraging grounds for shorebirds and fish are lost following seawall construction, leading to diminished trophic transfer between

terrestrial and marine food webs (Dugan and Hubbard, 2006, 2010). Similarly, where the replacement of natural rocky reef with seawalls decreases the area of hard substrate available for growth of fouling organisms, trophic transfer to grazers and predators may be expected to decrease. Further, structures may weaken trophic interactions operating across habitat boundaries where they prevent tidal or seasonal movement of predators out of foraging grounds. This is significant as the movement of fish, decapods and other species between different habitats plays a major role in energy transfer (Deegan and Garritt, 1997; Kneib, 2003). Exclusion of estuarine dwelling species from culverted wetlands may decrease the transfer of wetland-derived production to estuarine and offshore ecosystems (Boys and Williams, 2012).

Structures such as artificial reefs, deep-water oil rigs and offshore wind farms may weaken the impact of human activities on marine food webs by limiting the spatial and temporal extent of harmful processes. Artificial reefs have been successfully used to discourage illegal trawling in seagrass beds in Western Europe (González-Correa et al., 2005), as well as to passively enforce marine parks and fishery-protected areas in Hong Kong (Wilson et al., 2002). These and other successes has led to oil rigs and offshore wind farms being proposed as "de facto marine protected areas" (*sensu* Inger et al., 2009) because they exclude trawl fishing and their large internal spaces offer shelter to fish and other organisms (e.g. Macreadie et al., 2011; Witt et al., 2012; Ashley et al., 2014; Campbell et al., 2014).

3.3.2. Detrital subsidies

Detritus is a source of energy and nutrients to living organisms in most food webs and can also provide habitat (Moore et al., 2004). In many instances, detritus is not remineralised at its site of production, but is transported across habitat boundaries where it subsidises recipient ecosystems (Polis et al., 1997; Bishop et al., 2010; Franzitta et al., 2015). Hence factors that influence its production, its movement across habitat boundaries, its accumulation and retention, can strongly influence the structure of populations, communities and ecosystems (Polis et al., 1997).

Just as the effects of ocean sprawl on predator-prey interactions can be positive or negative, so too can its effects on detrital subsidies. Structures that provide hard-substrate for the growth of macroalgae and invertebrates in a previously sedimentary environment can enhance production of detritus and its deposition in adjacent sediments (Airoldi et al., 2010). Similarly, aquaculture operations that concentrate taxa at artificially high densities may enhance subsidies of organic matter to the benthos (Midlen and Redding, 1998; MacGarvin, 2000). The accumulation of biological debris at the base of the structures may modify local seabed communities (Boehlert and Gill, 2010), attracting scavengers such as flatfish, mobile crustaceans, and echinoderms, and enriching communities within the soft sediment (Coates et al., 2012). Similarly, the periodic sloughing off of animals from structures can lead to enhanced deposition of shell material on sediments below (Love et al., 1999; Goddard and Love, 2010; Heery et al., 2017-in this issue). The shell mounds that form under long-deployed structures such as oil platforms represent an extreme case of benthic habitat modification, and can comprise productive fish habitat (Love et al., 1999; Goddard and Love, 2010). In the worst case, subsidies of organic matter can result in hypoxic environments establishing under fish farms (Midlen and Redding, 1998; MacGarvin, 2000).

Where the construction of artificial structures results in loss of natural habitats that are key sources of detritus, there may be significant negative effects of ocean sprawl on detrital subsidies. Heatherington and Bishop (2012) found that the width of mangrove forests was substantially narrower along stretches of shoreline with seawalls compared to those without, and the amount of leaf litter found within the mangrove forest was also significantly less at the armoured sites. In some instances, a reduced contribution of terrestrial leaf litter to wrack may also be seen on armoured shorelines (Heerhartz et al., 2014) because

armouring is often associated with the replacement of riparian vegetation with lawns on the landward side of walls and revetments (Higgins et al., 2005).

Structures such as wind turbines and other offshore energy generating devices may not only modify detrital pathways by affecting living biomass (much of which eventually becomes detritus, Moore et al., 2004), but also by increasing the mortality rate of some species. For example, bird collisions with offshore wind turbines may increase carrion subsidies to scavengers, particularly in areas where collision rates are high. Recorded rates of collision vary from between 0.01 and 23 birds per turbine, annually (Drewitt and Langston, 2006). In some cases, carrion may spatially subsidise other habitats. In the northeast of England, bird carcasses have been found washed up on a beach adjacent to a pier hosting wind turbines, although the sources of birds were unclear (Newton and Little, 2009). Damage to or death of organisms around marine renewable energy devices during construction or operation may attract scavengers to the site to feed (Hiscock et al., 2002).

Even in the absence of changes in detrital production, ocean sprawl may influence detrital subsidies by modifying detrital transport processes, and the accumulation and retention of detritus in recipient habitats. As discussed in Section 3.1, structures, such as groynes and breakwaters, which act as barriers can modify patterns of wrack transport, leading to unnaturally high accumulations of detritus on some beaches, and starvation on others (Oldham et al., 2010; Pattiaratchi et al., 2011). Additionally, where shoreline-armouring by structures such as seawalls lowers the interface between marine and terrestrial zones and/or reduces the width of the intertidal transition, accumulation of wrack on shorelines may be reduced (Sobocinski et al., 2010; Heerhartz et al., 2014). In a survey of 29 pairs of armoured and unarmoured sites, Heerhartz et al. (2014) found about 50% as much wrack in the upper zone of armoured beaches than unarmoured beaches with similar characteristics. The altered profile of armoured shorelines increased the mobility of wrack and its decomposition rate, leading to lower retention times on armoured shorelines (Harris et al., 2014).

4. Ecological ramifications of changes to connectivity

In combination, the multiple effects of ocean sprawl on ecological connectivity can affect the structure and functioning of ecological systems at different spatial, temporal and biological scales, from genes to ecosystems. In this section, we review the potential ecological impacts of changes in connectivity, and the direct and indirect evidence for impacts from studies to date.

4.1. Altered genetic structure of populations

Migration between populations is a key process that influences the genetic structure of populations (Pannell and Charlesworth, 2000), such that artificial structures that connect or disconnect existing meta-populations (or allow the establishment of new ones) have the potential to modify genetic structure (e.g. Dethier et al., 2003). Yet, despite long recognition of the impact artificial structures may have on population genetic structure, relatively few studies have investigated their impacts at this level of biological organisation (but see Mauro et al., 2001; Atchison et al., 2008; Smith et al., 2008; Fauvelot et al., 2009, 2012).

Of the few studies examining the effects of ocean sprawl on population genetic structure, most have focused on hard substrate organisms, comparing aspects of their population genetic structure between artificial and natural substrates, at a single point in time (e.g. Mauro et al., 2001; Atchison et al., 2008; Fauvelot et al., 2009, 2012). Studies on the limpet *Patella caerulea* found lower genetic diversity on artificial than natural substrate along the Adriatic coast (Fauvelot et al., 2009) and significant differences in the genetic structure of two out of 12 enzymatic systems investigated (Mauro et al., 2001). Similar results were found

for the serpulid *Pomatoceros triqueter* colonizing offshore platforms in the same regions (Fauvelot et al., 2012). Fauvelot et al. (2009) hypothesised that the reduced genetic diversity on artificial structures may be due to selection resulting from the differing environment of the structures themselves, because they found no evidence of recent population bottlenecks on artificial structures that would be expected in the event of a founder effect (Barton and Charlesworth, 1984). In the Gulf of Mexico, however, the genetic similarity between coral population on offshore oil platforms and natural coral reefs decreased with distance (Atchison et al., 2008). Hence, it remains possible that at larger scales (e.g. 10s to 1000s of kilometres), structures that are infrequently colonized by larvae derived from natural habitats may develop genetic structures that deviate from natural populations due to genetic drift and founder effects (Johannesson and Warmoes, 1990; Atchison et al., 2008).

Several studies have used spatial surveys to assess how the genetic structure of fish populations relates to barriers, mostly focusing on dams and weirs in freshwater as opposed to coastal systems. These studies suggest that dispersal barriers reduce genetic diversity and increase genetic differentiation, by fragmenting species into small, partially independent populations that are strongly affected by genetic drift (Wofford et al., 2005; Heggenes and Røed, 2006). In the coastal environment, hybridization of closely related marine and estuarine species was greater in coastal lagoons that have predominantly open entrances, as compared to lagoons that are mostly closed to the ocean (Roberts et al., 2010). This suggests that the construction of breakwaters to permanently open the entrances of naturally intermittently open coastal lagoons may enhance hybridization of closely related marine and estuarine species.

4.2. Altered population sizes, resulting from changes in birth and death rates

Three main factors influence the population size of organisms – birth rate, death rate and migration. The alteration of landscape or trophic connectivity by ocean sprawl may influence birth rate by modifying the condition of organisms, which in turn may determine the amount of energy they have available to allocate to reproduction, and by altering access to or the availability of suitable habitat for breeding. Limpets on seawalls, for example, show reduced reproductive output as compared to limpets on natural rocky shores, producing fewer and smaller egg masses (Moreira et al., 2006). Artificial structures may influence death rates by altering resource availability and predator-prey interactions. Further, where ocean sprawl acts as a partial or full barrier or conduit to dispersal, migration may be affected.

Where structures provide a barrier to movement, organisms must either exert time and energy navigating their way around or else die as a result of failing to locate a suitable habitat. A number of structures act as a barrier, for example, top-hung tide gates delay up-stream migration of sea trout (Wright et al., 2014) and downstream migration of eel (Wright et al., 2015); bulkheads may cause terrapins to travel longer distances, and along more convoluted paths to reach shore-based nesting sites (Winters et al., 2015); and offshore wind farms may cause birds to alter their migratory paths in order to avoid collisions (Masden et al., 2009). Increased expenditure of energy during migration has been hypothesised to reduce the availability of energy for reproduction (Winters et al., 2015), although this has not been tested. Additionally, longer paths of migration may potentially increase risk of predation. The extent of these impacts will, presumably, be dependent on the extent to which the migration path is lengthened or impeded and the proportion of a species range that is affected. Avoidance by eiders of a Danish offshore wind farm increased their migration path of 1400 km by a trivial 500 m (Masden et al., 2009), such that in this case, it would be unlikely to greatly influence their condition and fitness. Nevertheless, construction of further wind farms along the migration route could have cumulative effects on the population, especially

when considered in combination with other human actions (Masden et al., 2009).

In addition to influencing birth rates by determining the energy organisms have available for reproduction, ocean sprawl may also modify access to suitable habitat for breeding. Shoreline armouring that impedes the migration of turtles from water to the high shore of beaches to breed may negatively influence birth rates, if a high proportion of a species' breeding habitat is affected. Fewer loggerhead turtles attempt to nest on armoured than unarmoured shorelines (Rizkalla and Savage, 2011) and the emergence of loggerhead hatchlings is lower on armoured than unarmoured shorelines (Witherington et al., 2011). Conversely, in other instances, ocean sprawl has benefited populations of species, such as jellyfish, that have a benthic phase that is dependent on hard-substrate (Boero et al., 2008). In soft-bottomed habitats, populations of jellyfish are limited by the availability of natural hard substrate for polyps (Duarte et al., 2012). Artificial structures have been hypothesised to contribute to a global trend towards an increased frequency and intensity of jellyfish blooms by facilitating survival of a greater numbers of polyps (Duarte et al., 2012). Artificial structures may be particularly favourable substrates for polyps where they provide a shaded surface (Pitt, 2000; Holst and Jarms, 2007), or where they protect polyps from wave scour (Duarte et al., 2012).

Several empirical studies provide evidence that at local scales, artificial structures modify the size of prey populations by altering rates of predation (see Section 3.3). For example, reduced abundances of sea pens (Davis et al., 1982), sand dollars (Kurz, 1995), and infauna (Ambrose and Anderson, 1990) have been observed in the vicinity of reefs with abundant predators, with accompanying observations of predation suggestive that patterns are at least partially trophically driven. Similarly, surveys indicate that the abundance of recruits and juveniles of some recreationally and commercially important fish as well as some seaweed species are negatively correlated to high predator abundances around artificial reefs (Herrera et al., 2002; Ferrario et al., 2016). Factors other than predation (e.g. behavioural avoidance) may, however, also contribute to this pattern. Predator populations may, conversely, benefit from increased prey availability around artificial structures, but the extent to which enhanced abundances are a consequence of enhanced production versus behavioural attraction to structures is a topic of considerable debate (Pickering and Whitmarsh, 1997). Recent studies, using stable isotopes to track trophic linkages, indicate that artificial reefs are indeed an important supplier of food to higher trophic levels (Cresson et al., 2014). Similarly, the observation of all size and age classes of fish on artificial reefs suggests that they are not just attracting individuals produced elsewhere (Fowler and Booth, 2012).

4.3. Altered distributions of species

Ocean sprawl may cause changes in species distributions when it introduces new bridges or barriers to dispersal. The distribution of opportunistic colonists of hard substrates, which have larvae present in the water column for much of the year, often are tolerant to a wide range of environmental conditions, and are therefore able to rapidly recruit to new substrates, including artificial structures. The proliferation of coastal defence structures is thought to have played a key role in the establishment and spread of *Codium* along the coast of the north Adriatic Sea by providing suitable habitat for its settlement (Bulleri and Airoldi, 2005). Along the southeastern coast of the USA, artificial structures such as pontoons, bridges and seawalls have allowed colonization and spread of the non-native mussel, *Perna viridis*, in a predominantly sedimentary environment (Baker et al., 2007; Spinuzzi et al., 2013). The mussel is thought to have been initially introduced to the area by ballast water (Power et al., 2004), but is presently limited in spread by cold weather events that will presumably decrease in frequency with climate warming (Firth et al., 2011; Urian et al., 2011; McFarland et al., 2015).

The effects of artificial structures on the ranges of species are not, however, limited to non-indigenous species. Oil and gas platforms around the Flower Garden Banks (northern Gulf of Mexico) have facilitated regional biogeographic expansion of scleractinian corals and coral reef fishes into locations that previously lacked hard substrate (Rooker et al., 1997). Artificial structures may also play an important role in facilitating climate migrants. For example, many intertidal species are presently showing poleward range expansions along the coast of the United Kingdom (e.g. Herbert et al., 2003; Mieszkowska et al., 2006; Herbert et al., 2007; Keith et al., 2011). Although these range expansions are in part driven by climate change, artificial coastal defences are also playing a role by providing suitable substrate for migration (Moschella et al., 2005; Hawkins et al., 2008; Firth et al., 2013b, 2015, 2016a).

4.4. Altered community structure and ecosystem functioning

Modification of landscape and trophic connectivity by ocean sprawl can modify the structure and function of communities through species-specific effects on distribution and abundance and by modifying species interactions. Additionally, artificial structures may cause major changes in community structure by modifying resource subsidies.

Surveys of port facilities, marinas, seawalls, breakwaters and other forms of coastal defence as well as offshore infrastructure associated with renewable energy generation have repeatedly shown that artificial structures disproportionately favour non-indigenous over native hard-bottomed species (Tyrrell and Byers, 2007; Ruiz et al., 2009; Sheehy and Vik, 2010; Mineur et al., 2012; Airoldi et al., 2015; de Mesel et al., 2015). This may be because non-indigenous species, with r-selected life history strategies, are able to rapidly colonise new substrates (Glasby et al., 2007), or because the vectors by which non-indigenous species are translocated select for species that are tolerant of the contaminants that typify urbanised coastlines (McKenzie et al., 2011). The communities establishing on artificial structures may influence those of nearby natural substrate by modifying the relative importance of competitive ability versus stochastic colonisation success (Didham et al., 2007). In the Mediterranean, the proliferation of non-native mussels, *Brachidontes pharaonis*, on nearshore beach rock habitats > 120 years after first introduction is thought to have been precipitated by a combination of habitat degradation and proliferation of the mussel on offshore platforms (Rilov et al., 2004). Prior to 1995, the non-native mussel was rare on natural rocky reefs because it is an inferior competitor to native mussel *Mytilaster minimus*. Following habitat degradation that made beach rock less suitable for perennial algae and more suitable for mussels, the non-native mussel was able to rapidly colonize due to a large spawning-stock biomass on offshore structures, resulting in a shift from *M. minimus* to *B. pharaonis* (Rilov et al., 2004).

The novel species assembly on artificial structures may also influence the structure and function of communities in adjacent habitats, by altering trophic connectivity and cross-habitat resource subsidies. For example, modelling suggested that 7–18 fold increases in the biomass of mussels on the Nysted offshore wind farm in Denmark would modify sediment communities by enhancing sedimentation through mussel egestion of fecal pellets, and enhance phytoplankton productivity through mussel excretion of ammonium waste (Maar et al., 2009). Empirical studies have found that soft sediment communities surrounding artificial reefs differ from those further away (e.g. Ambrose and Anderson, 1990; Fabi et al., 2002), presumably because some species are more susceptible to reef-associated predators than others (Langlois et al., 2005) or because some, deposit feeding, organisms benefit more than others from the trapping and production of organic matter by the reef (Falcão et al., 2007). Additionally, as the community structure of sediment-dwelling infauna is strongly coupled to sediment properties, alteration of sediment distribution and grain size by structures such as breakwaters and groynes typically leads to changes in macrofaunal diversity, abundance and species composition which are

Table 2
Some potential solutions for mitigating effects of ocean sprawl on connectivity.

Mechanisms of impacts	Impacts	Mitigation/Management strategy	Examples (where available)
Physical barriers	- Coastal defences such as groynes, breakwaters and seawalls serve as a barrier to movement of organisms, sediments, water and detritus	- Replace hard- with soft- engineering approaches, that do not involve hard barriers	- Beach nourishment (Finkl and Walker, 2004; Hanson et al., 2002; Cooke et al., 2012) and beach scraping (Kana and Svetlichny, 1982; Wells and McNinch, 1991) have been used as alternatives to hard engineering
		- Utilise designs that allow overtopping or penetration of water, sediments and organisms between structural units	- Low-crested coastal structures (Hawkins et al., 2010), seabee seawalls constructed of hollow hexagonal blocks (Charlier et al., 1989)
		- 'Living Shorelines'	- Use of natural elements such as oyster reefs and wood to protect shorelines from erosion (Davis et al., 2006).
	- Culverts and floodgates impede migrations of mobile species into coastal wetlands	- Reverse engineering: remove physical barriers to restore tidal inundation to wetlands	- Implementation of development set-backs that preserve natural barriers (e.g. dune systems) and allow for shoreline retreat under sea-level rise (Ferreira et al., 2006)
		- Modify floodgates so that they remain open for longer periods	- Following removal of culverts, the richness and abundance of fish immediately increased in one tidal creek while in a second, recovery occurred over a 16 year period (Boys and Williams, 2012)
		- Fishways or fishladders, i.e. structures placed on or around constructed barriers to give fish the opportunity to migrate. May include pool-type, denil, lock, trap and transport, rock ramp, bypass or eel fishways	- Use of retarders, side-hung doors, or self-regulating gates allow gates to remain open for a longer proportion of the tidal cycle, providing greater opportunity for migration of species and less time for generation of environmental gradients that deter migration (Williams et al., 2012; Boys et al., 2012)
- Dams and weirs prevent ontogenetic migrations of mobile species between freshwater and coastal systems	- Environmental flows; water releases. Intensify natural high flow to restore connectivity between main channel and floodplain habitats	- Typically effective only for allowing upstream passage of a sub-set of fish species (Crook et al., 2015)	
- Water retaining structures reduce flow to estuaries and coastal environments	- Replace nets with shark surveillance and warning systems (e.g. sonar, drones, light aircraft etc) or electrical shark shields	- Managed flow prevented the accumulation of sand and resultant formation of sand bar barriers across estuary mouths in Victoria, Australia (Lloyd et al., 2012)	
Deterrents to migration	- Shark nets prevent movement and cause entanglement of non-target species	- Use of new technology such as gravity or suction foundations instead of pile-driven ones	- Shark spotters programme, Cape Town, combines surveillance with flag and alarm warning system
	- Pile driving during construction of artificial structures deters marine mammals and fish	- Spatial planning	- Sweden's largest offshore wind energy farm, Lillgrund, used concrete gravity foundations
	- Offshore structures alter migrations patterns of birds and marine mammals	- Incorporate skylights into the design of jetties, pontoons and coastal walkways (Dafforn et al., 2015a)	- Offshore installations should be built as close as possible to minimise development footprint (Drewitt and Langston, 2006)
Habitat fragmentation	- Shading by coastal structures deters fish passage	- Use of ecologically friendly moorings	- Avoid construction on migratory paths of birds or marine mammals; and avoid building on protected or key areas of conservation (Drewitt and Langston, 2006)
		- Incorporate skylights into the design of jetties and pontoons	- Fibreglass grating used in the construction of jetties, pontoons and coastal walkways on the Central Coast of New South Wales, Australia
	- Loss of 'source' habitat	- Spatial planning	- Replacement of the block and chain system of swing mooring buoys with a mooring post with load spreaders and shock absorbers prevents seagrass damage from chain drag (Demers et al., 2013)
Conduits to the movement of organisms and resources	- Artificial structures serve as stepping stones for species invasions and range expansions	- Pre-seed structures with native habitat-forming species that pre-empt space	- See above, under deterrents to migration
		- Use materials that promote settlement of native species	- Avoid construction on key areas of conservation value
		- Spatial planning	- Transplantation of the threatened species of algae <i>Cystoseira barbata</i> on breakwaters in the Mediterranean Sea (Perkol-Finkel et al., 2012; Ferrario et al., 2016); transplant of corals and sponges to intertidal seawalls in Singapore (Ng et al., 2015)
			- ecologically active concrete enhanced recruitment of native habitat-forming species (Perkol-Finkel and Sella, 2014)
			- Avoid long continuous corridors of artificial structures that may provide corridors for non-native species

(continued on next page)

Table 2 (continued)

Mechanisms of impacts	Impacts	Mitigation/Management strategy	Examples (where available)
Alteration of trophic connectivity	- Paucity of microhabitats on artificial structures renders resident biota more susceptible to predation	- Incorporate complexity into design of artificial structures and/or enhance complexity of existing structures	- Addition of pits and crevices to seawalls (Martins et al., 2010; Chapman and Underwood, 2011) and wave energy foundations (Langhamer and Wilhelmsson, 2009)
	- Limited availability of intertidal space on vertical structures results in new biological interactions	- Design structures with enhanced intertidal surface-area	- Addition of artificial rockpools to seawalls and breakwaters (Browne and Chapman, 2011, 2014; Firth et al., 2013a, b, 2014a, b, 2016b; Evans et al. 2016);
	- Increased production of detritus on artificial structures, enhancing deposition in adjacent sediment	- Traps to avoid organic matter falling to adjacent soft-sediments	- Transplantation of native habitat-forming species onto artificial structures (Perkol-Finkel et al., 2012; Ferrario et al., 2016; Ng et al., 2015)
	- Reduced detrital production as a consequence of habitat loss	- Construction of structures from materials that deter unwanted growth	- Stepped structures such as seawalls (Chapman and Blockley, 2009; Chapman and Underwood, 2011; Dyson and Yocom, 2015); seawall texturing (Martins et al. 2010; Chapman and Underwood, 2011)
	- Hybrid designs, that incorporate coastal vegetation into structures	- Dykes coupled with vegetation to reduce wave impacts in Netherlands (Cheong et al. 2013); revetments being coupled with saltmarsh restoration in Chesapeake Bay, USA (Duhring, 2006; Bilkovic and Mitchell, 2013); mangroves coupled with breakwaters in Malaysia (Kamali et al., 2010; Hashim et al., 2010)	
- Alteration of detrital transportation and deposition	- Design structures of short length and high spacing to minimise retention of materials		
	- Incorporate hydrologic modelling in design phase to ensure structures will not have adverse effects on material transport		
- Bird collisions with blades of offshore wind farms increase carrion subsidies to offshore waters	- Wind farm design		- Orientate blades so that they are parallel to main flight paths and there are corridors between clusters of turbines; paint or mark blades and turbines so they are more visible to birds (Drewitt and Langston, 2006)

most pronounced in the immediate vicinity of the structure (Martin et al., 2005; Moschella et al., 2005; Walker et al., 2008).

Wrack is an important source of carbon, nutrients and shelter for invertebrate communities of intertidal and supratidal shorelines (Griffiths and Stenton-Dozey, 1981; Polis and Hurd, 1996; Dugan et al., 2003). Hence, where the physical barrier provided by coastal armouring reduces wrack accumulations on estuarine or coastal shorelines, it typically results in reductions in populations of invertebrate fauna (Sobocinski et al., 2010; Heerhartz et al., 2016). Such decreases in the abundance of invertebrates may, in turn, negatively influence the shorebird, fish and small mammal populations that depend on wrack-inhabiting invertebrates as a source of nutrition (Kirkman and Kendrick, 1997; Rose and Polis, 1998; Carlton and Hodder, 2003; Dugan et al., 2003). In other areas where wrack (and rubbish) accumulations build up behind coastal defences (e.g. groynes, breakwaters) and other structures, major changes in the community structure of infauna may, conceivably, result from organic enrichment. Whereas moderate detrital loads might enhance benthic productivity and the species richness of invertebrate communities, the supply of large quantities of rapidly decomposing organic material to already enriched environments may induce sediment anoxia and community collapse (Pearson and Rosenberg, 1978).

5. Potential solutions and considerations for mitigating effects of ocean sprawl on connectivity

Strategies to maintain the connectivity of habitats in urban landscapes remain a relatively new topic of research for urban ecologists, which has thus far received more attention in terrestrial systems (Goddard et al., 2010; LaPoint et al., 2015), than in marine systems. In

terrestrial systems, the addition of green roofs to buildings, for instance, has been shown to restore some connectivity of arthropod communities (Braaker et al., 2014). Similarly, wooded streets have been shown to maintain a greater connectivity of birds in urban landscapes by providing alternative habitat for feeding and nesting during breeding season (Fernandez-Juricic and Jokimäki, 2001).

Parallel approaches can be applied to marine infrastructure to mitigate some of their impacts on the connectivity of organisms and resources (Table 2; Fig. 1c; Dafforn et al., 2015a). For example, seeding structures with native species, such as vegetation or coral, can pre-empt space that may otherwise be rapidly colonised by non-native species, potentially slowing their range expansion, whilst also preserving native biodiversity (e.g. Stachowicz et al., 2002; Perkol-Finkel et al., 2012; Ng et al., 2015; Ferrario et al., 2016). Use of environmentally friendly materials in structures may not only improve performance and durability, but also reduce ecological stress and encourage the development of natural communities (e.g. Coombes et al., 2011; Coombes and Naylor, 2012; Coombes et al., 2013). Recent attempts to ecologically design concrete mixes used in marine and coastal infrastructure have been encouraging, with higher invertebrate and fish diversity reported on and around structures built using EConcrete® than on those built using traditional Portland cement (Sella and Perkol-Finkel, 2015). Similarly, the incorporation of microhabitats into artificial structures can promote diversity of species and provides refugia from both abiotic and biotic stress (Chapman and Blockley, 2009; Martins et al., 2010; Browne and Chapman, 2011, 2014; Chapman and Underwood, 2011; Firth et al., 2014a,b, 2016b; Coombes et al., 2015; Evans et al., 2016; Loke et al., 2017-in this issue). In the long run, ecological considerations in the design of marine infrastructures

need to be integrated into careful planning of repair and maintenance during the lifetime of the structure. [Airoldi and Bulleri \(2011\)](#) found that the regular maintenance of breakwaters caused a marked decrease in the cover of dominant space occupiers, such as mussels and oysters, and a significant increase in opportunistic and invasive forms, such as microbial films and weedy/non-indigenous macroalgae. They also found that if interventions were made at certain times of the year the system recovered to the original state more rapidly compared to when interventions were done in other periods of the year, reflecting the reproductive biology windows of the dominant native species, ultimately limiting the spread of the invasive species.

Strategies to mitigate impacts of structures that can introduce physical barriers, such as dams and breakwaters, may include designs and management strategies that maximise permeability, allowing movement of water (and preferably also sediments) across the barrier, either as a result of frequent overtopping or water penetration through pores ([Table 2](#)). In minimising impacts on water quality and sediment characteristics, such approaches may also minimise impacts on associate fauna and flora ([Martin et al., 2005](#)). In the case of coastal defences, impacts of structures on ecological connectivity may be reduced by minimising their length and height and increasing their spacing (e.g. [Tait and Griggs, 1990](#); [Engelhardt et al., 2004](#); [Burcharth et al., 2007](#); [Uijtewaai, 2005](#)). Management responses such as the implementation of ‘environmental flows’ from dams may be used to restore longitudinal connectivity by providing sufficient depth for passage of organisms over shallow habitats ([Arthington et al., 2010](#)) or prevent the accumulation of sand and, consequently, the formation of sand bar barriers across estuary mouths ([Lloyd et al., 2012](#); [Crook et al., 2015](#)). Simulating the ‘right’ regimes (e.g. flow magnitude, flood frequency, timing and duration) required to maintain sediment dynamics within and between habitats, ecological processes and ecological connectivity within and across habitats, is however, still a challenge ([Arthington et al., 2010](#)).

Mitigation strategies to reduce barrier effects of offshore wind farms on bird, fish and marine mammal migrations include orientating the blades so that they are parallel to main flight paths of birds, ensuring there are corridors between clusters of turbines and timing construction to avoid particularly sensitive periods ([Drewitt and Langston, 2006](#); [Snyder and Kaiser, 2009](#)). Additionally, increasing the visibility of rotor blades to birds, by creating high contrast patterns or by applying UV paint, may reduce collisions and hence modification of carrion subsidies ([Drewitt and Langston, 2006](#)). Some of the impacts caused by the noise associated with construction of offshore structures can be overcome by modifying construction methods ([Table 2](#); [Snyder and Kaiser, 2009](#)). Pile-driven foundations - known to affect several species of marine organisms - can be replaced, for example, by gravity or suction foundations ([Snyder and Kaiser, 2009](#)). Gravity foundations are simple concrete structures with large diameter bottoms that rest on the sea floor whereas suction foundations are simple steel baskets that form a seal with the ocean bottom. Suction is then applied to the inside of the basket and the resulting pressure difference causes the basket to bury itself in the sediment, much like a driven monopile. Both alternatives do not require piling operations and therefore have less potential to disturb marine mammals and fish ([Snyder and Kaiser, 2009](#)). Also, gravity foundations have more complex structure than monopiles, which may favour colonisation by native organisms.

In some coastal areas, however, the ideal management response may be to reduce dependence on artificial structures by conserving, restoring and creating natural habitats ([Fig. 1c](#); [Table 2](#); [Temmerman et al., 2013](#); [Dafforn et al., 2015b](#)). Mangroves, salt marshes, shellfish and coral reefs provide natural defence against storms and flooding (e.g. [Koch et al., 2009](#); [Borsje et al., 2011](#); [Gedan et al., 2011](#)) and their restoration can be a desirable alternative to coastal engineering for stabilising shorelines and protecting coastal infrastructure. “Living shorelines” (also termed “ecosystem-based adaptation”), the use of natural elements such as oyster reefs and wood to protect shorelines from erosion, help to maintain ecological connectivity by minimising loss and

fragmentation of habitats (e.g. [Davis et al., 2006](#)). The effectiveness of these approaches for adaptation to climate change and maintaining ecosystem connectivity has recently been reviewed ([Dowald et al., 2014](#)), with success contingent on a strong understanding of the geomorphic processes that control erosion and accretion at a site ([Rotman et al., 2008](#); [Friess et al., 2013](#)) and which underpin ecological function ([Spencer and Harvey, 2012](#)). Recent studies have also highlighted that long-distance interactions between ecosystems (e.g. oysters facilitating salt marsh) can be important for the maintenance of natural coastal defences against globally rising seas and increased storm frequencies (reviewed by [van de Koppel et al., 2015](#)) and so should be considered in the design of resilient ecosystem-based defences ([Bouma et al., 2014](#)).

Equally, soft-engineering, such as beach nourishment and scraping, is in some instances a more desirable method for coastal protection than hard engineering because it maintains beach width (see extensive discussion in [Dafforn et al., 2015b](#)). Beach nourishment does not, however, eliminate impacts on land-sea connectivity (see [Peterson and Bishop, 2005](#); [Peterson et al., 2006](#)) and can introduce impacts as a result of mismatch of the granulometry of fill with native beach sediments ([Manning et al., 2014](#); [Peterson et al., 2014](#)). Where soft-engineering strategies are not feasible, artificial structures should be built or retrofitted in ways to decrease their impacts on ecological connectivity (e.g. [Chapman and Underwood, 2011](#)).

In instances where the need for the barrier has been superseded, “reverse engineering”, which may include restoration of natural hydrology and/or removal of the barrier itself, can have considerable ecological benefits ([Table 2](#); [Fig. 1c](#); [Boys and Williams, 2012](#); [Boys et al., 2012](#)). For example, removal of dams has been shown to restore connectivity, increasing species richness and recruitment ([Rolls et al., 2013](#)). When full removal of barriers is not possible, construction of infrastructure for fish passage (e.g. fish ladders) can be incorporated into the design of dams and weirs to allow connectivity between upstream and downstream and might aid in restoring connectivity of mobile species between freshwater and coastal environments ([Table 2](#); [Crook et al., 2015](#)).

Solutions to ocean sprawl need to take into account changes in climate and societal demand, which requires a combination of robust, resilient and cost-effective strategies ([Cheong et al., 2013](#)) and, ideally, a multi-disciplinary team of experts and effective knowledge brokers ([Naylor et al., 2012](#)). In the Netherlands, for example, dykes built to prevent flooding have been planted with willow trees to reduce wave impacts on the dykes, increasing their integrity and reducing environmental impacts (e.g. [Borsje et al., 2011](#)). In Malaysia, a combination of low crested breakwaters and a mangrove restoration plan was applied to an intertidal beach, successfully rehabilitating the coast and facilitating the natural recovery process of the coastal ecosystem ([Kamali et al., 2010](#); [Hashim et al., 2010](#)). “Hybrid” designs, in which natural habitats are combined with hard structures, have also been successfully used in Chesapeake Bay, USA (e.g. revetments being coupled with saltmarsh restoration, [Duhring, 2006](#)). The habitat included within hybrid-designs does not, however, always support the same biodiversity and ecosystem functions as equivalent natural habitat ([Bilkovic and Mitchell, 2013](#)), and hybrid designs must consequently balance loss of existing habitats with shoreline stabilisation.

In addition to designing structures to minimise their connectivity impacts at a local scale, spatial planning is imperative if we want to efficiently reduce impacts of ocean sprawl on connectivity around the globe ([Table 2](#); [Fig. 1c](#); [Dafforn et al., 2015b](#)). Spatially explicit consideration of the multiple human uses in the marine and estuarine systems are critical to support current and future uses of the ocean and maintain the delivery of valuable ecosystem services ([Foley et al., 2010](#)), which is dependent, among other things, on the connectivity of organisms and resources. In terrestrial systems, comprehensive and integrated land use planning is commonly used as a central component of developmental and environmental planning ([Douvere, 2008](#)). In marine systems,

however, current governance is by sector, which leads to uncoordinated, fragmented and, often, disjointed rules and regulations (Foley et al., 2010; Crowder and Norse, 2008). Because connectivity in marine and estuarine systems operates at scales ranging from microns to 1000s of kilometres (Sheaves, 2009; LaPoint et al., 2015), so too will the effects of ocean sprawl. Hence, planning and management of construction in the sea needs to be considered at the scale of ecosystems, and should consider the spatial arrangement of structures. For instance, artificial structures that are built across entire sedimentary coastlines without virtually any spacing (e.g. North Adriatic) can facilitate the introduction and dispersal of non-indigenous species, while offering unsuitable habitat to many natives (Airoldi and Bulleri, 2011; Airoldi et al., 2015). On the other hand, it may be desirable to build wind farms as close together as possible to minimise their development footprint (Drewitt and Langston, 2006).

Management of ocean sprawl should ensure that key areas of conservation significance and sensitive areas are avoided as sites for artificial structures (Table 2). Construction of wind farms, for instance, should be avoided in areas known to be bottlenecks on the migratory routes of large numbers of birds (Snyder and Kaiser, 2009). Similarly, planners should consider migration routes of marine mammals and turtles when selecting a site (Snyder and Kaiser, 2009). In particular cases, construction of offshore structures in deeper waters might have lesser impacts on connectivity than those built near shore. Areas considered essential habitat for threatened or endangered species should be excluded from development plans (Snyder and Kaiser, 2009). Furthermore, whether potential sites of construction are considered 'sink' or 'source' areas should also be evaluated before construction is allowed. In theory, structures built in source areas will have greater impacts than those in sink areas (e.g. Crowder et al., 2000). In any case, guidelines need to be set that incorporate development footprints as well as context-specific spatial planning – i.e. each type of structure should have specific guidelines and regulations depending on the type and magnitude of its impact (Dafforn et al., 2015b).

6. Research gaps and opportunities to investigate how ocean sprawl modifies ecological connectivity

The development of effective strategies for minimising undesirable impacts of ocean sprawl is contingent on a mechanistic understanding of how structures individually and interactively modify ecological connectivity. Our review has revealed that there are major deficiencies in our understanding of how ocean sprawl influences connectivity, resulting from the limited number, scale and scope of studies, their failure to consider interactive effects of multiple structure types, and their predominantly descriptive (as opposed to experimental) approach to assessing effects on connectivity.

6.1. Scales of connectivity

Our current understanding of the temporal and spatial scales across which ocean sprawl influences ecological connectivity is hindered by inconsistencies in the methods used to address impacts at local and regional scales. At local scales (1–100 km), studies have predominately used surveys (e.g. Tyrrell and Byers, 2007; Sobocinski et al., 2010; Heerhart et al., 2014), often done at a single time point (e.g. Mauro et al., 2001; Atchison et al., 2008; Fauvelot et al., 2009, 2012), to assess impacts of ocean sprawl. In some instances, these surveys have been accompanied by small-scale experiments (e.g., Posey and Ambrose, 1994; Harris et al., 2014), but rarely do these assess changes in connectivity from before to after the construction of structures. At regional scales (1000s of kms), and particularly offshore, impacts have generally been assessed using modelling approaches (e.g. Adams et al., 2014), due to the constraints of access inherent to distant and deep water (Hilário et al., 2015). By using a combination of surveys, experiments (such as before-after-control-impact assessments) and modelling approaches,

at both local and regional scales, more robust conclusions, based on multiple lines of evidence, may be reached. The advent of a variety of "big data" tools provides new opportunities for remote collection and integration of large amounts of information over a variety of temporal and spatial scales (Dafforn et al., 2016). Where modelling approaches are appropriate, then "big data" has the potential to better parameterise these models (Dafforn et al., 2016) and create more holistic models. For example, species distribution models that incorporate effects of the artificial structure with both species-species interactions and species-resource interactions would go some way to addressing knowledge gaps.

Independent of their approach, the majority of studies have focused on the effects of a single structure (e.g. seawalls or offshore platforms) rather than the combined consequence of ocean sprawl (but see Duarte et al., 2012). Frequently, the focus of studies has been limited to a particular zone or habitat of a particular structure (i.e. intertidal or subtidal, benthic or pelagic, e.g. Bulleri and Airoldi, 2005; Fauvelot et al., 2009, 2012). Connectivity acts across multiple scales, habitats and trophic levels and could be affected by the interactions between different structures (Blockley, 2007). Studies are needed that consider cumulative effects of multiple artificial structures on the condition and fitness of organisms, and their habitats, across their range.

6.2. Types of connectivity

The vast majority of studies examining effects of artificial structures on ecological connectivity have focused on the role of hard substrates as stepping stones for fouling organisms. These studies have predominantly used surveys of communities on artificial structures, in order to infer range expansions (e.g. Tyrrell and Byers, 2007; Ruiz et al., 2009; Sheehy and Vik, 2010; Mineur et al., 2012; Airoldi et al., 2015; de Mesel et al., 2015). Approaches that directly assess connectivity are needed in order to ascertain whether species are subsequently dispersing from artificial structures to historically inhabited or novel locations of natural habitat.

Genetic studies assessing the relatedness of populations and their provenance would build a stronger case for the role of artificial structures in facilitating species range expansions of species that are substrate or dispersal limited. It is important not to confound ecological connectivity between populations (i.e. some interchange in most years) with the level of genetic interchange needed to produce panmictic populations (some interchange most generations, see Hawkins et al., 2016 for discussion). Moreover, to causally attribute changes in the genetic structure of populations to ocean sprawl, temporal and spatial replication of sampling is needed. To our knowledge, there has not yet been a study that has tracked changes in the genetic structure of populations at the time-scale of years, from before to after the addition of artificial structures, at unaffected control and impacted locations. Molecular techniques such as environmental DNA (eDNA) have the potential to rapidly collect information about the distribution of species and their propagules from benthic and pelagic collections (Ardura et al., 2015a, b; Bott et al., 2010; Pochon et al., 2013) and their spread (Ardura et al., 2015a,b). Modelling studies might also be helpful in predicting the ramifications on species ranges of new installations of artificial structures. For example, hydrodynamic models showed that proposed developments of offshore renewable energy in the area around the Firth of Lorn (a fjordic region in western Scotland) is likely to affect the dispersal, and hence the abundance, of organisms with planktonic larvae, allowing those presently restricted to Northern Ireland to invade the Scottish coastline (Adams et al., 2014).

A broad range of tagging methodologies is available for assessing the movement of larvae and adults (Gillanders, 2005), all of which are under-utilised with respect to investigating effects of artificial structures. These include external tags, external marks, internal tags, telemetry and natural tags (Gillanders, 2005, 2009; Lechner et al., 2013). In particular, elemental signatures in the otoliths of fish have been used

as a natural tag to determine connectivity between estuarine and coastal habitats (Gillanders, 2005), and may be used to assess how structures are influencing connectivity at intermediate scales. Tools such as Unmanned Aerial Vehicles and marine mammal tracking devices may prove useful for recording movements of larger species (reviewed by Dafforn et al., 2016). Knowledge of how the behavior of mobile species influences their response to artificial structures would assist with developing mitigation strategies. For example, the development of effective fishways requires biological knowledge of how the behaviour of fish responds to variable environmental conditions, such as flow, as well as hydraulic and civil engineering knowledge and expertise to develop facilities that provide appropriate conditions that fish will utilize (Williams et al., 2012).

Overall, most studies on effects of artificial structures on populations of predators and prey have been done at the site-scale using caging experiments or visual observations to compare predation between artificial and natural hard substrate, or artificial structures of varying design (Jackson et al., 2008; Munsch et al., 2014; Ferrario et al., 2016). There is need for research that address how alteration of trophic connectivity by artificial structures influences population sizes at larger, regional scales. In estuarine and coastal systems, predator/prey interactions and trophic connectivity have been effectively investigated at scales of meters to tens of kilometres through the use of gut content analyses, fatty acids, stable isotopes, and tracer studies (Guest et al., 2004; Alfaro et al., 2006; Wernberg et al., 2006). Such approaches have been used to trace the carbon sources of terrestrial invertebrates to marine ecosystems (Mellbrand et al., 2011), but it is unknown how coastal structures interfere with this energy flow.

To build and test hypotheses about ecological connectivity and ocean sprawl, we also need an extensive understanding of structural connectivity. This includes the physical connection between “habitats” or structures and resultant modifications to contaminants, sedimentary transport pathways and budgets. A variety of resources now exist including land use data that can inform coastal assessments of artificial structures and remote sensing tools that can be used to map offshore structures. These remote data sources could be complemented by detailed surveys of sediment transport, accumulation and erosion and mapping and the geomorphological systems in which they are placed. There is also the potential to use passive samplers to remotely collect physico-chemical data relating to water column changes or stable isotope analyses to investigate detrital subsidies from wrack.

6.3. Ecological connectivity and eco-engineering

Connectivity is crucial to eco-engineering designs that include a restoration objective. To ensure natural recruitment processes are adequate for any restoration objectives to be met, we need to understand the potential for colonisation by investigating potential dispersal pathways and connections to adult reproductive populations. Where information on these factors is limited, or natural recruitment processes are likely to be slow, strategies that include “seeding” of eco-engineered structures (see Section 5) might be explored. This option would require research into how “seeding” and transplants to eco-engineered structures alter genetic connectivity (Reynolds et al., 2013) or may aid the spread of parasites and pathogens (Villareal et al., 2007; Firth et al., 2017-in this issue). Eco-engineering designs should also consider the influence of physical characteristics on connectivity and restoration success (Balke and Friess, 2016), for example, adding substrate or habitat types that do not occur naturally could enhance problems with connectivity. For example, hard substrate eco-engineering designs that are used in areas that should be primarily soft sediments may enhance reef type assemblages, but at the expense of potentially replacing or creating a barrier for soft sediment organisms (see Heery et al., 2017-in this issue).

Similarly, the scale of eco-engineering designs is an important consideration for ecological connectivity that has not been explored in

great detail (but see Loke et al., 2015; Loke and Todd, 2016). The incorporation of microhabitats into artificial structures has been found to promote diversity of species and provide refugia from predators (e.g. Chapman and Blockley, 2007; Chapman and Underwood, 2011; Firth et al., 2014b; Evans et al., 2016), but there is the potential to optimise these designs further by investigating the density and scale of microhabitats (Loke et al., 2015) and the level of structural connectivity.

7. Conclusions

Assessing the impacts of ocean sprawl in the near and offshore marine environment is a significant, and burgeoning, challenge for ecologists. Early work on this problem concentrated on local changes to systems. As ecological thinking embraced the connections between organisms and their landscape of habitats, so too biologists and engineers have started to consider the implications of sprawling artificial structures for ecological connectivity. This is the first review to comprehensively assess how the introduction of artificial structures to estuarine and marine environments may structurally and functionally alter connectivity. Importantly, artificial structures can inhibit ecological connectivity by acting as physical barriers to the movement of organisms and/or resources within and among habitats, or by altering environmental conditions in a way that deters species migrations or movement of resources. Conversely, artificial structures may enhance connectivity by weakening or removing existing barriers. For example, artificial structures can serve as stepping stones for the movement of hard-substrate dependent organisms across otherwise sedimentary habitat. Ocean sprawl may not only influence connectivity by introducing or removing physical barriers to species and resource dispersal, but it may also do so by destroying, fragmenting or modifying natural habitats (Boström et al., 2011). We have presented key examples of how ocean sprawl alters the strength and nature of trophic interactions that transfer energy across habitat boundaries. In many instances, due to the inherent interconnectedness of ecological systems, there are downstream consequences of artificial structures that cannot be easily predicted.

Although our review paints a compelling picture of the potential impacts of ocean sprawl across a wide variety of temporal and spatial scales, the actual magnitude and scale of impacts of artificial structures on marine connectivity is largely unknown. Moreover, it is unclear how the impacts of artificial structures will be affected by other consequences of ocean sprawl, for example pollution, or by global climate change. For all ecological systems, global climate change is associated with elevated temperatures, greater weather variability and increases in storm frequency and/or intensity (Pachauri et al., 2014). Not only will the consequences of a changing climate modify the scale of impacts as governments and land managers increase the extent of sprawl associated with defences against the sea, but we will also see changes in variability influencing the consequences of sprawl. For example an increase in the frequency of storm surges will see tidal barriers close more frequently, which means the general impacts of barriers may not be predictable from current patterns and so ecologists will need to propose, and test, new models and hypotheses (Underwood, 1995).

The other grand challenge identified by our review is a need for ecological science to consider impacts and effects beyond changes in local abundance or simple trophic interactions. The multiple effects of ocean sprawl on connectivity have significant ecological ramifications including the potential to alter genetic structure of populations, as a result of changes to migration patterns. Apart from effects on genetic structure, population sizes may also respond to altered landscape or trophic connectivity, for example when birth rates, death rates or migration patterns are modified by ocean sprawl. Migration and dispersal patterns are key factors that influence the distributions of species and, when these patterns are interrupted or modified by artificial structures, there may be consequences for community structure and ecosystem functioning. However, despite the links and inferences we are able to draw from the literature, we still lack clear quantification of how

changes in assemblages associated with ocean sprawl may influence key ecosystem functions and services.

With the anticipated increase in artificial structures there is a pressing need to address the lack of primary data that directly investigates the effects of ocean sprawl on ecological connectivity. This will be crucial in enabling managers to effectively use engineering and spatial planning solutions to the problems we have identified in this review. We have highlighted a range of research gaps including a need for research that looks more holistically at impacts of ocean sprawl on connectivity across multiple scales, habitats and trophic levels through large-scale survey work and exploiting an increasing range of “big data” tools available to interpret these impacts. Approaches to collecting information that will enhance our understanding of how ocean sprawl affect ecological connectivity include modelling, genetic studies, eDNA, tagging and remote sensing.

The increasing investment in solutions-based research to mitigate the problems associated with ocean sprawl has resulted in impressive growth of strategies such as restoration, soft engineering and ecological engineering, which all seek to increase the ecological sustainability of building into the ocean. To date, none of these strategies have specifically addressed the issue of connectivity, although the importance is increasingly being recognised (Dafforn et al., 2015b; Loke and Todd, 2016). In the future, solutions-based strategies underpinned by high-quality science will offer solutions and generate new understanding for managers of ocean sprawl. The significant task for experimental ecologists is to work with engineers, managers and government in the context of climatic change, to maximise the effectiveness of ecological knowledge in solving the problems so clearly identified in this review.

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