

The outsized trophic footprint of marine urbanization

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Artificial structures are proliferating along coastlines worldwide, creating new habitat for heterotrophic filter feeders. The energy demand of this heterotrophic biomass is likely to be substantial, but is largely unquantified. Combining in situ surveys, laboratory assays, and information obtained from geographic information systems, we estimated the energy demands of sessile invertebrates found on marine artificial structures worldwide. At least 950,000 metric tons of heterotrophic biomass are associated with commercial ports around the world, emitting over 600 metric tons of carbon dioxide into the atmosphere and consuming 5 million megajoules of energy per day. We propose the concept of a trophic “footprint” of marine urbanization, in which every square meter of artificial structure can negate the primary production of up to 130 square meters of surrounding coastal waters; collectively, these structures not only act as energy sinks and carbon sources, but also potentially reduce the productivity of coastal food webs.

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Barges, piers, seawalls, and other artificial structures used for transportation, recreation, and coastal defense are becoming increasingly prevalent on coastlines around the world. Today, nearly 40% of the global population lives within 100 km of a coastline (Firth *et al.* 2016), and approximately half the coastline of Europe, the US, and Australasia are now modified by artificial structures (Dafforn *et al.* 2015). This accumulation of marine construction is known as marine urbanization and has a number of consequences for the function of coastal ecosystems, some of which are better recognized than others.

Marine urbanization is often associated with negative ecological and economic impacts, including declines in water quality and habitat productivity, spread of invasive species, and proliferation of jellyfish and toxic algal blooms (Duarte *et al.* 2013;

Dafforn *et al.* 2015; Lagos *et al.* 2017a). Changes in physical conditions contribute to these impacts and affect communities that colonize artificial and natural habitats (Connell 2001; Glasby and Connell 2001). One general but rarely recognized effect of marine urbanization is that most artificial structures increase the proportion of shaded and vertical-facing substrata compared to natural habitats (Dafforn *et al.* 2015; Firth *et al.* 2015). Floating platforms, barges, piers, pontoon, seawalls, or port quays decrease access to direct sunlight, thereby reducing the ability of autotrophic organisms to colonize the available space and promoting the formation of dense communities of filter-feeding sessile invertebrates (eg barnacles, mussels, ascidians, polychaetes; Dafforn *et al.* 2015; Firth *et al.* 2015; Pardal-Souza *et al.* 2017). These communities, forming on human-made habitats, can achieve densities of up to 270 kg m⁻² in a single year (Figure 1; Rajagopal *et al.* 1991) and can alter the natural trophic pyramid. However, the impact of this additional biomass on energy flows through coastal ecosystems remains largely unquantified.

The abnormal increase in encrusting (fouling) biomass favored by marine urbanization is likely to affect coastal food webs. By reducing light availability, the construction of artificial structures creates new shaded environments in which energy-producing autotrophic organisms are replaced by energy-consuming heterotrophic species. Byrnes *et al.* (2007) predicted that the invasion of benthic filter feeders associated with marine urbanization might increase the intensity of resource usage at lower trophic levels, a prediction that has not been tested but is plausible; for example, a typical mussel bed of 15 kg dry weight m⁻² can filter up to 100,000 L m⁻² of water per day (Jorgensen 1980), feeding on large amounts of plankton in the process. Indeed, suspension-feeding organisms can consume 40–95% of the total primary production in the water column each day (Gerritsen *et al.* 1994), and fouling communities on artificial structures are more energetically demanding than those on natural structures (Lagos *et al.* 2017b).

In a nutshell:

- Artificial structures in marine coastal environments increase the availability of hard surfaces that can be colonized by sessile invertebrates (mussels, barnacles, anemones, etc)
- The world's ports have created new habitat for about 950,000 metric tons of sessile invertebrates, which release ~600 metric tons of CO₂ and consume roughly 5 million megajoules of energy daily
- Every square meter of artificial structure cancels out the primary production of up to 130 square meters of coastal waters, essentially robbing marine ecosystems of their productivity

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and nine sites in Moreton Bay (WebPanel 1a). The amount of biomass growing on artificial structures ranged between 2.4 and 39.36 kg m⁻² across the 160 communities sampled (Figure 2). Using these estimates, we calculated that a total of 7607 metric tons and 1846 metric tons of biomass occur over all the artificial structures in Port Phillip Bay and Moreton Bay, respectively. To put this in perspective, the biomass on artificial structures in both bays is equal to approximately 3151 female African bush elephants (*Loxodonta africana*, each ~3000 kg).

How much energy is consumed by fouling biomass on artificial structures?

Sample communities were weighed, then transported to the laboratory to measure mean daily energy consumption (kilojoules per day; see WebPanel 1b). Our isometric metabolic relationships are quantitatively consistent with previous reports of fouling communities in the same region (Ghedini *et al.* 2018). The total energy consumption of the fouling community living on artificial structures in Port Phillip Bay and Moreton Bay was estimated by multiplying the mean metabolic rate of a quadrat by the total man-made underwater surface area in each bay (WebPanel 1b). In Port Phillip Bay, the fouling biomass on artificial structures consumes 25,148 megajoules (MJ) and produces 2.46 metric tons of CO₂ daily, with a carbon flux of 1.45 g C m⁻² day⁻¹ (7.6 × 10⁶ MJ and 898 metric tons of CO₂ annually). In Moreton Bay, the fouling biomass on artificial structures consumes 10,878 MJ of energy and produces 1.06 metric tons of CO₂ daily, with a carbon flux of 1.254 g C m⁻² day⁻¹ (3.97 × 10⁶ MJ and 388 metric tons of CO₂ annually).

How much ocean is required to feed fouling communities on artificial structures?

One way to quantify the impact of human activities on a natural ecosystem is to use an “ecological footprint” framework (Wackernagel *et al.* 1999). The ecological footprint of an artificial structure is the amount of primary production required to support the metabolic demands of the heterotrophic community growing on the underwater portion of its surface (WebPanel 1, c and d). Using depth-integrated satellite data, we estimated that primary productivity in Port Phillip Bay fixes 55,912 metric tons of carbon (C) each month (with monthly variability from 46 to 74 × 10³ metric tons), which converts to approximately 1.8 × 10⁹ MJ (from 1.5 to 2.4 × 10⁹ MJ) of energy. Moreton Bay produces 37,867 metric tons of C (from 27 to 52 × 10³ metric tons), which converts to around 1.2 × 10⁹ MJ (from 0.9 to 1.7 × 10⁹ MJ) of energy. Based on our estimates, biomass on artificial structures consumes 0.042% and 0.027% of the total annual energy production in Port Phillip Bay and Moreton Bay, respectively. Given that artificial structures such as jetties, piers, and pontoons cover 0.0027% and 0.005% of the total area of Port Phillip Bay and Moreton Bay, respectively, the trophic footprint of these artificial structures is ~16 (Port Phillip Bay)

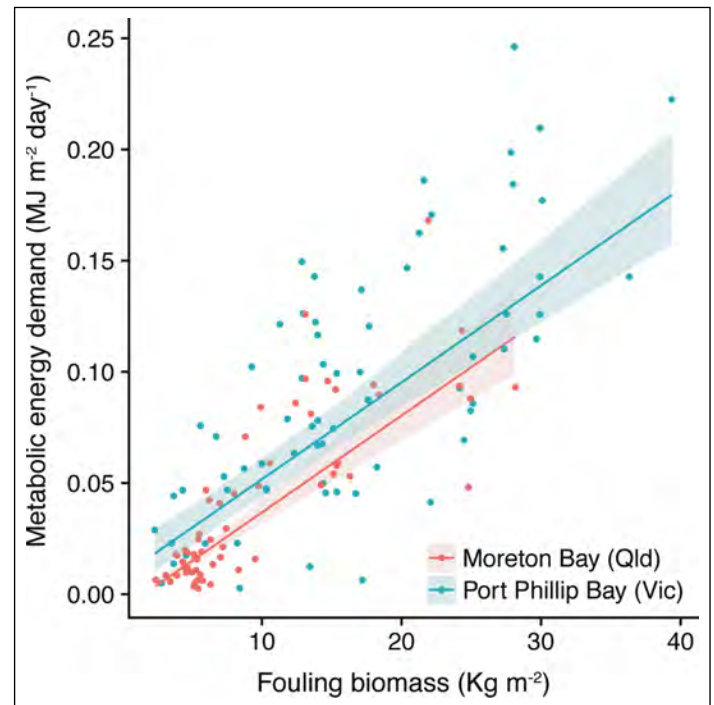


Figure 2. Energy demand of fouling biomass from Moreton Bay (Queensland [Qld], Australia) and Port Phillip Bay (Victoria [Vic], Australia) measured in the laboratory at 20°C. Metabolic energy demand was calculated from rates of dissolved oxygen depletion. All combinations of nested linear models were examined after forcing the same intercept, the same slope, or both, between Port Phillip Bay and Moreton Bay. Lines (± 95% confidence intervals) show the best-fitting model (ie same slope and different intercept between sites) estimated using conventional model selection with Akaike information criteria and assuming log-normal error distribution ($F_{2,129} = 126$, $P < 0.001$, $r^2 = 0.66$). To account for as many sources of variation as possible, we collected community samples from sites scattered across the entire extension of both bays (11 sites across 210 km of coast in Port Phillip Bay; nine sites across 143 km in Moreton Bay; eight replicates at each site), selecting communities from a wide variety of structures (ie main pier, marina pier, pier extensions, side jetty harbor, next to station pier, boat ramp jetty, and public pontoon), artificial substrates (ie cement, wood, and plastic), and salinity levels (from 27–40 parts per thousand). By collecting replicate communities from various habitats, our relationship between fouling biomass and metabolic rate has a moderate r^2 but is likely to be representative of the average fouling community present on an artificial structure.

and ~5 (Moreton Bay) times as large as their physical footprint. In other words, invertebrates on 1 m² of artificial structure consume the same amount of energy produced by around 16 m² and 5 m² of the respective bay's photic layer.

■ Estimating the total trophic footprint of commercial ports worldwide

The trophic footprint of a port is the area of ocean (in square meters) that is required to generate enough primary productivity to meet the metabolic energy demand of all sessile invertebrates growing on its associated artificial

structures (see WebPanel 1). First, we estimated the total submerged urbanized area of port infrastructure using geographic information system data on total quay length (ie meters of quay available for container ships to dock) and mean quay depth for all major 357 commercial ports listed in the 2015 World Port Rankings published by the American Association of Port Authorities (AAPA; see WebFigure 1). Second, we relied on information available in the scientific literature to estimate the mean total biomass of fouling communities that live on artificial structures in ports around the world (see WebFigures 3 and 4). Third, we used the relationship between fouling biomass and invertebrate energy demand for Port Phillip Bay and Moreton Bay to infer the total fouling energy consumption on each port (MJ day^{-1}), after correcting for local sea-surface temperatures (National Oceanic and Atmospheric Administration [NOAA] temperature dataset; see sensitivity analysis in WebFigure 2). Fourth, we used satellite data of depth-integrated primary productivity (NOAA global primary productivity dataset) to estimate total primary productivity in the coastal ocean adjacent to each port ($\text{MJ day}^{-1} \text{ m}^{-2}$). Finally, we divided the energy demand of fouling communities with the energy generated from primary production to calculate the trophic footprint of each major port worldwide.

In total, these ports occupy 4565 km of coastline, creating 57 million m^2 of underwater artificial structures (Figure 3; see WebTable 2 for all port data). We estimated that this human-

made habitat supports over 944,000 metric tons of sessile invertebrate biomass, which emits over 600 metric tons of CO_2 in the atmosphere and consumes 5 million MJ of energy every day, which is equivalent to the primary production of over 120 million m^2 of ocean surface (see WebPanel 1e for details). Each square meter of underwater port quay covered by invertebrates consumes an average of 26 m^2 of ocean primary productivity, but annual averages vary in trophic footprints by more than one order of magnitude among ports (from 2–130 m^2 for every square meter of port artificial structure; Figure 3). For example, one square meter of artificial structure in cold, highly productive regions can require as little as 0.9 m^2 of ocean (eg St Petersburg, Russia), whereas one square meter of artificial structure in the oligotrophic tropics depletes all of the productivity in the surrounding $\sim 120 \text{ m}^2$ of ocean (eg Honolulu, Hawaii). This variability is magnified when consumption rates are calculated for different months (from 0.8 m^2 to greater than 300 m^2). Around 80% of ports worldwide are located in cooler, more productive areas, featuring low trophic footprints of 10–40 m^2 (Figure 3). The remaining 20% of ports are typically located around the equator, particularly in Asia, eastern Africa, and Brazil. These ports have large trophic footprints (from 40 m^2 to greater than 100 m^2 ; Figure 3) and are responsible for around one-third of the total energy consumed by sessile invertebrates growing in those ports, although they only contribute to 13% of the worldwide port economic traffic (WebTable 2).

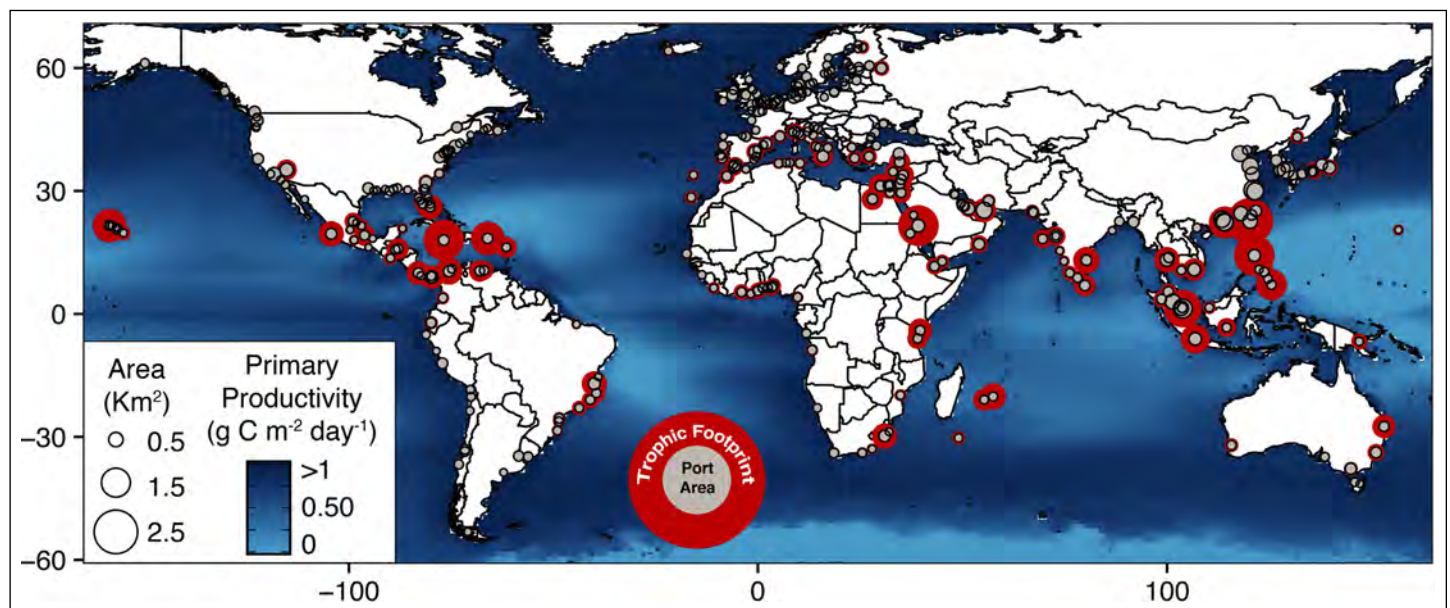


Figure 3. Distribution of all major commercial ports worldwide, with associated area of underwater artificial structures (size of gray dot) and trophic footprint (size of red border). Trophic footprints indicate how much ocean surface is required to supply the energy demand of the sessile fouling community growing on all artificial structures of the port, averaged over the year. Trophic footprints depend on local conditions of ocean primary productivity and temperature. Ports located in cold, nutrient-rich waters (dark blue) will have a lower footprint than ports in warm-oligotrophic waters (light blue). Ocean productivity was calculated on a regular grid size with a definition of 0.25° latitude/longitude, by averaging weekly carbon fixation rates between 1997 and 2007, using the National Oceanic and Atmospheric Administration global primary productivity dataset (see WebPanel 1 for methods and WebTable 2 for data).

■ Impacts of artificial structures on food chain dynamics

Habitat productivity is strongly influenced by the available energy from primary production (Blanchard *et al.* 2012), which implies that **artificial structures could substantially reduce phytoplankton density** and alter food web dynamics by concentrating a heterotrophic biomass of filter feeders with high metabolic demands. For example, the invasion of the clam *Potamocorbula amurensis* in San Francisco Bay in the late 1980s coincided with radical changes to the local food web, as well as a fivefold reduction in chlorophyll concentration (an indirect measure of phytoplankton biomass), the complete elimination of periodic spring algal blooms, a 50–90% reduction of planktonic copepod species, and circumstantial evidence pointing to a decline in the density of small fish (Alpine and Cloern 1992; Herbold *et al.* 1992). Marine urbanization is likely to act in a similar way, by increasing the density of sessile filter feeders and intensifying top-down control on primary productivity. An illustrative example can be seen in Dubai, where natural hard substrates along the coastline are limited and mostly found in areas with emergent limestone or rocky shores; however, recent coastal developments have lengthened the Dubai shoreline from 50 km to more than 1600 km (Hansen 2005), greatly expanding the suitable habitat for sessile organisms. For Dubai, we estimated that up to 40 m² of phytoplankton are required to meet the energy demand of sessile invertebrates growing on each meter of port quay. Assuming fouling communities homogeneously occupy the shoreline, we would predict that fouling communities on artificial structures in Dubai went from depleting the primary production over an area half the size of New York City's Central Park (1.75 km²) to that of the entire island of Manhattan (56 km²). Human-related activities are altering trophic pyramids, and many of these activities disproportionately favor filter feeders and scavengers instead of top predators and primary producers (Byrnes *et al.* 2007; O'Connor *et al.* 2009); we believe that marine urbanization is also contributing to this trend.

■ Are there food web benefits of marine urbanization, as well as costs?

Urbanization often goes hand in hand with eutrophication: nitrogen (N) and phosphorus (P) levels are 5–14 times above natural rates in many coastal habitats in the US (Cloern 2001; Compton *et al.* 2011). The heterotrophic biomass associated with urbanization could possibly capture the increased productivity of highly modified coastlines and thereby reduce the negative effects of eutrophication, but such conclusions are premature. While examples of strong correlations between N and P concentrations and phytoplankton biomass have been reported (Smith 2006), in other cases nutrient loading

is a poor predictor of primary productivity (Borum 1996). For instance, San Francisco Bay has low algal biomass despite high N and P concentrations (Alpine and Cloern 1992; Cloern 2001). Other factors involved with urbanization can influence primary productivity, such as pesticides (DeLorenzo *et al.* 2001), heavy metals (Rai *et al.* 1981), or suspended sediments (Wofsy 1983). When eutrophication does stimulate aquatic primary production, decomposition of phytoplankton-derived organic matter also enhances depletion of dissolved oxygen from bottom waters, with negative effects on food chain productivity (Smith *et al.* 1992; Cloern 2001). Further research is needed to clarify the interactions between marine urbanization and eutrophication.

■ Future predictions on the impacts of artificial structures

The trophic footprint of artificial structures is likely to worsen in the future due to warming temperatures. Climate model simulations suggest that marine biological productivity in the tropics and mid-latitudes will decline substantially (Bopp *et al.* 2001; Behrenfeld *et al.* 2006), primarily because global warming is predicted to inhibit mixing of the water column, reducing the supply of nutrients to the euphotic zone (Doney 2006). At the same time, animal metabolism is temperature-dependent, with respiration increasing faster than photosynthesis in response to warming (Dillon *et al.* 2010; Hoegh-Guldberg and Bruno 2010). There are also instances where climate change promotes an increase in the mean body size of sessile fouling organisms, which intensifies their total energy consumption (Nawrot *et al.* 2017). Global warming is therefore expected to have a multidimensional effect on the energy flux of marine ecosystems, not only by reducing aquatic primary production but also by increasing the energy demands of sessile fouling communities.

We found that ports with high trophic footprints (>40 m²) are often distributed into clusters near highly populated tropical areas (eg Caribbean, northern Red Sea, southern East Asia). Countries in Asia and East Africa are characterized by fast-growing economies, estimated at a 5–6% increase in real GDP per annum (double and triple the rate of North American and European countries, respectively; data from www.worldbank.org, as of 10 Dec 2017). These factors combine to exacerbate the negative effects of artificial structures in many coastal regions and will accelerate in the future. This is particularly concerning given that subsistence fishers rely on coastal fisheries in these regions as their major source of protein.

■ Caveats

Our sensitivity analysis on model predictions showed that energy demands of invertebrate communities are robust with regard to uncertainty in main input parameters (change by <20%; see WebFigure 2). There are, however, major potential

sources of error in a number of our calculations, including temporal and spatial variation in mean biomass, relative composition of fouling communities, their metabolic rates, and the area available for colonization. Throughout the estimation process, we tended to assume conservative values that erred toward the lower end of estimates. For instance, we chose the conservative approach of assuming 100% energy assimilation efficiency of sessile invertebrates on phytoplankton, although the actual value is likely to be below 50%, so that trophic footprints are likely to be at least double those calculated here (Dame and Patten 1981; van der Veer *et al.* 2006). Furthermore, the metabolic rates we measured for sessile communities represent only the energy required to maintain life, as any additional allocation of energy beyond this maintenance will need additional consumption of food. Our energy-equivalency approach therefore represents the absolute minimum amount of food consumed by invertebrate biomass on artificial structures. Given that, to the best of our knowledge, our study is the first of its kind, and we believe these estimates are valuable despite the considerable uncertainty, as there are currently no baseline assessments of the trophic footprint of any artificial structures.

■ Conclusions

Our analysis represents an important first step toward recognizing the role of marine artificial structures as energy sinks and carbon sources. A large percentage of the ocean shoreline has been modified by human engineering (Dafforn *et al.* 2015), and burgeoning coastal human populations are expected to increase demands on fisheries in the future, while food web productivity is expected to decline due to the effects of climate change (Blanchard *et al.* 2012). Understanding the trophic impacts of artificial structures on marine environments is therefore becoming increasingly urgent.

Temperature and primary productivity are the most influential factors in our model to explain differences in the trophic footprints among ports worldwide, together accounting for 78% of the total variability. We predict that food webs in warmer, oligotrophic locations (eg Central America, the Caribbean, eastern Mediterranean, the Red Sea, southeastern Asia) will be most affected by the accumulation of fouling biomass on artificial structures. In these regions, it is important to consider the trophic impact of artificial structures.

How might the trophic impacts of artificial structures be reduced? Increasing light penetration into the more shaded portions of the structures should reduce the percentage cover of heterotrophs relative to autotrophs. Maintaining higher seawater flow rates around structures will also favor native species (Lagos *et al.* 2017a). In extreme cases, periodic removal of fouling biomass might be necessary.

Paradoxically, the outsized trophic footprint of artificial structures in some areas might actually be beneficial. Heavily

modified coastal zones suffer from eutrophication and nutrient loads. However, it may be that under specific circumstances, fouling biomass on artificial structures might reduce the incidence or intensity of algal blooms. An important next step will be to determine whether the sessile organisms on artificial structures feed on all available primary producers in the system or reduce certain groups disproportionately. For now, it seems that managers should no longer assume that the impacts of artificial structures are restricted to their physical footprint, given that their trophic footprint extends much further.

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■ Supporting Information

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