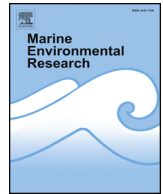




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Building up marine biodiversity loss: Artificial substrates hold lower number and abundance of low occupancy benthic and sessile species

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ABSTRACT

Ocean sprawl is replacing natural substrates with artificial alternatives. We hypothesized that, after submersion, high occupancy, high mobility species colonize artificial substrates faster than low occupancy, low mobility species, a biodiversity divergence that will slowly fade out with time. Using quantitative visual census of species in 10 artificial and their adjacent natural substrates, we tested for the existence and temporal evolution of this divergence. Assigning species to one of three occupancy and one of three mobility categories, we found that artificial substrates increased the performance of high mobility, high occupancy species while decreased the performance of low mobility species with medium and low occupancy. This biodiversity divergence remained unchanged over the 50-year underwater timespan of the artificial substrates investigated. Our results suggest that proliferation of artificial substrates is building up a biodiversity loss driven by the least conspicuous and uncommon benthic and sessile species that is undermining coastal marine biodiversity.

1. Introduction

Coastal environments are critical components of the Earth support system. They provide us with goods and services that surpass those provided by any terrestrial ecosystem (Costanza et al., 1997). The relevance of coastal systems stems from their specific biological and environmental traits. Coastal waters up to 200 m deep are about 5–10% of the world surface, yet they account for 25% of the primary production of the oceans, 79% of marine fish species, and 90% of marine exploitation (Barnabé and Barnabé-Quet, 2000; Ray and McCormick-Ray, 2009). In short, coastal waters hold the greatest variety and abundance of marine species (Gray, 1997) but they also are among the most threatened by anthropogenic stressors (Halpern et al., 2007).

Demographic pressures on coastal ecosystems are steadily increasing as coastal zones are home to a large and growing proportion of the world's population, which could rise by more than 50% between 2000 and 2030 (Neumann et al., 2015). Human-induced changes of the coastal environment occur through a variety of activities such as overfishing, pollution, or habitat destruction. Habitat degradation, fragmentation, and loss are major threats to biodiversity (Sih et al., 2000). These are widespread phenomena in coastal areas with over 50% of the world and 86% of Europe's coasts at moderate or high risk of

degradation (Bryant et al., 1995). Given the high value of the coastal services to humans, coastal degradation may cause a great environmental burden with important implications to our society (Costanza et al., 2014). A better understanding of the effect of human alterations on the marine coastal diversity will certainly help minimize the negative consequences of coastal development and promote more efficient biodiversity conservation and management.

Ocean sprawl, the proliferation of artificial structures in the sea, is an important component of coastal degradation in marine environments (Duarte et al., 2012; Firth et al., 2016). Breakwaters, dykes, coastal defense structures, and other human-made constructions are increasingly present in coastal areas to meet the growing demand for commercial, touristic, and residential activities of the last decades (Bulleri and Chapman, 2010; Firth et al., 2016). Artificial structures are becoming a significant habitat for marine organisms in detriment of their natural counterparts (Airoidi and Beck, 2007; Dugan et al., 2011; Duarte et al., 2012; Bishop et al., 2017). Beyond some striking examples of ocean sprawl scattered over the world (e.g., Dubai or Qatar in the Persian Gulf, Penang Is or Singapore in the Malay Peninsula, Firth et al., 2016; Chee et al., 2017), the phenomenon is truly widespread and a cause of environmental concern. The Mediterranean coasts of France, Italy, and Spain have over 1500 km of artificial structures (Airoidi and

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Beck, 2007), which represents about 15% of their coastline. Ocean sprawl causes loss of coastal habitats (e.g., Airoldi and Beck, 2007) and shifts in species abundance and distribution (Clynick et al., 2008; Airoldi and Bulleri, 2011; Burt et al., 2011; Heery et al., 2017). Yet, we are far to understand the ecological importance of artificial habitats and whether, given enough time, artificial substrates will have the capacity to hold communities equivalent to those on natural substrates.

Artificial habitats may add new variables and habitat types (e.g., material, rugosity, or dark sciaphilic habitats in shallow communities) with important implications in community organization and functioning (Chapman, 2003; Bulleri and Chapman, 2010; Ponti et al., 2015). High mobility species such as fish may colonize new habitats sooner than species with more limited mobility such as mobile invertebrates or sessile organisms, which may rely more strongly on reproductive traits (Kinlan and Gaines, 2003; Perkol-Finkel and Benayahu, 2007; Lin et al., 2008; Miller et al., 2009; Gothland et al., 2014). Species abundance and size of the organisms may also determine their capacity to colonize new habitats, with common (i.e., abundant) species having numerical advantage over uncommon species in terms of space occupation (MacKenzie et al., 2003; Strain et al., 2017). Similarly, widely distributed species that inhabit numerous locations (frequent, high occupancy species) are more likely to colonize artificial habitats because surrounding natural reefs may act as a “pool source” (Svane and Petersen, 2001). On the other hand, irregularly distributed species inhabiting few locations (infrequent, low occupancy species) may need longer time periods to colonize artificial habitats, underpinning a secondary successional diversity (Tilman, 1988). Colonization of artificial habitats by common and high occupancy species may create a false state of similarity with natural substrates because the less conspicuous species (uncommon and low occupancy species) are easier to overlook. Yet, the less conspicuous species are bound to represent a significant percentage of the overall biodiversity (Whittaker, 1965) and play critical roles in ecosystem functioning (Grime, 1998), so their absence in artificial habitats would tone down biodiversity severely.

It is unclear whether artificial habitats deviate significantly from natural substrates or they can function as their natural counterparts given enough time (Carr and Hixon, 1997; Glasby and Connell, 2001; Perkol-Finkel et al., 2006). We herein hypothesized that species composition and abundance in artificial habitats deviate from natural reefs. Artificial substrates will favor some species and disfavor others, resulting in significant community differences between natural and artificial habitats. These differences, however, may decrease over the long term making artificial substrates suitable environments to maintain current levels of marine biodiversity. In our study, we selected 10 artificial substrates that have been underwater from 0 to 54 years and tested whether the number and abundance of species differed with their associated natural reefs.

2. Material and methods

We quantified species composition and abundance in 10 locations in Tenerife, Canary Islands (Fig. 1, Table 1). At each location, we surveyed hard bottom habitats with either artificial or natural substrates. All artificial structures in our study were breakwaters, mostly built to provide shelter for boats. None of the artificial structures investigated in our study aimed to enhance species, to restore habitats, to prevent areas from trawling or fishing, or to promote recreational fishing or diving. In this regard, all the artificial substrates investigated were located in the seaward site of the breakwaters, had similar exposure, orientation, slopes, and depths than their natural counterparts and resembled their nearby rocky reefs but with big quarry rocks or concrete boulders added to provide coastal defense (Table 1). The artificial boulders did provide a sciaphilic habitat mostly missing in the natural reefs of our study due to the large number of dark spaces created by the three-dimensional artificial structures. We obtained from official sources (Cabildo de Tenerife, Autoridad Portuaria de Tenerife, and City

Councils) the year of construction of each artificial structure to calculate the number of years they have been underwater until we surveyed them. At each site, we ran three visual censuses that quantified fish, invertebrate, and sessile species using the Reef Life Survey methodology (Edgar and Stuart-Smith, 2014) during summer 2012 (June–September). Briefly, the first visual census quantified number and abundance of demersal fish species in an area of 50 × 10 m. The second visual census quantified macro invertebrate and cryptic fish species in a 50 × 2 m. Finally, to quantify sessile species, we took 25 × 25 cm photoquadrat (PQ) every 2.5 m along the 50 m long transect, for a total of 20 PQs. Then, for each PQ, we generated 20 random points with the software CPCe V. 4.1 (Kohler and Gill, 2006) to quantify the percent cover of sessile species. These three methods also represent degree of mobility, as the first method targets the highly mobile, swimming, demersal fish community (high mobility), the second method targets the benthic invertebrate and cryptic fish community (medium mobility), and the third method targets the fixed-to-the-substrate invertebrate and algal sessile community with highly restricted or no mobility as adults (low mobility).

Because we quantified species abundances in artificial substrates and adjacent natural reefs, we “paired” for every species in our study the abundance data in each artificial substrate to its natural counterpart using the following abundance based index:

$$NAR = \frac{Natural - Artificial}{\max(Natural, Artificial)}$$

where *Natural* is the number of specimens of a single species present in the natural substrate, *Artificial* is the number of specimens of the same species present in the artificial substrate, and $\max(Natural, Artificial)$ is the largest of these abundances. NAR computation for sessile species, quantified through the use of PQs, was identical except for the use of percent cover instead of abundance.

For every species, NAR (*Natural-Artificial Ratio*) is the proportion of change in the number of specimens (or percent cover) found in artificial as compared to natural substrates. NAR values range between 1 and -1, with positive values when the species is more abundant in the natural substrate and negative values when the species is more abundant in the artificial substrate. Therefore, a NAR value of 0.75 represents a situation where the abundance of one species in the artificial substrate is 75% less than that in the natural reef, while the opposite is true for a NAR value of -0.75 (i.e., abundance in the natural substrate is 75% less than that in the artificial substrate). For any given species, NAR equals 0 when the number of specimens in both substrates is identical.

Finally, we also categorized species as low, medium, or high occupancy species based on the number of locations (including both substrate types) where every species was found. Out of the 10 locations we sampled, we defined low occupancy species as those that occurred in 3 or less locations, high occupancy species as those that occurred in 8 or more locations, and medium occupancy species as those that occurred in 4–7 locations. It is important to note that these three categories classified species independently of the actual number of specimens quantified for each species. For example, a high occupancy species may have a very small number of specimens, being considered “rare” under an abundance criterion. Similar, a low occupancy species could be present in very large numbers and be considered common or frequent. For this reason, and to avoid misinterpretation, in this study we avoid the terms “frequent, common, and rare” and refer to high, medium, and low occupancy species to unambiguously state that these categories do not refer to abundance but to the small-scale geographic distribution in our study.

We used five analytical approaches to test for a number of hypotheses. First, we ran paired t-tests to test for differences in richness (number of species), diversity (Shannon Diversity Index), abundance (number of specimens), and number of exclusive species between artificial and natural substrates. We defined exclusive species as those that, for every location, were present in either the natural or the

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