Towards an urban marine ecology: characterizing the drivers, patterns and processes of marine ecosystems in coastal cities

Peter A. Todd[1], Eliza C. Heery[1], Lynette H. L. Loke[1], Ruth H. Thurstan[2], D. Johan Kotze[3] and Christopher Swan[4]

[1]Experimental Marine Ecology Laboratory, Dept of Biological Sciences, National Univ. of Singapore, 16 Science Drive 4, 117558, Singapore

[2]Centre for Ecology and Conservation, College of Life and Environmental Sciences, Univ. of Exeter, Penryn, UK

[3]Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, Univ. of Helsinki, Lahti, Finland

[4]Dept of Geography & Environmental Systems, Univ. of Maryland Baltimore County, Baltimore, MD, USA

Corresponding author: Peter A. Todd, Experimental Marine Ecology Laboratory, Dept of Biological Sciences, National Univ. of Singapore, 16 Science Drive 4, 117558, Singapore. E-mail: dbspat@nus.edu.sg

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Abstract

Human population density within 100 km of the sea is approximately three times higher than the global average. People in this zone are concentrated in coastal cities that are hubs for transport and trade – which transform the marine environment. Here, we review the impacts of three interacting drivers of marine urbanization (resource exploitation, pollution pathways and ocean sprawl) and discuss key characteristics that are symptomatic of urban marine ecosystems. Current evidence suggests these systems comprise spatially heterogeneous mosaics with respect to artificial structures, pollutants and community composition, while also undergoing biotic homogenization over time. Urban marine ecosystem dynamics are often influenced by several commonly observed patterns and processes, including the loss of foundation species, changes in biodiversity and productivity, and the establishment of novel assemblages, ruderal species and synanthropes. Further, we discuss potential urban acclimatization and adaptation among marine taxa, interactive effects of climate change and marine urbanization, and ecological engineering strategies for enhancing urban marine ecosystems. By assimilating research findings across disparate disciplines, we aim to build the groundwork for urban marine ecology – a nascent field; we also discuss research challenges and future directions for this new field as it advances and matures. Ultimately, all sides of coastal city design: architecture, urban planning, and civil and municipal engineering, will need to prioritize the marine environment if negative effects of urbanization are to be minimized. In particular, planning strategies that account for the interactive effects of urban drivers and accommodate complex system dynamics could enhance the ecological and human functions of future urban marine ecosystems.

Keywords: climate change, ecological engineering, ocean sprawl, pollution pathways, resource exploitation

1. Introduction

The world's population is urbanizing rapidly (Bloom 2011, UN 2017) with mass migration towards coastlines (Creel 2003) and policy reforms that favour densification (Dallimer et al. 2011, Kyttä et al. 2013). Population density at the coast (≤ 100 km from the sea) and ≤ 100 m above sea level is approximately three times higher than the global average and is increasing (Small and Nicholls 2003). Most people are concentrated in coastal cities that, as hubs for trade and/or due to a fertile delta, are frequently situated where river and sea meet (Konishi 2000). Many of these cities have expanded into megacities of more than ten million people (Nicholls 1995, Li 2003). For ecologists, coastal cities are of particular interest and concern, not only from a terrestrial perspective, but also in terms of consequences in the marine environment (Dafforn et al. 2015).

Understanding of the effects of urbanization on marine ecosystems and ecological processes is growing (Burt 2014, Mayer-Pinto et al. 2015, Firth et al. 2016). Human density is strongly related to resource exploitation, and one of the early effects of marine urbanization is the depletion of nearby fishery resources (Li 2003, Kirby et al. 2004). Coastal cities create marine pollution, including that from sewage and urban runoff (Hoffman et al. 1983, Nixon 1995, Cornelissen et al. 2008). They also lead to nearshore development, usually starting with a harbour, but also including hard coastal defences to reduce erosion of valuable land, whether it be pre-existing or reclaimed (Charlier et al. 2005, Lotze et al. 2005, Tian et al. 2016). The combination of development and shore protection results in the proliferation of artificial coastal structures, such as seawalls, breakwaters, piers, and groynes (Bulleri and Chapman 2010, 2015). These structures have significant effects on the ecology of shorelines, especially when entire habitats are replaced with novel materials such as concrete and granite (Firth et al. 2014, Dyson and Yocom 2015, Loke et al. 2019a).

Several recent reviews have separately highlighted urban-related pollution and physical modifications of urban shorelines as critical components of urban marine ecosystem dynamics (Dafforn et al. 2015, Firth et al. 2016, Heery et al. 2018b), but exploitation of marine resources is rarely emphasized in an urban context (though see Li 2003, Baum et al. 2016). The overarching characteristics of urban marine ecosystems that result from each of these factors and their potential combined effects have yet to be thoroughly considered. There is considerable need to integrate findings relating to marine urbanization across subdisciplines of ecology; this effort would be aided by conceptual frameworks that integrate multiple variables, identify potential interactions and feedbacks, incorporate historical trajectories, and facilitate the development of testable hypotheses regarding the response of urban marine ecosystems to further environmental change. Frameworks meeting this need would not only broadly support marine research in the Anthropocene, as nearly all coastal zones are now strongly impacted by anthropogenic stressors, but would also help build a foundation for urban marine ecology—a field in its nascence. Inevitably, urban marine ecosystems are coupled social-ecological systems and are heavily influenced by what is happening 'upstream' in the urban fabric, by physical modifications nearshore and offshore, and by current and future consequences of climate change, such as sea-level rise and punctuated extreme weather events. As such, the dynamics and prevailing ecological paradigms for these systems have yet to be tested experimentally, and it is only through expanded field manipulations that it will be possible to understand the core properties of urban marine ecosystems: how they are structured, how they function, and the key parameters that drive the ecosystem services they provide.

In this paper, we outline the primary drivers of marine urbanization and identify the known patterns exhibited by marine ecosystems in urban areas. Empirical testing of the underlying processes that create these patterns and further research in areas we highlight in this paper can help build a framework for understanding multifaceted impacts of marine urbanization, and future trajectories of urban marine ecosystems in the face of climate change.

2. Three main drivers of marine urbanization

The process of marine urbanization comprises three primary drivers (Fig. 1). The first is exploitation of both living and non-living resources (Section 2.1) and includes recreational, subsistence and commercial fishing, as well as dredging and mining for minerals (Table 1). In post-industrialized nations, this may largely be historical, but with long lasting effects that are still relevant today. The second is pollution (Section 2.2), including sediments, industrial waste (often toxic), municipal waste (e.g. landfill leachate), domestic water and waste (baths, washing machines, kitchen waste), animal/slaughterhouse waste, fecal matter, street dust, oil from automobiles and other contaminant sources, pharmaceuticals (especially hormones and antibiotics), light pollution, and noise pollution (Table 2). The third is the wholesale conversion of natural habitats into a different state (Section 2.3), such as reclaimed land, seawalls, jetties, piers, marinas, groynes, breakwaters, port and harbor infrastructure and bridges (collectively termed as “ocean sprawl”, Table 3). These three drivers are presented in the chronological order in which they often begin to occur, though their timing and relative scope can vary substantially between cities (Fig. 2). Further, the three drivers can have interactive effects, with potential additional consequences for marine ecosystems (Section 2.4). Other factors relating to urbanization, such as elevated propagule pressure and invasion risk, can also be particularly intense in coastal cities (Carlton 1996, Ruiz et al. 1999, 2000, Mineur et al. 2012, but see Tan et al. 2018 and Wells et al., 2019), however, we discuss these primarily as they relate to one or more of the three drivers presented below.

2.1 Resource exploitation (both living and non-living)

It is increasingly well documented that the overexploitation of living coastal and marine resources is one of the earliest observable forms of human disturbance within coastal ecosystems (Jackson et al. 2001, Pandolfi et al. 2003, Lotze et al. 2006;). Moreover, coastal systems that have endured the longest period of intense human impacts and that contain the highest human populations are among the most degraded (Lotze et al. 2006). Yet, awareness of the magnitude of changes that previously occurred as a result of the exploitation of living and non-living marine resources is generally poor. This is due to exploitation usually commencing prior to regular monitoring of these systems, coupled with the pervasiveness of the shifting baseline syndrome, where a lack of knowledge of past ecological conditions facilitates a gradual ratcheting down of expectations as to what constitutes a healthy ecosystem (Pauly 1995, Shepherd 1995).

Coastal population growth and development has impacted a wide variety of living marine resources (Table 1). For instance, oyster reefs and maerl beds have dramatically declined or been extirpated in coastal ecosystems around the world due to destructive fishing methods aimed at providing food and/or building material for increasingly urbanized populations (Airoldi and Beck 2007, Claudet and Fraschetti 2010). Human population growth facilitated the establishment and expansion of industrialized commercial harvesting for marine mammals, turtles and fin-fish species, ultimately resulting in the decline or loss of marine megafauna, and of diadromous and large demersal fish species (e.g., Lotze et al. 2005, Van Houtan and Kittinger 2014). Targeted fin-fish assemblages, although constrained by environmental factors (e.g., availability of suitable habitat), have been shown to decline in abundance and richness along increasing gradients of human pressure or proximity to urban centres in a range of habitats (e.g., coral reefs: Aswani and Sabetian 2009, Brewer et al. 2009, Williams et al. 2008; surf zones of exposed sandy beaches: Vargas-Fonseca et al. 2016). Fishing effort also impacts intertidal species abundance, for example, the majority of known sandy beach invertebrate fishery stocks are fully exploited, overexploited or depleted due to commercial, subsistence or recreational harvesting (e.g., Defeo and Alava 1995, Defeo 2003).

Overexploitation often follows a predictable spatial-temporal pattern that is tied to urban growth. This is particularly evident among exploited sessile species. On the East Coast of the United States, historical oyster fishery collapses demonstrated sequential depletion beginning in urbanized estuaries and spreading along the coast away from urban centres (Kirby et al. 2004). Many European native oyster reefs adjacent to urban conurbations became ecologically extinct prior to the mid-20th century (Airoldi and Beck 2007). Oyster (*Ostrea angasi*) reefs in South Australia disappeared less than 200 years after the first records of commercial oyster landings from this region by early Europeans (Alleway et al. 2015). A total of five species of giant clam were historically recorded in the coastal seas around Singapore, but now only two remain, and these only exist in very low abundances. The intensification of giant clam exploitation in the 19th century, followed by extensive coastal development from the 1960s onwards, are considered to be the main drivers in the decline and extirpation of these charismatic invertebrates (Guest et al. 2008, Neo and Todd 2012).

The historical legacy effects of overexploitation, combined with pollution and coastal development, means that the present day commercial exploitation of living marine resources adjacent to urbanized regions, at least in more economically developed countries (MEDCs), is often far lower than its historical peak (Lotze et al. 2005, 2006). The search for resources has thus moved further offshore and into less exploited regions (Anderson et al. 2011, Swartz et al. 2010). Recreational fishing participation rates in MEDCs have also seen a decline in the last two decades as a result of factors related to urbanization, such as increased urban sprawl, demographic change, and a reduction in fishable water resources (Poudyal et al. 2011). In contrast, within less economically developed countries (LEDCs), small-scale and subsistence fishing often remains a significant source of livelihood for coastal communities in or near urban areas (Smit et al. 2017). The maintenance of these traditional activities is, however, under pressure from factors such as declining water quality and coastal development (Smit et al, 2017), as well as enhanced access to education and alternative employment opportunities for children of fishing families (Teixeira et al. 2016). In some cases, urbanization may enhance economic opportunities for small-scale fishing communities. In southern Brazil, for example, the proximity of small-scale fishers to urban centres has expanded opportunities for subsistence fishers to access additional markets, as the presence of high numbers of fishers enables them to supply enough fish to meet supply chain demand (Hellebrandt 2008).

Urbanization also coincides with increases in the exploitation of non-living resources, including the extraction of marine aggregates (sand, gravel, rocks) for use in construction and beach renourishment, mineral resources for industrial applications, and the extraction of energy resources (oil and natural gas, and wave and tidal resources). Nearshore aggregate dredging may occur for mud, rock, shells, corals or sand for construction purposes, or for the heavy or precious minerals they contain (Charlier and Charlier 1992). Potential negative effects arising from the extraction of coastal marine aggregates include an increased risk of flood events and coastal erosion. For example, aggregate extraction from the coasts of Kiribati in the South Pacific resulted in beach structure being degraded, exposing coastal conurbations to enhanced risk of flood events (Webb 2005, In: Holland and Woodruff 2006). Similarly, beach mining, nearshore dredging and quarrying have contributed significantly to coastal erosion in the Marshall Islands (Holland and Woodruff 2006), France, and Bali (Charlier and Charlier 1992). The extraction of sand for the renourishment of urban beaches is commonly undertaken for aesthetic and erosion control purposes (Fletemeyer et al. 2018). Knowledge of the direct and indirect effects of this activity on the local biota and ecological processes remains incomplete (Peterson and Bishop 2005), but beach renourishment has been shown to negatively impact nearshore coral reefs (Hernández-Delgado and Rosado-Matías 2017), marine invertebrate prey availability and nesting behavior in sea turtles (Peterson and Bishop 2005). Coastal urbanization also facilitates the expansion of maritime port operations, which often dredge nearshore channels to maintain deep-water access for commodity and passenger transport (Lemay 1998).

Dredging and mining represent a major area of overlap between exploitation and pollution (Figure 1) due to the release of toxicants and sediments that occurs during these operations.

The establishment of oil and natural gas rigs can be broken down into four stages: seismic exploration, exploratory drilling and installation, operation, and decommissioning (Khan and Islam 2008). Each of these stages involves some form of extractive activity, although the consequences for marine life (with the exception of pollution effects, covered in the following section) are particularly strong during the installation and decommissioning stages. The installation and decommission of rig infrastructure may also degrade or destroy the seabed (Macreadie et al. 2011). However, their establishment introduces a source of hard substrate, potentially increasing local biodiversity, as well as non-native species, which can alter community dynamics at local or regional levels (Burt et al. 2009, Feary et al. 2011, Macreadie et al. 2011). The establishment of renewable energy infrastructure presents many of the same ecological issues and opportunities as oil and gas, yet the installation of some structures, such as tidal barrages, has the potential for generating highly significant physical and thus ecological impacts at the local scale, including the loss of intertidal habitats, modification of water flow, and sediment resuspension (Gao et al. 2013, Hooper and Austen 2013).

2.2 Pollution pathways (both industrial and domestic)

Urbanization and pollution are tightly linked; whereas as air and soil pollution are major concerns for terrestrial conurbations, contaminated water and sediments are the main pollution issues for coastal cities (Table 2). Originating from both point (e.g. wastewater discharge) and non-point (e.g. wind-blown debris and dust) sources, pollution impacts marine life at individual, population, and ecosystem levels, often bioaccumulating and then biomagnifying up the trophic pyramid (Erftemeijer et al. 2012, Johnston et al. 2015, Langston 2017). Chronic marine pollution effects tend to be sub-lethal (e.g. Browne et al. 2015), but they frequently interact with others stressors in ways that ultimately cause mortality (Yaakub et al. 2014, Bårdsen et al. 2018).

Urban sediment pollution, commonly the result of runoff from construction work and disturbance via dredging (Rogers 1990, Eggleton and Thomas 2004, Erftemeijer et al.

2012), as well as other sources such as beach nourishment and land-use changes that alter catchment runoff (Colosio et al. 2007, Zhang et al. 2010), affects marine life in multiple ways. The resulting increase in turbidity reduces light penetration, photosynthesis (e.g., Falkowski et al. 1990), and the maximum depth at which photosynthetic organisms can grow (Heery et al. 2018b). Suspended sediments can also reduce fish hatching success and larval survival (Auld and Schubel 1978), impede zooplankton feeding (Sew et al. 2018), affect mobile fauna that rely on visual cues (Weiffen et al. 2006), and alter a wide range of benthic ecosystem processes and patterns (Airoldi 2003), including the settlement and successful recruitment of organisms, the diversity of species, and competitive interactions—such as those between foundation macrophyte species and low-lying algal turfs (Gorgula and Connell 2004, Russell and Connell 2005, Gorman and Connell 2009, Knott et al. 2009, Bauman et al. 2015). Smothering by sediment further reduces light and physically interferes with the functioning of benthic organisms, including corals (Rogers 1990, Junjie et al. 2014), seagrasses (Erftemeijer and Lewis 2006), and certain life stages of kelps (Devinny and Volse 1978, Geange et al. 2014).

High nutrient concentrations are frequently attendant with sediments but, in urban settings, inputs come also from wastewater treatment plants, industrial discharges, stormwater runoff, dust from land, domestic detergent use, and human sewage (McClelland et al. 1997, Braga 2000, Atkinson et al. 2003, Cole et al. 2004, Gaw et al. 2014, Vikas and Dwarakish 2015) and can be particularly hazardous in bays and harbors with limited circulation (Gomez et al. 1990). Resultant eutrophication can have positive feedbacks on nutrient loads and localized acidification (Howarth et al. 2011) and leads to many undesirable ecological effects (Bell 1991, Orth 2017), including phytoplankton blooms and/or shifts toward noxious cyanobacteria, macroalgal blooms that can outcompete foundation species such as corals, and increases in the occurrence and severity of marine diseases (Bowen and Valiela 2001, Balestri et al. 2004, Lapointe et al. 2005, Reopanichkul et al. 2009, Haapkylä et al. 2011, Redding et al. 2013). Human sewage and wastewater creates additional problems due to the release of fecal coliform, antibiotics, and other pharmaceuticals (Jiang et al. 2001a, Shibata et al. 2004, Rose et al. 2009, Jia et al. 2011, Watkinson et al. 2011, Rizzo et al. 2013, Gaw et al. 2014).

Toxic pollutants, including organochlorine compounds (e.g. PCBs and HCH), heavy metals, tributyltin (TBT), polybrominated diphenyl ethers (PBDEs) and compounds from oil (e.g. petrogenic PAHs, plastics and microplastics), are strongly associated with industrial activities and urban run-off (Kennish 1997, Shazili et al. 2006, Todd et al. 2010, Cole et al. 2011, Tayeb et al. 2015), as well as from shipping and other sea-based sources (Tornero and Hanke 2016). Many of these substances bioaccumulate in animals, especially in top predators and humans (Tanabe 1988, Wolff et al. 1993, Bayen et al. 2003) and can interfere with cellular and biochemical functions and disrupt hormonal, reproductive, neurological and nervous systems (Portmann 1975, Wolff et al. 1993, Frigo et al. 2002, Bosch et al. 2016). Lead, cadmium, copper, tin, nickel and iron are among the metals commonly found in sediments near industrial areas (Williamson and Morrisey 2000, Buggy and Tobin 2008, Amin et al. 2009). Copper is especially toxic to marine invertebrates, including poriferans, cnidarians, molluscs and arthropods (Reichelt-Brushett and Harrison 1999, Johnston and Keough 2000, Reichelt-Brushett and Harrison 2000, Brown et al. 2004, Rainbow 2017). The impacts of lead and cadmium on economically important invertebrates such as oysters and crabs are also well established in the literature (Ramachandran et al. 1997), however, recent studies suggest deleterious effects from a wide range of metals (Langston 2017), particularly when combined with other anthropogenic stressors (Burton and Johnston 2010). Other industrial discharges that can have negative effects, albeit usually localized, include brine from desalination plants and heat from industrial cooling. Often the most deleterious impacts from these discharges are toxicants (especially metals, hydrocarbons and anti-fouling compounds) that enter the sea with the effluent (Lattemann and Höpner 2008, Roberts et al. 2010).

Urban noise pollution usually originates from boat traffic and in-water construction (Middel and Verones) while urban light pollution comes from street lights, buildings, shipping, airports, and vehicle headlights (Hölker et al. 2010). For fish and some marine mammals, noise pollution can potentially inhibit communication, affect predator-prey interactions, and have negative effects on growth and reproduction (Slabbekoorn et al. 2010, Houghton et al. 2015). It may also impact various other taxa that are sensitive to sound, including oysters (Charifi et al. 2017), clams (Mosher 1978, Peng et al. 2016), mussels (Roberts et al. 2015), cephalopods (André et al. 2011, Fewtrell et al. 2012), shrimp and other invertebrates (Solan et al. 2016). Night lighting includes both direct glare and overall increased illumination, and can disrupt marine ecosystems in a number of ways (Hölker et al. 2010). Organisms that use light to navigate, such as birds and sea turtles, can become disorientated (Davies et al. 2014), as can fish and fish larvae.

Artificial lighting can also affect predator and prey behavior, disrupt larvae settlement, alter distribution patterns, and de-synchronize broadcast spawning species from normal lunar phases (Becker et al. 2013, de Soto et al. 2013, Wale et al. 2013, Navarro-Barranco and Hughes 2015, Bolton et al. 2017).

A gradient of decreasing levels of various pollutants with increasing distance from urban sources has been described multiple times, for example: heavy metals (Qiao et al. 2013), sediments (Todd et al. 2004), marine debris (Evans et al. 1995, Andrades et al. 2016), and PAHs (Assunção et al. 2017). Whereas the effects of urban (land-based) light and noise pollution and some contaminants are limited to a few decimeters to kilometers from the source (Zaghden et al. 2005, Burton and Johnston 2010), other pollutants can have impacts that extend much further (Heery et. al. 2017). For example, PCBs have been found in Arctic waters far from any urban or industrial centres, albeit at very low levels (Gioia et al. 2008). An important example of urban pollution being transported huge distances but still having a substantial negative impact is marine debris, especially plastics. Like other forms of marine debris, plastics have a very high dispersal potential (Carlton et al. 2017), particularly as they can take decades to biodegrade (Moore 2008) and are often buoyant. They can maintain their structural integrity for many years, resulting in negative effects, via ingestion or entanglement, to animals such as seabirds, turtles, marine mammals, crustaceans and cnidrians (Azzarello and Van Vleet 1987, Moser and Lee 1992, Bjorndal et al. 1994, Jones 1995, Laist 1997, Lamb et al. 2018, Mecali et al. 2018) far from their point of origin. Due to ultraviolet rays, mechanical and microbial degradation, plastics eventually fragment into microplastics (Barnes et al. 2009) that are bioavailable to suspension feeding marine organisms, including zooplankton (Wright et al. 2013, Barboza et al. 2018, Botterell et al. 2018).

2.3 Ocean sprawl (both coastal and offshore)

"Ocean sprawl" is a term used to describe the proliferation of human-made hard structures in the marine environment (Firth et al. 2016, Table 3). This includes offshore infrastructure (e.g. wind farms, oil and gas platforms, aquaculture facilities, submarine cables/pipes) and coastal infrastructure such as artificial shore defences (e.g. seawalls, breakwaters, groynes), as well as facilities associated with ports, docks and marinas. Ocean sprawl is a fundamental and dominant feature of urbanized marine environments

(Bulleri and Chapman 2010, Duarte et al. 2013, Dafforn et al. 2015, Firth et al. 2016). Artificial structures comprise the bulk of shorelines in many coastal cities (Lai et al. 2015, Dafforn et al. 2015) and modify benthic habitats well into the subtidal zone (Airoldi and Beck 2007, Heery et al. 2018a, Heery and Sebens 2018).

As a habitat, artificial shorelines are quite distinct from natural rocky shores (Glasby and Connell 1999, Rilove and Benayahu 2000, Perkol-Finkel and Benayahu 2004, Bulleri et al. 2005, Moschella et al. 2005, Clynick et al. 2008, Lam et al. 2009, Bulleri and Chapman 2010, Lai et al. 2018). One of the most obvious differences is the slope of hard substrates; while shoreline armoring structures such as seawalls are generally very steep, natural rocky shores tend to be more gently sloping with longer and wider intertidal areas (Gabriele et al. 1999, Knott et al. 2004, Andersson et al. 2009, Chapman and Underwood 2011, Firth et al. 2015). The smaller area of intertidal zone typical of seawalls is probably an important contributor to species loss (Chapman and Underwood 2011, Perkins et al. 2015). It can also lead to greater overlap in the distribution of individuals (Klein et al. 2011) or to superimposed distributions of species that normally would not overlap (Loke et al. 2019b). Wave impact is also more intense on steep shores (Gaylord 1999, Cuomo et al. 2010), potentially dislodging intertidal organisms and/or impeding their settlement (Blockley and Chapman 2008, Iveša et al. 2010). Compared to natural hard-bottom habitats, seawalls have few microhabitats, such as pits, rock-pools, overhangs and crevices (Chapman 2003, Chapman and Bulleri 2003, Moreira et al. 2007), which are important for the occurrence and survival of many intertidal and benthic species (Chapman and Underwood 2011, Loke and Todd 2016, Loke et al. 2017). When considering these multiple effects in combination, it is unsurprising that many direct comparisons between rocky shores and seawalls often reveal the latter host lower species richness, reduced functional and genetic diversity, and different community compositions (e.g. Chapman 2003, Bulleri et al. 2005, Moschella et al. 2005, Fauvelot et al. 2009, Lai et al. 2018).

The consequences of ocean sprawl at large spatial scales are not yet well understood, but they are likely to be considerable given its prominence and extent (Lotze et al. 2006, Airoldi and Beck 2007). In some heavily urbanized regions, entire habitats have been lost as artificial structures proliferate over vast distances (Dong et al. 2016). Even where coastal transformation is not ubiquitous, clusters of artificial structures can serve as corridors that facilitate species invasions (Airoldi et al. 2015) and alter ecological connectivity, with significant impacts on marine assemblages (Bishop et al. 2017). The spatial scale of impacts from artificial structures depends on the type of impact in question, the type of structure, local hydrodynamic conditions, and a variety of other parameters (summarized by Heery et al. 2017). For instance, fluxes of exogenous detritus from artificial structures typically affect marine communities within meters to tens of meters only (Heery and Sebens 2018), while infrastructure that creates major impediments to circulation and sediment transport tends to impact marine assemblages across a much larger area (Bishop et al. 2017).

2.4 Overlap, interactions, and feedbacks

The three key drivers described above are not limited to urban areas, yet their relative magnitude and spatial and temporal overlap is often augmented near high-density coastal development (Jiang et al. 2001b, Kennish 2002, Finkl and Charlier 2003, Mayer-Pinto et al. 2015). This overlap can have important consequences for marine organisms and communities, as effects from multiple anthropogenic stressors are often cumulative and non-linear in the marine environment (Adams 2005, Crain et al. 2008, 2009), leading to complex changes in ecosystem condition (Conversi et al. 2015, Halpern et al. 2015, Mollmann et al. 2015). It can also feedback to influence the key drivers themselves, which are each the result of dynamic, interacting socioeconomic and biophysical forces (*sensu* Alberti et al. 2003), and closely interrelated in the coupled social-ecological systems that characterize coastal cities (Liu et al. 2007, Alberti 2008, Grimm et al. 2008a, Pickett et al. 2011). Such feedbacks and interactions are widely recognized as shaping urban ecosystem function (Wu 2014, McPhearson et al. 2016), and are central in nearly all current models of urban ecosystem dynamics (e.g. Pickett et al. 2001, Alberti et al. 2003, Grimm et al. 2013). In this section, we highlight some known and likely interactions among the three drivers (exploitation, pollution, and ocean sprawl) of marine urbanization. Each interaction fits conceptually within the overlapping regions of the Venn diagram in Fig. 1.

One of the best examples of complex interactions and feedbacks among the drivers of marine urbanization and ecosystems is the relationship between habitat conversion, contaminants, and invasion risk. Artificial structures associated with port infrastructure and shoreline protection tend to both concentrate environmental contaminants by altering hydrodynamics patterns and reducing water movement (Waltham et al. 2011, Rivero et al. 2013), and by facilitating increased contaminant influx, for instance from antifouling paints (Schiff et al. 2004, 2007, Warnken et al. 2004, Sim et al. 2015). Copper emissions from antifouling paints then have both direct and indirect consequences for marine organisms (Rygg 1985, Perrett et al. 2006). The toxin enters the food web by accumulating in algal tissues (Johnston et al. 2011) or being consumed directly by non-selectively feeding animals, which can additionally accelerate the leaching and burial process in adjacent sediments (Turner 2010). While toxic effects from copper negatively impact many marine organisms and reduce diversity (Rygg 1985), differential responses to copper contamination among invertebrates (Piola and Johnston 2006) combined with the novel colonization habitat that is provided by floating docks and other marina structures can disproportionately favor non-indigenous taxa, thus facilitating marine invasions (Piola and Johnston 2008, Dafforn et al. 2009, Piola et al. 2009, Airoldi and Bulleri 2011, Edwards and Stachowicz 2011, Cordell et al. 2012, MacKenzie et al. 2012).

The trajectory of marine resource exploitation in urban areas is also closely tied to that of pollution pathways and marine habitat conversion (Inglis and Kross 2000, Jiang et al. 2001b, Cundy et al. 2003) (Fig. 2). In the early developmental stages of many cities, shoreline habitats were converted by artificial structures to facilitate resource exploitation industries and the economic growth they fueled (Squires 1992). Overwater structures that housed cannery facilities and seafood markets were prominent drivers of early waterfronts in San Francisco (Walker 2001), Singapore (Chang and Huang 2010), and many other coastal cities globally (West 1989, Portman et al. 2011). Various shoreline armoring structures were also part of facilities for resource exploitation industries, such as oil and gas (Minca 1995), and remain important drivers in adaptation plans for protecting these industries from future sea level rise (French et al. 1995, Ng and Mendelsohn 2005). Pollution associated with resource exploitation and habitat conversion continues to be problematic in many urban and suburban areas, for instance surrounding shellfish aquaculture farms, oil refineries, port infrastructure, and dredged waterways that harbor contaminants (Board 1997, Pereira et al. 1999, Jones 2001, Strand and Asmund 2003, Tolosa et al. 2004, Medeiros et al. 2005, Casado-Martinez et al. 2006, Paisse et al. 2008, Knott et al. 2009), and alters system dynamics via multiple biogeophysical pathways, trophic levels, and functional groups (Paisse et al. 2008, Weis et al. 2017).

As coastal cities grow, and effects from various aspects of marine urbanization increasingly overlap (Fig. 2), the system's potential for feedbacks appears to intensify (Fernando 2008, Grimm et al. 2008b). For instance, as impervious surfaces proliferate on land, increased delivery of stormwater can accelerate the accumulation of contaminants in receiving waterbodies (Lee et al. 2006, Jartun et al. 2008, 2009, Jartun and Pettersen 2010, Walsh et al. 2012). Similarly, as resource exploitation and shoreline alteration expand, so too does the spatial extent and magnitude of marine debris and contaminants (Garcia-Sanda et al. 2003, Wake 2005, Ng and Song 2010, Märkl et al. 2017), which can in turn impact exploitable marine resources (Islam and Tanaka 2004). Additional biogeochemical and ecological feedbacks have also been important historically, in some cases leading to losses in a system's capacity to absorb urban impacts over time (Cloern 2001, Nyström et al. 2012). For instance, the loss of oyster reefs due to overharvest and eutrophication is thought to have reduced the filtration capacity of urban estuaries in the United States (Zimmerman and Canuel 2000, Kemp et al. 2005, Wilberg et al. 2011, zu Ermgassen et al. 2013), potentially inhibiting their ability to accommodate further pollution influx. Similar feedbacks surrounding challenges such as harmful algal blooms and marine diseases may be increasingly likely as ecosystems are further altered by marine urbanization (Prins et al. 1998, Sunda et al. 2006, Heisler et al. 2008, Crain et al. 2009). However, such feedbacks can be difficult to predict and may obfuscate efforts to effectively anticipate ecosystem response to further environmental change (Elmgvist et al. 2003).

3. Key ecological patterns

The convergence of exploitation, pollution and ocean sprawl that typifies urban marine environments may lead to shifts in ecosystem characteristics and several key ecological patterns, which are just beginning to emerge in the literature.

3.1 Homogenized systems, comprising heterogeneous mosaics

A common theme in the terrestrial urban ecology literature is the spatial heterogeneity that occurs across landscapes as a result of urbanization (Pickett et al. 1997, Dow 2000, Cadenasso et al. 2009, Pickett and Cadenasso 2008). The resulting "mosaics" of habitat types, biophysical characteristics, and land use are temporally dynamic and influenced by multiple interacting social and ecological drivers (Pickett et al. 2017). At the same time, there are considerable similarities across cities in the underlying processes and trajectory of urbanization, leading to an overall homogenization among urban ecosystems regionally and globally (Alberti 2005, McKinney 2006). Even though research supporting these concepts is far more comprehensive in terrestrial environments, there are several indications of comparable patterns among urban marine ecosystems based on the current literature (Dafforn et al. 2015).

Most coastal cities are positioned in estuaries and bays that were historically dominated by soft sediments. As artificial structures are added to these sedimentary environments, a checkerboard of hard and soft habitats is created, with each supporting distinct biotic assemblages (Connell and Glasby 1999, Glasby 2000, Connell 2001, Barros et al. 2001). This can alter ecosystem dynamics in several ways. In some regions, artificial structures can support a larger standing stock of benthic macroalgae and other hard-bottom organisms, which then enter adjacent sediments as detritus and may alter sedimentary community dynamics (Boehlert and Gill 2010, Heery and Sebens 2018, Heery 2018). Artificial structures can also act as “stepping stones” for dispersal, particularly of non-indigenous taxa (Bulleri and Airoldi 2005, Glasby et al. 2007, Vaselli et al. 2008, Sheehy and Vik 2010, Airoldi et al. 2015, Foster et al. 2016) and alter genetic population structure of marine fauna (Fauvelot et al. 2012). Marine species vary in dispersal potential, and many taxa encounter barriers to dispersal at relatively small spatial scales (Darling et al. 2009, Costantini et al. 2013, Maas et al. 2018, Sefborn et al. 2018). Dispersal limitation can therefore also interact with local stressors and abiotic conditions to result in compositionally very different assemblages across patches of hard substrata (Bulleri and Chapman 2004, Munari 2013). This may be accentuated where urban habitat conversion has significantly altered hydrodynamic patterns or created other additional barriers to dispersal and subsequent settlement (Bishop et al. 2017).

Spatially heterogeneous mosaics also form in urbanized seascapes as a result of fine-scale gradients in nutrient enrichment and sediment pollution (Airoldi 2003, Baumet et al. 2015, Ling et al. 2018), particularly in low flow environments and enclosed estuaries and embayments (Balls 1994, Dauer et al. 2000). For instance, physical disturbance from swing moorings, which are ubiquitous in shallow sedimentary environments in Sydney Harbor, leads to depressed concentrations of metal contaminants within a highly localized area (Hedge et al. 2017). This may result in complex, fine-scale spatial patterns in microbial, meiofaunal, and macrofaunal taxa that are sensitive to metal contamination (Coull and Chandler 1992, Stark 1998, Lindegarth and Hoskin 2001, Mucha et al. 2003, Gillan et al. 2005, Sun et al. 2012). It is likely this is complicated further by localized gradients in other abiotic conditions, such as granularity, that commonly occur in the vicinity of artificial structures (Martin et al. 2005, Seitz et al. 2006). While swing moorings and other structures that increase physical disturbance and scour increase sediment grain size (Hedge et al. 2017), structures such as pilings that reduce flow speeds and increase deposition tend to reduce the grain size of nearby sediments (Heery et al. 2018c). Grain size, contaminant concentrations, and a variety of other flow-related metrics are known to have strong effects on sedimentary composition and diversity (Mannino and Montagna 1997, Hewitt et al. 2005), which likely therefore varies considerably in urban seascapes over small spatial scales.

Studies of marine diversity and connectivity relative to urbanization remain relatively limited, and there is need for expanded work in this area. In particular, study designs that allow for the assessment of alpha, beta, and gamma diversity could be helpful for beginning to distinguish between the ecological processes that shape marine assemblages in spatially heterogeneous urban seascapes. In their eDNA study on seagrass beds, Kelly et al. (2016) found decreases in beta diversity even while species richness increased with the intensity of urbanization. Landscape-scale homogenization in urban assemblages has some precedents in freshwater and terrestrial systems (McKinney and Lockwood 1999, Holway and Suarez 2006, Urban et al. 2006, Groffman et al. 2017), but less so in the marine literature (Balata et al. 2007). For instance, by creating urban freshwater reservoirs/dams many cities have inadvertently fragmented their catchments and resulted in biotic homogenization (Olden and Rooney 2006, Olden et al. 2008). The straightening or "linearization" of shorelines through armoring (Dyl 2009) may homogenize intertidal communities at certain scales, though this has not been demonstrated empirically. Sedimentation may also cause marine communities to become more homogenous under certain conditions (Balata et al. 2007). However, more thorough characterization of diversity measures relative to resource exploitation, pollution, and ocean sprawl should advance understanding of ecological processes in urban marine environments.

3.2 Loss of foundation species

Urban stressors can be particularly detrimental for sensitive foundation species such as oysters, reef-building corals, seagrasses, mangroves, and canopy-forming kelps, which structure marine ecosystems via the provisioning of biogenic habitat (Dayton 1972, Bertness and Callaway 1994). Even though the dynamics of decline vary across taxa and across locations (Terrados et al. 1998, Waycott et al. 2009, Polidoro et al. 2010, Heery et al. 2018b), loss in foundation species is generally tied to one or more of the three major drivers of marine urbanization (Rogers 1990, Hastings 1995, Airoldi 2003, Balesetri et al. 2004, Kirby et al. 2004, Connell et al. 2008, Strain et al. 2014, Alleway and Connell 2015). In temperate areas, nutrient-rich, high sedimentation conditions can limit the recruitment and survival of canopy-forming kelps while supporting opportunistic, turf-forming algal species that can act as kelp competitors (Airoldi 1998, Bendetti-Cecchi et al. 2001, Gorgula and Connell 2004, Russell and Connell 2005, Coleman et al. 2008, Gorman and Connell 2009). Similarly, in the tropics, sediment pollution has multiple negative effects on corals. These decrease coral cover and disproportionately impact competitive, branching coral genera such as *Acropora*, which ultimately lowers reef complexity in urban areas (Heery et al. 2018b). Ocean sprawl can also be an important driver of foundation species loss. For instance, despite the numerous ecosystem services they provide to urban communities (Benzeev et al. 2017), mangrove forests are cleared in many coastal areas to make way for urban development (Harper et al. 2007, Martunizzi et al. 2009, Lai et al. 2015, Richards and Friess 2016). Where urban mangroves are left intact, they are often heavily impacted by artificial structures constructed nearby; mangrove forests adjacent to seawalls tend to be narrower, with less leaf litter and fewer saplings than those without seawalls (Heatherington and Bishop 2012). Coral reefs and seagrass beds are also frequently built over (Chou 2006, Burt et al. 2013, Yaakub et al. 2014). Furthermore, urban losses in foundation species often involve feedbacks that prevent subsequent population recovery (Altieri and Witman 2006, de Boer 2007, Moore et al. 2013). For instance, seagrass loss can be tied to sediment pollution and eutrophication (Waycott et al. 2009, Orth et al. 2017) and deforestation and altered hydrodynamic regimes from coastal construction (Silva et al. 2004), as well as possible indirect effects from top-down reductions in grazers that control seagrass epiphyte loads (Duffy et al. 2005, Myers et al. 2007). The reduction of seagrass bed cover can lead to destabilization of sedimentary substrata, which can then further increase turbidity (de Boer 2007) and potentially inhibit recolonization (Moore et al. 2013).

There is increasing evidence that multiple, often interacting, urban-related drivers affect both foundation species and ecological response to foundation species loss (Lenihan and Peterson 1998, Jackson 2008, Claudet and Fraschetti 2010, Nyström et al. 2012, Strain et al. 2014, Ferrario et al. 2016, Orth et al. 2017), although studies evaluating multiple stressors simultaneously are rare (O'Brien et al. In press). The abundance of kelps and other important habitat-forming macroalgae is negatively correlated with human population density in several regions, including temperate coasts in Australia and North America (Connell et al. 2008, Scherner et al. 2013, Feist and Levin 2016), and this is likely linked to gradients in sedimentation and nutrients (Fowles et al. 2018). Yet, ocean sprawl may also be an important factor in macroalgal community dynamics. Reduced topographic complexity, changes in substrate type, and altered substrate profiles are all factors that can limit kelp abundance (Toohey 2007, Schroeter et al. 2015) and correlate with urban habitat conversion. Artificial structures not only support distinct macroalgal assemblages compared with natural rocky shores (Glasby 1999) – the kelps that inhabit them also support distinct epifaunal and microbial communities and erode at different rates (Marzinelli et al. 2009, 2018, Mayer-Pinto et al. 2018). Habitat conversion thus likely influences ecological processes in urban areas where canopy-forming kelps persist. The interaction of resource extraction, pollution, and ocean sprawl as drivers of foundation species loss, and the ecological responses to this loss, are important future areas of research. Importantly, these processes are highly dynamic, with ecological legacies from past impacts, and future scenarios linked to rising temperatures and pCO_2, that are challenging to ascertain (Ramalho and Hobbs 2011, Davis et al. 2017, Gao et al. 2017, Heldt et al. 2018, Fig. 2).

3.3 Changes in biodiversity and productivity

Patterns of biodiversity in urban marine environments are complex. Resource extraction, sediment pollution, and habitat modification are important drivers of marine biodiversity declines globally (Sala and Knowlton 2006), and there are many examples from the literature of reduced species richness and altered community composition at heavily urbanized sites (Pearson and Rosenberg 1978, Long et al. 1995, Lindegarth and Hoskins 2001, Lotze et al. 2006, Airoldi and Beck 2007, Poquita-du 2019). Even through the diversity of marine assemblages in some regions is negatively correlated with human population density (Scherner et al. 2013, Neo et al. 2017), this pattern is not universal, and varies considerably between regions, cities, the taxa and type of diversity considered, and the methods used. For instance, using eDNA from water samples, Kelly et al. (2016) found that species richness was positively correlated with land-based urbanization in intertidal seagrass beds. Similarly, while some studies have reported higher species diversity on artificial shorelines than on their natural counterparts (Chou and Lim 1986, Connell and Glasby 1999, Munsch et al. 2015), others have found artificial shorelines to be relatively depauperate (Firth et al. 2013, Aguilera et al. 2014, Lai et al. 2018).

There are similar complexities surrounding productivity in urban marine environments. In nutrient-rich marine estuaries, like those in most coastal cities, climate variables, such as major precipitation events and interannual fluctuations in weather patterns, tend to be particularly important drivers of temporal patterns in primary production (Mallin et al. 1993, Rodrigues and Pardal 2015), as these events deliver land-based sources of nitrogen to coastal waters. However, the relationship between nutrient load and primary production is highly variable (Borum and Sand-Jensen 1996), and urban-related increases in nutrient loads can have different effects depending on tidal regimes, the system's trophic structure, as well as other factors (Alpine and Cloern 1992, Monbet 1992). Nutrient loading therefore does not manifest comparable, elevated marine production across cities. Moreover, broader ecosystem responses to primary production also vary across urban marine ecosystems. In some locations, nutrient enrichment can trigger micro- and macroalgal blooms that are highly detrimental to important foundation species (McGrathey 2001) while, in other places, the same process may increase secondary production (Leslie et al. 2005) and species richness (Whittaker and Heegaard 2003).

3.4 Novel assemblages

Novel assemblage structure tends to emerge as species move and change in abundance and dynamics in response to environmental change (Hobbs et al. 2018). The most obvious manifestation of this phenomenon in urban marine environments is among sessile assemblages on artificial shorelines. Conversion from natural shores to hard artificial structures creates new habitats for colonization and supports novel assemblages of hard-bottom organisms (Chou and Lim 1986, Connell and Glasby 1999, Bulleri et al. 2005, Moschella et al. 2005, Clynick et al. 2008, Lam et al. 2009, Airoldi et al. 2015, Munsch et al. 2015). These assemblages differ from nearby rocky shores with respect to composition (Chapman 2003, Bulleri and Chapman 2010, Airoldi et al. 2015, Lai et al. 2018) and genetic diversity (Fauvelot et al. 2009). Differences in species abundance between artificial and natural rocky shores may be biased towards some functional groups, such as mobile primary consumers (Chapman 2003, Pister 2009). However, human-made habitats in urban areas also provide a foothold for a variety of non-indigenous species, many of which are non-motile (Glasby et al. 2007, Vaselli et al. 2008, Ruiz et al. 2009, Sheehy and Vik 2010, Simkanin et al. 2012, Airoldi et al. 2015, Foster et al. 2016).

3.5 Ruderal species and potential synanthropes

On land, urbanization is strongly associated with the proliferation of ruderal and synanthropic species (McKinney 2006). Ruderal species, those that grow in contaminated soils or human wastes, typically include a variety of weedy plant species (Haigh 1980), while "synanthropes" is a term typically applied to mid-level consumers, such as raccoons and coyotes, that have higher densities and abundances in cities than in adjacent rural areas (McKinney 2002). Although not well studied, there is evidence of analogue taxa exploiting urban marine environments. Polluted sediments in urban areas appear to generate opportunities for certain marine microbes (Córdova-Kreylos et al. 2006, Cetecioğlu et al. 2009, Nogueira et al. 2015). For instance, *Alteromonadales*, *Burkholderiales*, *Pseudomonadales*, *Rhodobacterales*, and *Rhodocyclales* bacteria that are involved in the degradation of hydrocarbons, were found to be more abundant in polluted urban mangrove forests in Brazil (Marcial Gomes et al. 2008). Some macroalgae also respond opportunistically to polluted urban waters (Valiela et al. 1997, Raven and Taylor 2003). For instance, transplant experiments have demonstrated that the photosynthetic capacity of sea lettuce *Ulva lactuca* increases while that of canopy-forming brown seaweed *Sargassum stenophyllum* decreases in response to urban waters (Scherner et al. 2012). Differential photosynthetic responses to copper contaminants among different species of *Ulva* may connote a competitive advantage in contaminated urban areas (Han et al. 2008). Similarly, the combination of elevated sediment and nutrient loads increases the cover of filamentous turf-forming macroalgae in field manipulations (Gorgula and Connell 2004) and is thought to be central to turf proliferation in metropolitan areas (Airoldi 1998, Connell et al. 2008, Strain et al. 2014).

Evidence for synanthropic marine consumer species is more limited. Most of the studies on fish distribution patterns in urban areas and relative to coastal population density suggest primarily negative impacts of urbanization on major fish groups (Toft et al. 2007, Williams et al. 2011, Kornis et al. 2017, Munsch et al. 2017, Cinner et al. 2018). Although several well-recognized terrestrial synanthropes, such as raccoons and rats, are known forage in intertidal habitats (Carlton and Hodder 2003), degraded intertidal resources in urban areas are unlikely to be a major driver of synanthropic distribution patterns for these species. There is at least one record, however, of rats occurring in higher densities on artificial breakwaters than on natural shorelines (Aguilera 2018). Heery et al. (2018a) recently found that giant Pacific octopus that inhabit relatively deep subtidal environments (< 24m) were more common in urban areas than in rural areas in Puget Sound (northeast Pacific), while also demonstrating that octopus abundance was positively correlated with the density of anthropogenic structures on the seafloor. Artificial structures, such as floating docks and buoys, are also widely used as haul out sites for urban pinnipeds (Heath and Perrin 2009), and may play a key role in facilitating jellyfish blooms, by expanding the available habitat for polyp recruitment (Duarte et al. 2013). These lines of evidence suggest that, where synanthropic distribution patterns do exist among marine consumers, ocean sprawl may be an important underlying mechanism (Heery et al. 2018a).

In addition to ruderal macrophytes and synathropic consumers, the interacting drivers of marine urbanization appear to facilitate the establishment of opportunistic sessile invertebrates, many of which are non-indigenous. Opportunistic responses to multiple urban drivers may provide a particular advantage. For instance, the bryozoans, *Bugula neritina* and *Watersipora subtorquata*, and the ascidian, *Botrylloides violaceus*, have particularly high tolerances for copper toxicity (Piola and Johnston 2006), which may partially explain their successful invasion of urban marine environments beyond their endemic range (Piola et al. 2009, McKenzie et al. 2011, Osborne et al. 2018). In addition, larval dispersal for these taxa is aided by shipping activities between coastal cities, and they readily utilize artificial structures, such as floating docks, as habitat for settlement (Lambert and Lambert 1998, 2003, Piola and Johnston 2008, Dafforn et al. 2009, Piola et al. 2009, Airoldi and Bulleri 2011, Edwards and Stachowicz 2011, Gittenberger and van der Stelt 2011, Cordell et al. 2012, MacKenzie et al. 2012, Simkanin et al. 2012, Zhan et al. 2015). In this way, simultaneous positive responses to multiple urban drivers may help to facilitate invasion success in urban areas, although the strength of these responses likely vary between cities, taxonomic groups, and latitudes (Canning-Clode et al. 2011).

3.6 Acclimatization and adaptation

Urbanization is considered a major selective pressure (Alberti 2015, Donihue and Lambert 2015) leading to phenotypic changes at both the organismal and species levels (Alberti et al. 2017a). These changes may be phenotypically plastic (i.e. within-lifetime) responses such as acclimatization, or (population-level) adaptation via genetic change over multiple generations (Alberti et al. 2017b, Johnson and Munshi-South 2017). Recent advances in understanding evolutionary responses to urbanization have been driven largely by work in terrestrial systems (Partecke et al. 2006, Miranda et al. 2013, Johnson and Munshi-South 2017). However, there is ample precedent for rapid evolutionary change and phenotypic plasticity in response to anthropogenic stressors in the marine environment (Todd 2008, Sanford and Kelly 2011).

All three of the key drivers of marine urbanization are known to structure population genetics among a variety of marine taxa (examples – Resource exploitation: Smith et al. 1991, Hauser et al. 2002; Pollution: Suchanek 1993, López-Barea and Pueyo 1998, Nacci et al. 1999, Ma et al. 2000, Virgilio et al. 2003, Virgilio and Abbiati 2004, McMillan et al. 2006, Galletly et al. 2007, Moraga and Tanguy 2009; Ocean sprawl: Street and Montagna 1996, Fauvelot et al. 2012). In many cases, resource exploitation, pollution, and ocean sprawl lead to population bottlenecks and reduced genetic diversity (Nevo et al. 1986, Maltagliati 2002, Fauvelot et al. 2009, Ungherese et al. 2010, Neo and Todd 2012, Pinsky and Palumbi 2014). Yet evidence of micro-evolution in urban marine environments has been limited. Some of the best examples come from the ecotoxicology literature (Medina et al. 2007). For example, McKenzie et al. (2011) showed heritable copper tolerance in the bryozoan *Watersipora subtorquata*. Similarly, Galletly et al. (2007) found a significant geneotype × environment interaction in hatching success of the ascidian, *Styela plicata*, under different copper concentrations, yet hatching success at high concentrations had a different genetic basis than that at low concentrations, suggesting different genetic mechanisms for adaptation depending on pollution levels.

Trait plasticity in response to marine urbanization has been much more widely documented. Many marine organisms exhibit substantial capacity for acclimatization that may provide a fitness advantage; this could include changes in morphology, physiology, behavior, and/or life history (West-Eberhard 1989, Foo and Byrne 2016). Goiran et al. (2017) observed melanism in sea snakes inhabiting urban sites that may facilitate the excretion of trace pollutants. Phenotypically plastic responses to light in corals are well documented and can benefit colonies where sediment pollution and associated turbidity is prevalent (Hoogenboom et al. 2008, Todd et al. 2003, Ow and Todd 2010). Some marine invertebrates also exhibit transgenerational plasticity, wherein parents alter the phenotypes of gametes in response to factors such as copper and salinity to maximize gamete performance (Marshall 2008, Jensen et al. 2014). Several other examples of trait plasticity from natural rocky shores may be additionally relevant in the abiotically stressful environments created by seawalls and other artificial structures (Strain et al. 2018). For example, dog whelks *Nucella lapillus* and other gastropods have larger feet in high wave energy environments so they can adhere better to the substrate (Etter 1988, Trussell 1997), potentially an advantage on steep seawalls that intensify wave shock. Similarly, local adaptation for thermal tolerance in acorn barnacles *Semibalanus balanoides* (Bertness and Gaines 1993) and acclimatization to high temperatures in various intertidal gastropods (Williams and Morritt 1995, Marshall et al. 2010) may facilitate survival in novel thermal environments associated with ocean sprawl.

Urbanization-driven trait changes can have important effects on community interactions (Palkovacs et al. 2012, Alberti 2017a), yet much work remains to understand the nature of these effects in the marine environment, as well as their ultimate consequences for functioning in urban marine ecosystems. This work needs to be conducted across multiple organismal scales to account for potential urban-related acclimatization at the level of holobionts – host-microbial assemblages that function as an ecological unit (Ziegler et al. 2016, Evans et al. 2017). Further, the heritability of urban-driven adaptation should be considered through both genetic and epigenetic approaches, as acclimatization responses can be inherited via transgenerational maternal effects and methylation patterns (Sun et al. 2014, Suarez-Ulloa et al. 2015).

4. Climate change and marine urbanization

The effects of climate change interacting with marine urbanization range from reasonably established to complex and speculative possibilities. Atmospheric warming from greenhouse gases leads to the thermal expansion of the oceans and melting of glacial and polar ice, and is well-documented as the cause of current and predicted sea-level rise (Neumann et al. 2015). Increases in the severity, and possibly occurrence, of major storms have also been attributed to global warming (Walsh et al. 2016). This combination of rising seas and extreme weather pose direct flooding and erosion threats to coastlines and, together with coastal development, represent the main drivers of the current proliferation of sea defenses (Dafforn et al. 2015). Elevated temperatures, altered rainfall patterns, and other changes associated with climate change (Donat et al. 2016, Duffy et al. 2015) pose challenges for marine organisms that inhabit coastal defense structures (Ng et al. 2017), as well as for marine communities that provide sources of food and natural defenses for coastal cities, such as coral reefs and mangrove forests (Hoegh-Guldberg et al 2017, Ward et al 2016). Of course, coastal cities are also part of the problem as they contribute to climate change via high levels of greenhouse gas emissions, energy consumption, and changes in land use, hydrology and biodiversity (Grimm et al. 2008a), but these additional impacts of marine urbanization are beyond the scope of the current review.

One of the better studied interactions between urbanization and climate change is “coastal squeeze” first reported by Doody (2004), but later refined and defined by Pontee (2013, pg 206) as: “one form of coastal habitat loss, where intertidal habitat is lost due to the high water mark being fixed by a defence or structure (i.e. the high water mark residing against a hard structure such as a sea wall) and the low water mark migrating landwards in response to SLR” (sea level rise). Loss and/or fragmentation of tidal wetlands means a concomitant reduction in ecosystem services, including flood and erosion abatement, biodiversity support, water quality, carbon sequestration, and benefits to coastal fisheries (Torio and Chmura, 2013). Managed retreat (or realignment), where infrastructure is relocated inland to escape the effects of erosion and flooding (Alexandrea al. 2012), can alleviate coastal squeeze by moving back or removing hard artificial defences, thereby elimitaing the fixed high water mark back-stop. However, the distances required for coasal habitats to successfully move inland can be considerable—potentially being meters per year depending on rate of sea level rise (Pethick 2001).

Climate change will have a variety of effects on urban shoreline and nearshore environments, including increasing air and water temperature (both relevant for intertidal organisms) and altering rainfall (Wallace et al. 2014), and therefore possibly urban runoff patterns. Temperature is a critical stressor on rocky shores (Helmuth and Hofmann 2001) but little is known regarding the thermal landscape of artificial coast defenses (Zhao et al. 2019). The homogeneity of artificial structures may create thermal barrens that challenge intertidal organisms (Perkins et al. 2015) or, alternatively, provide refugia from thermally-limited predators. Helmuth et al. (2006), based on a comprensive study of the spatial and temporal patterns in the body temperature of the mussel *Mytilus californianus* on natural rocky shores, concluded that interacting factors such as tidal regime and wave splash can create complex thermal mosaics of temperature that are potentially more important locally than those of large-scale (e.g. latitudinal) climate effects. Hence, it will be difficult to predict or measure the broader impacts of global warming on the intertidal area of seawalls and similar structures. Shifts in patterns of rainfall and runoff, e.g. heavier rainfall and/or more prolonged rainfall (Wallace et al. 2014), could overwhelm drainage systems leading to peaks in the influx of pollutants. These unusual pollution spikes would likely be concurrent with increased sedimentation, eutrophication and low salinity, all of which could moderate species and community response and the toxicity of pollutants (Pearson and Rosenberg 1978, Šolić and Krstulović 1992, Verslycke et al. 2003).

Climate change is also likely to impact natural coastal defenses. Healthy coral reefs and mangrove forests are effective at protecting coastlines from wave impact and associated erosion in tropical and subtropical regions, but both are vulnerable to climate change. Extended periods of warmer than average sea temperatures causes coral bleaching that, when severe, kills colonies (Hoegh-Guldberg 1999) resulting in the loss of wave-absorbing complexity (Alvarez-Filip et al 2009, Graham and Nash 2013). As mangroves live within a narrow band of suitable habitat determined by local tidal regimes, they are susceptible to sea level rise if it exceeds the rate of soil accumulation, leading to shoreline retreat (Lovelock et al. 2015). Many tropical and subtropical towns and cities benefit from the protection that coral reefs and mangroves provide (Ferrario et al. 2014), and their loss may lead directly to the installation of alternative coastal defense measures, of which hard amour such as seawall, rip-rap and gabion are frequently chosen. There is also strong potential for additive or synergistic effects as coral reefs and mangroves near urban areas are likely to be heavily exploited as well as impacted by pollution (Wells and Ravilious 2006). In addition to these rather more predictable consequences of climate change, urban marine environments—as part of urban ecosystems—are shaped by a multitude of interacting social and ecological drivers (Alberti 2003) and are likely to exhibit non-linear dynamics characteristic of complex adaptive systems (Scheffer et al. 2001, Alberti 2008). The three major drivers of marine urbanization have gradually altered urban marine ecosystems in ways that may have reduced their capacity to absorb disturbance; for instance to a 100-year storm event, a sudden change in socio-economic variables such as a rapid loss in food security, a major marine disease epidemic, or various other pulse perturbations. Without considerably more research, it is unclear how urban marine ecosystems will respond to such disturbances, whether they are susceptible to future phase shifts, and what such shifts might mean for ecosystem functions and ecosystem services. While these should be focal points of future research (discussed below), approaches such as scenario planning (Peterson et al. 2003) that integrate and accommodate uncertainties directly into management of urban marine environments may be highly beneficial (Alberti et al. 2003).

5. Ecological engineering

It is predicted that by the next decade approximately three quarters of the world's population will reside in coastal zones (Small and Nicholls 2002, Bulleri and Chapman 2015). Coastal land is therefore in high demand and development and reclamation are occurring at unprecedented scales (Yeung 2001, Duarte et al. 2008). In addition, the risks of climate change, as outlined in the previous section, have resulted in an urgent need for greater shoreline protection, especially in low-elevation coastal zones (LECZ) (*sensu* Neumann et al. 2015). For instance, in China, Japan and Korea alone, 28% of the global population are currently living in LECZ and it is predicted that by 2070, 37 million people and assets worth $13 trillion are going to be exposed to coastal hazards such as storms, flooding and climate variability (Nicholls et al. 2013). Strategies that mitigate risk and help coastal cities adapt to sea level rise and climate change are already being implemented in many parts of the world (Zimmerman and Faris 2010, Hayes et al. 2018) and are predicted to increase in the coming decades (Neumann et al. 2015, Dangendorf et al. 2017). Such strategies, though multifaceted, include expanded coastal armoring and human-made structures such as seawalls (French and Spencer 2001, Hinkel et al. 2014), the integration of new stormwater capture and treatment systems, and a wide variety of other modifications to expand the capacity and resilience of urban infrastructure (Zimmerman and Faris 2010).

If the past is any indication, future proliferation of marine urbanization will further facilitate the formation of novel assemblages of marine organisms on an unprecedented scale. Currently, there is considerable debate in ecology regarding the concept of 'novel ecosystems' (Hobbs et al. 2014, Murcia et al. 2014), i.e. ecosystems shaped by human intervention that are distinct from their historical state, and that cannot be returned to their historical trajectory (Hallett et al. 2013). It is presently unclear whether urban marine ecosystems meet all criteria of 'novel ecosystems' (Morse et al. 2014), but their trajectory is undeniably shaped by the way in which coastal cities develop and modify the marine environment (Dafforn et al. 2015). Given the potential of marine assemblages to provide ecosystem services to urban populations, as well as recent success in the realm of eco-shoreline design (Morris et al. in press), it may be more helpful to consider urban marine ecosystems and their future trajectory within the framework of 'designed ecosystems' (Higgs 2017) or 'reconciliation ecology' (Rosenzweig 2003). While both of these frameworks arose with the realization that some systems have been so severely altered and/or degraded it is practically impossible to apply conventional restoration practices (or expect the system to shift back towards a "historic" or "pre-disturbed" state), conceptually they are fundamentally different in their intent, starting point and developmental trajectory (Hunter and Gibbs 2007, Higgs 2017). For instance, 'designed ecosystems' often involve large-scale intervention efforts to create and sustain the system whereas 'reconciliation ecology' is less reliant on long-term intervention and more based on the idea that "if you build it, they will come" (Rosenzweig 2003, p 6). 'Ecological engineering', i.e. the design and engineering of urban infrastructure congruent with ecological principles, can be viewed as straddling between these frameworks, as it often requires huge initial intervention but with less emphasis on subsequent management and maintenance (see recent review by Loke et al. 2019a).

Ecological engineering is currently being trialed, or attempted in earnest, in many locations around the world (Chapman and Blockley 2009, Mitsch 2012, Strain et al. 2018). Nature-based or soft-engineering approaches using "green infrastructure" for coastal defense are preferred over hard engineering approaches in many coastal cities as they have been shown to be more cost-effective in the longer term and can serve multiple functions in addition to flood risk reduction (Spalding et al. 2014, Temmerman et al. 2013, Reguero et al. 2018). However, these solutions are often not adopted due to feasibility (e.g. mangrove planting at sites with high wave energy or flow) or socio-economic reasons (e.g. lack of political will, support or resources). In addition, hard artificial coastal defenses have frequently already been built and cannot realistically be removed. Given that more human-made shorelines are expected to be built in the foreseeable future, it is critical to find ways to increase their ecological and social value while maintaining their engineering function (Borsje et al. 2011, Loke et al. 2019a). The ecological engineering of human-made shoreline structures is a new but dynamic field, and there is often a trade-off between taking time to understand these habitats as a system, and the urgency or desire to implement practical solutions (Morris et al. in press). Knowledge of urban shoreline ecosystems and of strategies that effectively enhance ecosystem functioning and services should improve over time, as ecological enhancement and blue/green infrastructure projects become more common and are applied in a broader variety of urban marine environments (Pontee et al. 2016). Developing and maintaining research collaborations with industry will be essential to ensure that lessons from each of these projects are shared and translated into subsequent designs and engineering solutions (Mayer-Pinto et al. 2017). Further, partnerships with city governments and planners will be needed to ensure that ecological enhancement projects are applied concurrently with broader improvements in water quality and at a sufficient scale to have long-standing benefits, and then carefully monitored over time.

6. Critical challenges and research directions

Awareness of the impacts of overexploitation, marine pollution, and ocean sprawl is growing (Chapman and Underwood 2011, Lotze et al. 2018). However, there remain many emerging issues, knowledge gaps, and research needs at numerous scales for understanding the dynamics of urban marine ecosystems (Airoldi et al. 2005, Kueffer and Kaiser-Bunbury 2014) and building urban marine ecology as a discipline. Here, we offer some critical research questions and areas for investigation that have yet to be fully addressed.

1. What are the interactive effects of multiple stressors, including feedbacks and changes over time?

2. Stronger characterization of spatial and temporal patterns of biodiversity in urbanized marine environments.

3. What are the mechanisms driving marine synanthropy?

4. Key ecosystem functions, their most essential drivers, and likely future trajectories—including implications for current and future provisioning of ecosystem services.

5. Assessment of the evidence for urban-driven trait selection in the marine environment.

6. What ecological enhancement approaches (ecological engineering, green- and blue-infrastructure, etc.) are most effective in urban settings?

There are also numerous questions related to the key ecological processes in Section 3 that need to be elucidated, especially disentangling the many co-varying stressors and determining the long-term responses of organisms and populations to marine urbanization. Ultimately, all sides of coastal city design: architecture, urban planning, and civil and municipal engineering, will need to prioritize the marine environment if the negative effects of urbanization are to be minimized. In particular, planning strategies that account for the interactive effects of drivers and accommodate complex system dynamics could enhance the ecological and human functions of future urban marine ecosystems.

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Figure Legends

Figure 1. Activities, installations, processes and issues that represent instances of overlap and interaction among the three major drivers of marine urbanization: resources exploitation, ocean spread and pollution pathways.

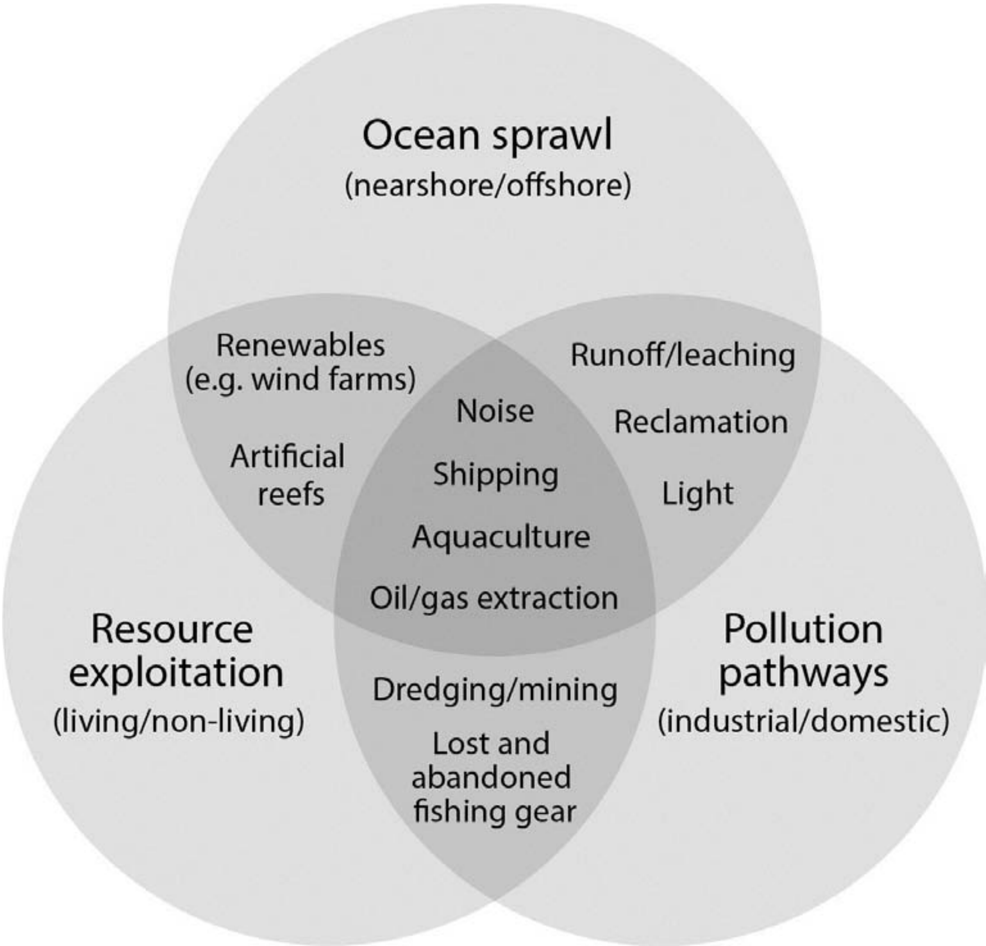

Figure 2. The trajectories of the three key drivers of marine urbanization over time are difficult to hindcast (or forecast) and are likely to be city-specific. However, they will almost certainly overlap, potentially creating non-linear interactions that are even more challenging to predict (and are not represented here). For illustration purposes only: (a) the exploitation of living resources could accelerate rapidly during the early development of many coastal cities, yet decrease in intensity as the resource is overexploited or inaccessible due to other factors, such as contaminants. Conversely, ocean sprawl may be more likely to follow an asymptotic trajectory, which reaches saturation as an increasingly large percentage of natural habitats are converted by the installation of artificial structures. (b) A possible alternative configuration of driver trajectories in a younger city with a shorter but equally intense history of marine urbanization.

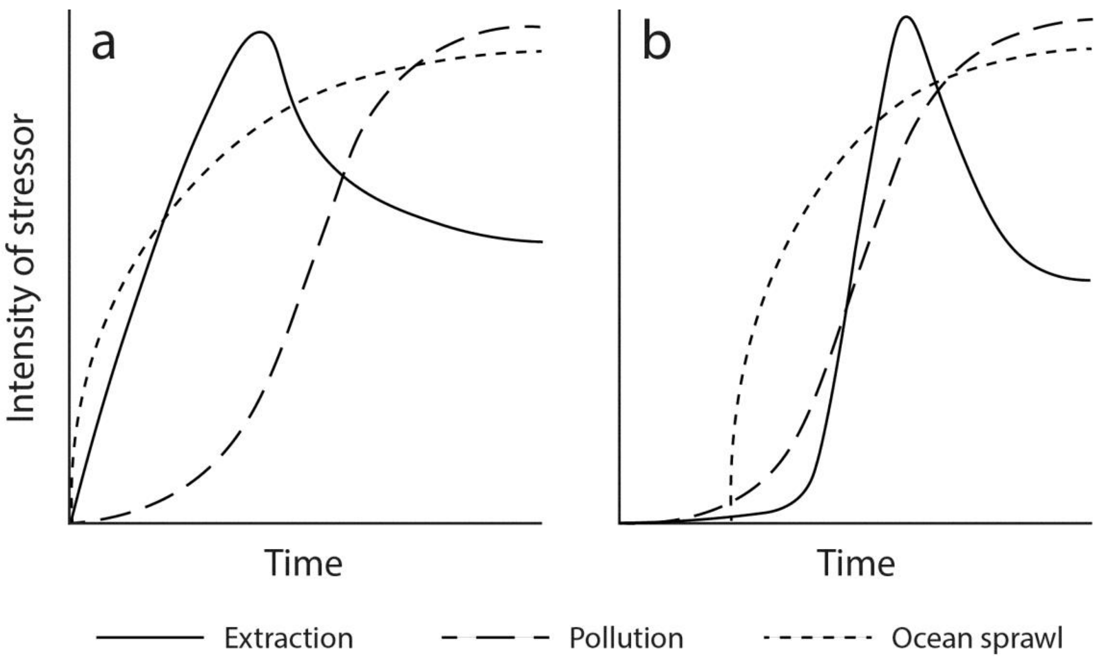

Table Legends

Table 1. Types of marine exploitation, their scale and scope, and their impacts.

Exploitation type	**Scope and scale**	**Potential effects on marine life and habitats**
Recreational fishing	Estuarine, inshore, offshore; scale can range from hundreds to tens of thousands of participants in a region.	Removal of target fish and shellfish, potentially leading to population- and/or ecosystem-wide impacts. Delayed mortality from catch and release practices; mortality of bycatch species; mortality or injury from boat collisions. Damage or degradation of sensitive habitats from contact fishing gear or the launching/recovery of boats. Lost and abandoned fishing gear issues (see Table 2).
Subsistence fishing and gleaning	Estuarine, intertidal, inshore; numbers unknown but likely to vary greatly by region.	Removal of target fish and shellfish, potentially leading to population- and/or ecosystem-wide impacts; mortality of bycatch species; mortality or injury from boat collisions. Damage or degradation of sensitive habitats from contact fishing gear and the launching/recovery of boats. Impacts from practices such as cyanide or dynamite fishing. Lost and abandoned fishing gear issues (see Table 2).
Commercial fisheries	Estuarine, inshore, offshore; scale variable by fishery and region but can range from tens to thousands of participants.	Removal of large numbers of target species, potentially leading to major population- and/or ecosystem-wide impacts; mortality of bycatch species; mortality or injury from boat collisions; damage or degradation of sensitive habitats from contact fishing gear and the launching/recovery of boats. Lost and abandoned fishing gear issues (see Table 2).
Mariculture	Estuarine, inshore (offshore in the future); scale varies widely and depends upon the species being farmed.	Transmission of disease and parasites between farmed and native species; eutrophication due to addition of nutrients (although shellfish farms may remove nutrients from water column); smothering of benthic fauna due to build-up of organic material (also leading to changes to sediment type/chemistry).
Dredging for minerals/ aggregates	Inshore and offshore; scale variable but can range from tens to hundreds of km^2.	Physical disturbance and removal of the substrate and associated benthic biota; changes to the composition of the sediment/substrate; changing bathymetry and sediment transport patterns; smothering of biota; reduced light and enhanced turbidity due to sediment suspension, toxicant release (see Table 2).
Beach mining	Inshore; usually conducted at the local scale	Direct removal of species and substrate; loss of soft-sediment habitat; lowering/loss of beach leading to erosion, changing sediment transport patterns, increased turbidity, changing conditions for fauna/flora and/or

	but with possible regional-scale effects.	saline water intrusion.
Oil and gas extraction	Inshore and offshore (mostly offshore in recent years); local to regional-scale effects.	Direct removal of species and substrate; smothering/physical alterations to habitat/substrate type (i.e., replacement of soft with hard substrate); chronic and acute toxic pollution events; noise pollution (see Table 2).
Water extraction for cooling and desalinatio n	Inshore, generally localized effects.	Fish and plankton killed during intake and processing (impingement and entrainment). Brine and heated water (thermal pollution) can impact communities near outflows, changing behavior and physiology. Toxicants can also be released with the effluent.

Table 2. Pathways and potential effects of pollution on marine life.

Pollutant type	**Main urban pathways**	**Potential effects on marine life**
Sediments	Construction sites (on the coast and within inland urban areas), dredging, land reclamation.	Turbidity resulting in less light for photosynthesis and visual predators/prey. Down welling sediments smother benthic organisms and create a substrate unsuitable for settling larvae.
Nitrogen and phosphoru s	Industrial discharge, human and animal waste, detergents, mariculture.	Eutrophication leading to both micro and macro algal blooms, reduced water clarity (see “sediments”), shifts toward noxious cyanobacteria and reduced fertilization success in corals.
Plastics (macro and micro), lost and abandoned fishing gear	Resin pellets and discarded end-user products. Fishing activities.	Ingestion and/or entanglement, leading to internal blockages/injuries, toxic poisoning, starvation due to false ‘stomach filling’, suffocation, lacerations, infections, reduced ability to swim.
Compound s from oil	Motor vehicles, shipping, industry.	Impairment of growth and developmental rates, reduced reproductive output and recruitment rates, increased susceptibility to disease. Carcinogenic.
Heavy/trac e metals	Industrial and vehicle emissions, leaching from landfills, urban runoff, sewage.	Can inhibit fertilization, recruitment, development, growth in marine microorganisms, invertebrates and vertebrates. Carcinogenic. Prone to undergo food chain magnification.
Tributyltin	Antifouling paint used in the maritime industry.	Causes imposex, and reduces growth and larval success, in various crustaceans and molluscs. Biomagnifies, leading to endocrine disruption in fishes, marine mammals and humans.
PCBs and PBDEs	Discharge from industry, especially electronics. Used in plastics, fire retardants and lubricants.	Prone to biomaginification. Interferes with neurological and hormonal systems of marine organisms and humans. Can lead to decreases in reproductive capabilities and pose immunotoxic risk in marine mammals.
Pharmaceu ticals	Industrial, hospital and domestic waste.	Interferes with reproduction and development in both animals and plants. Perturbs fish physiology.
Bacteria and viruses	Sewage (from land and boats/ships), runoff, aquaculture.	Diseases, especially acute gastrointestinal illnesses, e.g. salmonellosis. Viruses can cause hepatitis and respiratory infections.
Light	Streets, private and commercial buildings, vehicle headlights, airports.	Encourages unwanted fouling, affects migration, predator and prey behavior. Disrupts larval settlement. De-synchronization of broadcast spawning from lunar phase (e.g. corals).
Noise	Boat traffic, construction, machine operation.	Disrupts behavior (e.g. ability to find food, mates or avoid predators), reduces growth and fecundity.

Table 3. Types of human-made structures comprising ocean-sprwal, their functions and potential impacts. Note; all of these structures require some alteration and/or loss of natural habitat.

Structure type	**Function**	**Potential effects on marine habitats**
Reclaimed land and artificial islands	Alleviation of coastal squeeze and expansion of land for industry and development.	Directly results in habitat loss, and fragmentation. Sedimentation during construction, altered hydrodynamics interferes with connectivity at landscape and local scales.
Artificial coastal defenses	Engineered to protect shorelines from shoreline erosion, flooding, and impacts from waves.	Reduced intertidal extent and results in steeper slopes. Footprint of the structure removes existing natural habitat but effects may extend beyond structure (halo effect). Change in substrate material and altered hydrodynamics could result in different colonizing assemblages.
Commercial ports, docks and marinas	Industry, services, and recreation.	Elevated risk of species invasions, contaminants (oil, antifouling coatings, noise, light), disturbances associated with shipping (sediment resuspension, propeller injuries, etc.).
Oil shipping and refinery infrastructure	Non-renewable resource mining for energy.	Footprint of the structure removes existing natural habitat but effects may extend beyond structure (halo effect). Contaminants, risk of oil spills, noise and light pollution.
Tidal and wind energy infrastructure	Energy production.	Footprint of the structure removes existing natural habitat but effects may extend beyond structure (halo effect). Noise and light pollution, electromagnetic fields.
Submarine cables and pipelines	Telecommunications, power, water, oil.	Concrete mattresses are often used to stabilize and position cables on seafloor. Fragmentation of soft-sediment habitats due to introduction of hard substrates. Noise and light pollution during construction phase. Electromagnetic fields.