



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



Jose A. Sanabria-Fernandez^{a,b,*}, Natali Lazzari^{a,c}, Rodrigo Riera^{d,e}, Mikel A. Becerro^a

^a The BITES Lab, Center for Advanced Studies of Blanes (CEAB-CSIC), Acc Cala S Francesc 14, 17300 Blanes, Gerona, Spain

^b Department of Physical Chemistry, University of Cádiz, Avenida República Árabe Saharaui, s/n, 11510 Puerto Real, Cádiz, Spain

^c Univ Cádiz, Dept Biol, Fac Environm & Marine Sci, Marine Campus Int Excellence CEIMAR, Puerto Real, Spain

^d Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Casilla 297, Concepción, Chile

^e Centro de Investigación en Biodiversidad y Ambientes Sustentables (CIBAS), Universidad Católica de la Santísima Concepción, Concepción, Chile

ARTICLE INFO

Keywords:

Abundance based index
Anthropogenization
Artificial substrates
Biodiversity
Common and rare species
Marine ecology
Ocean sprawl
Rocky reef communities

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 occupancy species with medium and low mobility. 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 (Airoldi 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 (Airoldi and

* Corresponding author. The BITES lab, Center for Advanced Studies of Blanes (CEAB-CSIC), Acc Cala S Francesc 14, 17300 Blanes, Gerona, Spain.
E-mail address: jsanabriafernandez@gmail.com (J.A. Sanabria-Fernandez).

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

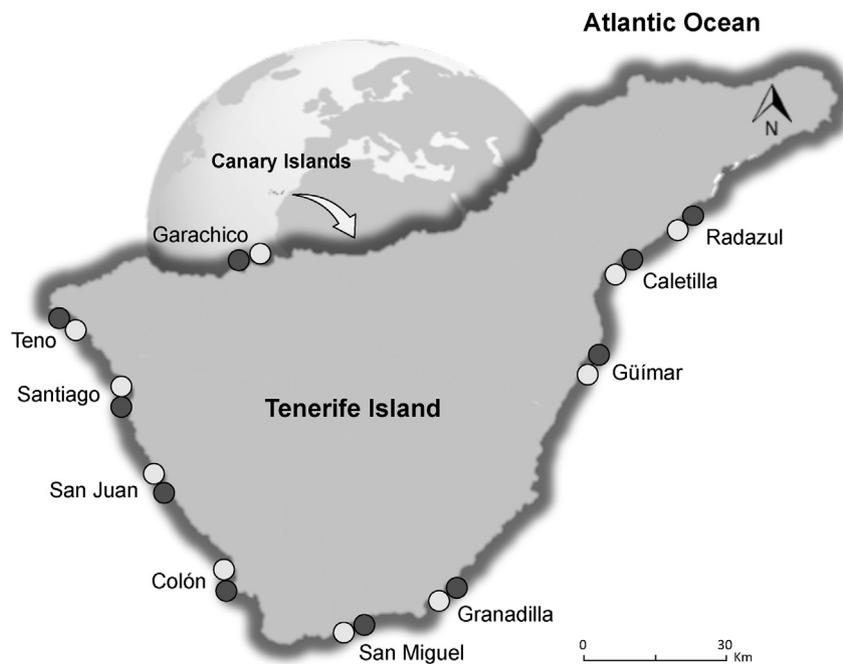


Fig. 1. Sampled artificial (dark circles) and adjacent natural substrates (light circles) scattered along the coast of Tenerife, Canary Islands. See Table 1 for additional site information.

artificial substrate, but not in both. It is possible that the same taxonomic species contributes multiple times as an exclusive species, regardless substrate type. For example, species “A” could be present exclusively in the natural substrate in one location and exclusively in the artificial substrate in another location, contributing as an exclusive species in both locations. Regardless the variable, all paired t-tests had 10 replicates, i.e., one natural and one artificial value for location. A second analytical approach used log-linear models to test for differences in richness, abundance, and number of exclusive species as a function of substrate type, species occupancy, and species mobility. Because log-linear models are a type of multiway frequency table analysis, data for each cell in the table was a single value with the total number of species, total abundance, or total number of exclusive species under each respective category. Log-linear models were run with the three variables of interest (substrate type, species occupancy, and species

mobility) and their two-way interactions. Third, we also tested for differences in richness, diversity, abundance, and number of exclusive species (all variables rank-transformed because of lack of assumptions) between artificial and natural substrates with a three-way analysis of variance applying “aov” function of the vegan package in R (Oksanen et al., 2016) with substrate type, species occupancy, and mobility as fully orthogonal, fixed factors (i.e., 180 data points for each variable; 3 levels of mobility x 3 levels of occupancy x 2 substrate types x 10 locations). We used a fourth analytical approach to test whether artificial substrates increasingly resembled their natural counterparts with time. To do so, we ran an analysis of covariance on the rank-transformed NAR using species occupancy and mobility as fixed factors and age of the artificial substrates as covariate. Because NAR was calculated for each species in our data set and many occurred in multiple locations, the total number of data points in this analysis was 492, i.e., there were

Table 1

Sampling locations (and numbers for their identification in Fig. 1) with average depth (m), latitude and longitude for both natural and artificial substrates, age of the artificial substrate (in years from submersion to sampling time) and type of material used for the construction of the breakwaters, i.e., material of artificial substrates.

Number	Location	Natural Substrate (NS)	Depth NS	Artificial Substrate (AS)	Depth AS	Age AS	Material AS
1	Garachico	28°22'17.38" N 16°45'10.33" W	5	28°22'24.13" N 16°45'09.62" W	2.5	0	Concrete
2	Teno	28°20'32.78" N 16°55'06.98" W	4.6	28°20'30.86" N 16°55'11.27" W	5.4	34	Concrete
3	Santiago	28°16'06.98" N 16°51'05.11" W	6.8	28°14'54.31" N 16°50'34.74" W	8.8	35	Concrete
4	San Juan	28°10'46.50" N 16°49'10.26" W	6.2	28°10'46.03" N 16°48'57.61" W	6.6	24	Concrete
5	Colón	28°06'00.46" N 16°45'20.83" W	7.9	28°04'47.04" N 16°44'17.59" W	7	27	Concrete
6	San Miguel	28°01'21.15" N 16°36'33.25" W	3.7	28°01'17.96" N 16°36'36.42" W	4.7	8	Concrete
7	Granadilla	28°05'16.07" N 16°29'25.39" W	6.5	28°05'14.39" N 16°36'37.25" W	3.3	18	Concrete
8	Güímar	28°17'42.79" N 16°22'21.10" W	3.8	28°17'16.32" N 16°22'42.67" W	3.2	4	Quarry rock
9	Caletillas	28°23'02.74" N 16°21'11.87" W	3.6	28°22'54.29" N 16°21'21.81" W	5.9	54	Concrete
10	Radazul	28°24'07.77" N 16°19'39.77" W	6	28°24'05.50" N 16°19'35.72" W	5.8	4	Quarry rock

multiple NAR values (multiple species) for each of the 10 age values (one for each location). Regressions in the analysis of covariance were highly replicated (between 32 and 93 data points depending on the mobility x occupancy combination). Finally, we also ran a permutational analysis of variance (PERMANOVA) of square-root transformed species abundance data to test for community level differences between natural and artificial substrates. We used a resemblance matrix based on Bray-Curtis distance and the “Adonis” function of vegan package (R Development Core Team, 2013; Oksanen et al., 2016) with 999 permutations.

3. Results

We found none non-indigenous or invasive species out of the 107 identified species quantified in our study (Appendix 1). Overall, seven out of the 10 natural substrates had more species than their artificial counterparts, yet the total number of species failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = -0.918$, $df = 9$, $p = 0.382$). The log-linear model fit well with the total number of species found in natural and artificial substrates (Likelihood Ratio $\chi^2 = 3.429$, $df = 4$, $p = 0.489$). The same model without occupancy had a poor fit ($\chi^2 = 18.548$, $df = 6$, $p = 0.005$), causing a significant change in the model ($\chi^2 = 15.119$, $df = 2$, $p = 0.001$). The number of low occupancy species with medium and low mobility in natural substrates doubled and tripled those found in artificial substrates (Fig. 2a). We also found that the average number of species found in natural and artificial substrates might vary as a function of species occupancy and mobility (three-way ANOVA, see probability of three-way interaction term between substrate type, occupancy, and mobility, and probability of substrate type in Table 2a).

Similarly, eight out of 10 natural substrates had higher Shannon Diversity Index than their artificial counterparts, yet diversity failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = -1.983$, $df = 9$, $p = 0.079$). We found that the average Shannon Diversity Index found in natural substrates was significantly larger than in artificial substrates (three-way ANOVA, significant substrate type, Table 2b), driven by the higher diversity values in natural than in artificial substrates for the low occupancy species with medium and low mobility (Fig. 3).

Seven out of the 10 natural substrates had more exclusive species than their artificial counterparts, yet the total number of exclusive

species failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = -0.918$, $df = 9$, $p = 0.382$). The total number of exclusive species that were found in either natural or artificial substrates varied as a function of occupancy and mobility (Fig. 2b, $\chi^2 = 9.886$, $df = 2$, $p = 0.007$). High occupancy species with high mobility were more often seen exclusively in artificial than in natural substrates (56 vs. 42) while the opposite was true for low occupancy species with medium (36 vs. 56) and low (19 vs. 37) mobility (Fig. 2b). Substrate type also had an effect on the average number of exclusive species, although its effect varied as a function of mobility and occupancy (three-way ANOVA, significant substrate type effect and its interaction with occupancy and mobility, Table 2c).

The total number of specimens also failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = 1.151$, $df = 9$, $p = 0.280$). Yet, the total number of specimens in natural and artificial substrates varied as a function of occupancy and mobility (Fig. 2c, $\chi^2 = 512.786$, $df = 4$, $p < 0.001$). High occupancy species with high mobility were more abundant in artificial than in natural substrates (25.4 vs. 9.2) while the opposite was true for low occupancy species with medium (17 vs. 56) and low (600 vs. 893) mobility (Fig. 2c). We also found that the average number of specimens found in natural and artificial substrates varied as a function of species occupancy and mobility (three-way ANOVA, significant interaction term between substrate type, occupancy, and mobility, Table 2d).

NAR varied as a function of species occupancy, species mobility, and their interaction ($p = 0.005$, $p < 0.001$, and $p = 0.005$, respectively, Table 3). Age had no effect on NAR, either directly ($p = 0.436$, Table 3) or through its interaction with species occupancy and mobility ($p = 0.121$, Table 3). Low occupancy species with medium and low mobility were more abundant in natural than in artificial substrates (Fig. 4). High mobility species showed negative NAR values regardless their occupancy (Fig. 4). Permutational analysis of variance (PERMANOVA) failed to detect differences in species abundances between natural and artificial substrates (Pseudo-F = 1.064, $df = 1$, $p = 0.354$, Fig. 5).

4. Discussion

Human alteration of coastal ecosystems is widespread and artificial substrates are becoming a significant habitat in shallow rocky communities (Airoldi and Beck, 2007). The proliferation of artificial

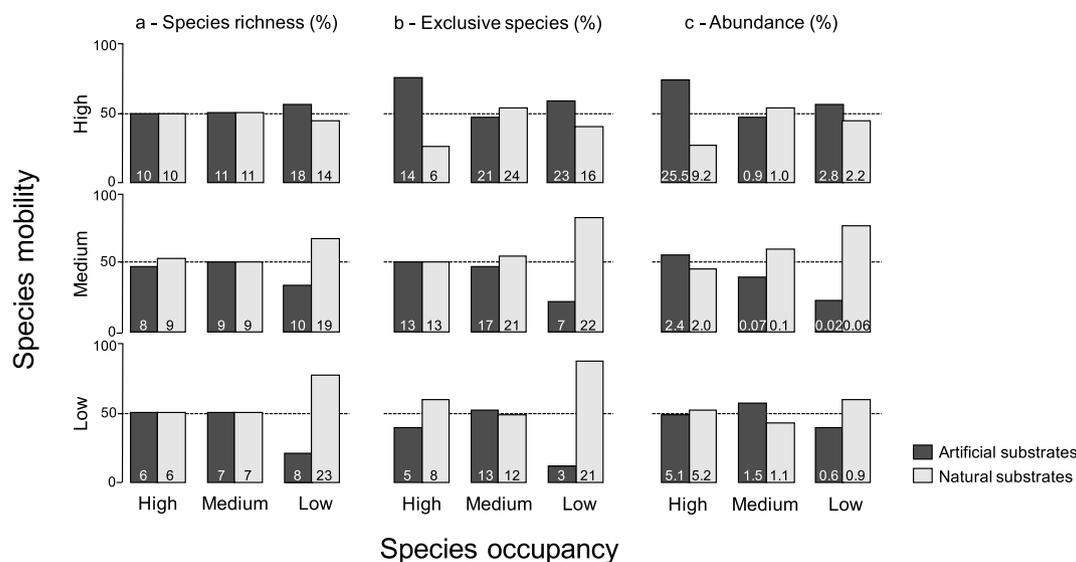


Fig. 2. Percentage of a) species richness, b) exclusive species, and c) total species abundance found in artificial (dark bars) and natural (light bars) substrates. Numbers within bars are a) total number of species, b) total number of exclusive species, and c) total abundance (x10³) pooled across substrates as a function of species occupancy (high, medium, and low occupancy, x-axis) and mobility (high, medium, and low mobility, y-axis).

Table 2

Summary of the three-way analysis of variance on a) species richness, b) Shannon diversity index, c) number of exclusive species, and d) total abundance of specimens with substrate type, species mobility, and species occupancy as fixed factors.

Variable	Factors	df	SS	MS	F	p
Richness	Substrate	1	3234	3234	3.46	0.064
	Mobility	2	11,193	5596	5.99	0.003
	Occupancy	2	287,973	143,987	154.22	< 0.001
	Substrate* <i>Mobility</i>	2	2873	1436	1.53	0.217
	Substrate* <i>Occupancy</i>	2	4024	2012	2.15	0.119
	Mobility* <i>Occupancy</i>	4	1,0408	2602	2.78	0.028
	Substrate* <i>Mobility</i> * <i>Occupancy</i>	4	8801	2200	2.35	0.055
	Residuals	162	151,245	934		
	Diversity	Substrate	1	7618	7618	5.27
Mobility	2	6210	3105	2.14	0.119	
Occupancy	2	200,250	100,125	69.31	< 0.001	
Substrate* <i>Mobility</i>	2	1855	928	0.64	0.527	
Substrate* <i>Occupancy</i>	2	5064	2532	1.75	0.176	
Mobility* <i>Occupancy</i>	4	14,217	3554	2.46	0.047	
Substrate* <i>Mobility</i> * <i>Occupancy</i>	4	11,800	2950	2.04	0.09	
Residuals	162	234,025	1445			
Exclusive species	Substrate	1	12,103	12,103	5.71	0.017
	Mobility	2	16,201	8100	3.82	0.023
	Occupancy	2	20,717	10,359	4.89	0.008
	Substrate* <i>Mobility</i>	2	8423	4211	1.98	0.14
	Substrate* <i>Occupancy</i>	2	20,099	10,050	4.74	0.009
	Mobility* <i>Occupancy</i>	4	9851	2463	1.16	0.329
	Substrate* <i>Mobility</i> * <i>Occupancy</i>	4	21,138	5284	2.49	0.044
	Residuals	162	343,088	2118		
	Abundance	Substrate	1	149	149	0.17
Mobility	2	276,597	138,299	160.2	< 0.001	
Occupancy	2	45,298	22,649	26.23	< 0.001	
Substrate* <i>Mobility</i>	2	958	479	0.55	0.575	
Substrate* <i>Occupancy</i>	2	1904	952	1.1	0.334	
Mobility* <i>Occupancy</i>	4	10,771	2693	3.11	0.016	
Substrate* <i>Mobility</i> * <i>Occupancy</i>	4	9928	2482	2.87	0.024	
Residuals	162	139,847	863			

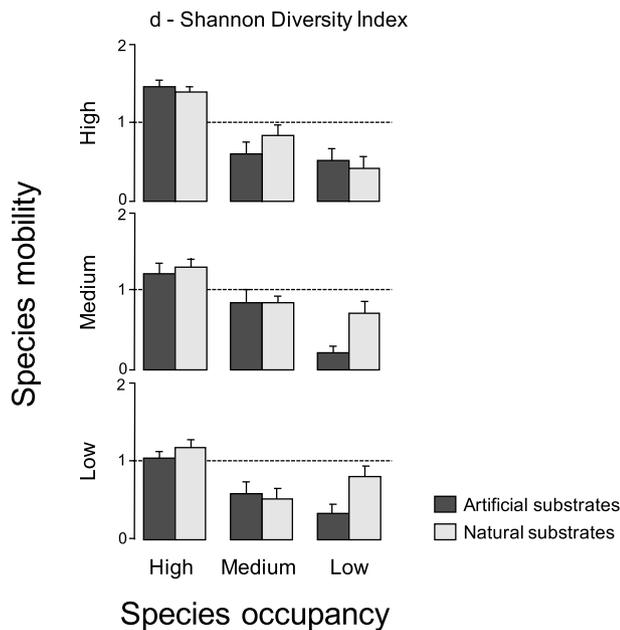


Fig. 3. Mean (\pm 1SE) Shannon diversity index of the species found in the 10 artificial (dark bars) and adjacent natural (light bars) substrates as a function of species occupancy (high, medium, and low occupancy, x-axis) and mobility (high, medium, and low mobility, y-axis).

structures in the sea, referred to as ocean sprawl (Firth et al., 2016), is a cause of concern because artificial substrates may not function as the natural substrates they often replace (Carr and Hixon, 1997; Airoidi and Beck, 2007; Burt et al., 2009). Many studies have evaluated whether communities in natural and artificial substrates differ, yet evidence is

Table 3

Summary of the two-way analysis of covariance on the *Natural-Artificial Ratio* (NAR) using species mobility and occupancy as factors and age of the artificial substrates as covariate.

Factors	df	SS	MS	F	p
Occupancy	2	194,601.6	97,300.8	5.281	0.005
Mobility	2	290,674.5	145,337.2	7.888	0.000
Age	1	11,182.5	11,182.5	0.607	0.436
Mobility* <i>Occupancy</i>	4	278,698.1	69,674.5	3.781	0.005
Mobility* <i>Occupancy</i> * <i>Age</i>	4	135,015.3	33,753.4	1.832	0.121
Error	478	8,807,322.7	18,425.3		

somehow contradictory and incomplete. For example, fish populations in artificial structures can be either larger (Jessee et al., 1985; Rilov and Benayahu, 2000; Granneman and Steele, 2015), similar (Santos et al., 2013; Ross et al., 2016), or smaller (Carr and Hixon, 1997; Rooker et al., 1997) than in natural reefs. Differences between natural and artificial substrates may vary depending on the variable recorded (e.g., species richness, species abundance, species diversity), the location investigated, the species quantified, or the complexity of the artificial structures, among others (Hunter and Sayer, 2009; Granneman and Steele, 2015). Our results showed biodiversity differences between adjacent natural and artificial substrates. These differences were majorly driven by the larger diversity of low occupancy species with medium or low mobility (i.e., rare benthic and sessile species) in natural substrates and the larger abundance of high occupancy and high mobility species in artificial substrates (i.e., common demersal fish species). Occupancy and mobility were, therefore, critical species traits to explain differences between substrate types. Failure to include these species traits resulted in non-significant differences between both substrate types. Our results suggest that the more common and mobile species create an illusion of natural communities in artificial substrates,

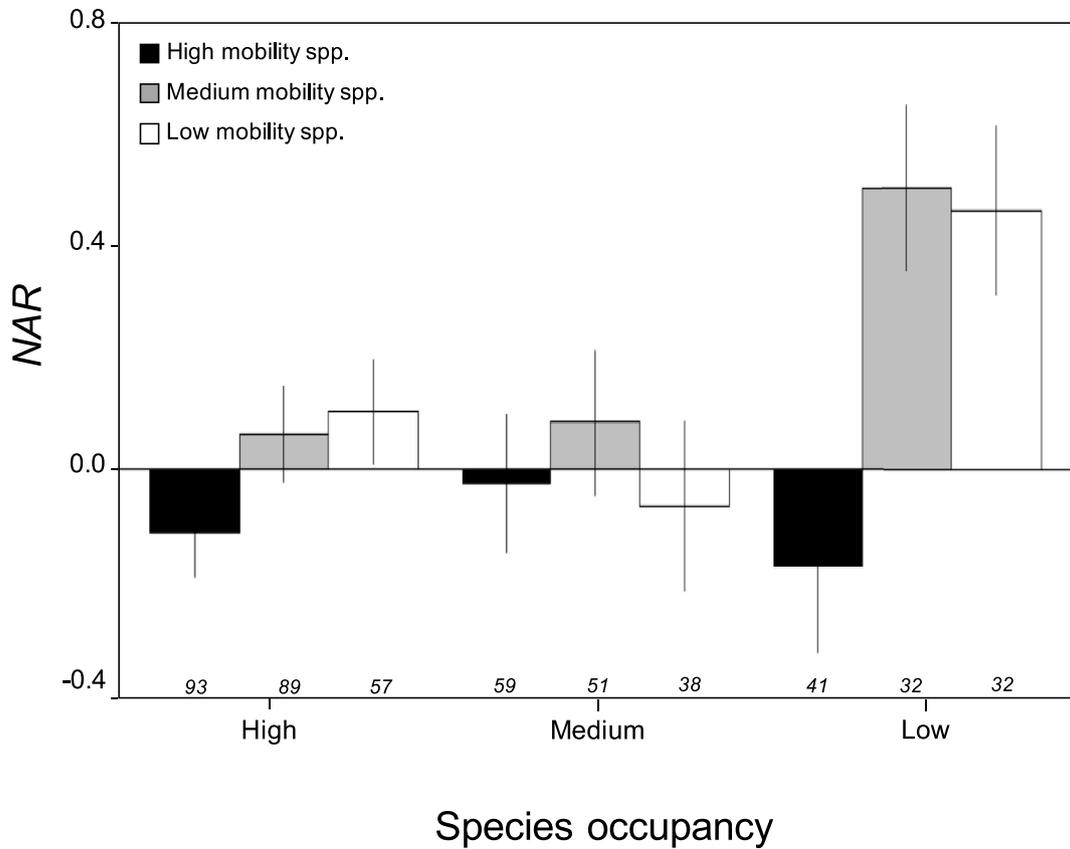


Fig. 4. Mean (± 1SE) *Natural-Artificial Ratio* (NAR, y-axis) of the species found in the 10 artificial and adjacent natural substrates as a function of species occupancy and mobility (x-axis). Positive NAR values are obtained with larger species abundance in natural than in artificial substrates, while negative NAR values are obtained with larger species abundance in artificial than in natural substrates. Numbers below bars are the number of NAR values (i.e., species) contributing to each occupancy*mobility combination. See Materials and methods for additional details.

by homogenizing both habitats and masking the negative effect that artificial substrates have in a large proportion of species. We found no evidence to support that these differences decreased over time, suggesting that artificial substrates are bad surrogates of their natural counterparts, at least over the 54-yr span investigated in our study.

There are reasons to expect that artificial substrates can mimic or surpass the biodiversity found in natural substrates (Baine, 2001). Artificial structures may provide additional habitats and refuge to those

available in natural reefs, which could result in increased species richness, abundance, or diversity (Menge, 1976; Jessee et al., 1985; Granneman and Steele, 2015). Out of the many possible artificial structures deployed in the ocean, artificial reefs have been widely used as a tool to help mitigate undesired trends such as habitat loss (Pickering and Whitmarsh, 1997) or to help preserve, restore, or enhance desired ecological functions such as diversity and production (Perkol-Finkel and Benayahu, 2005) or fisheries (Baine, 2001).

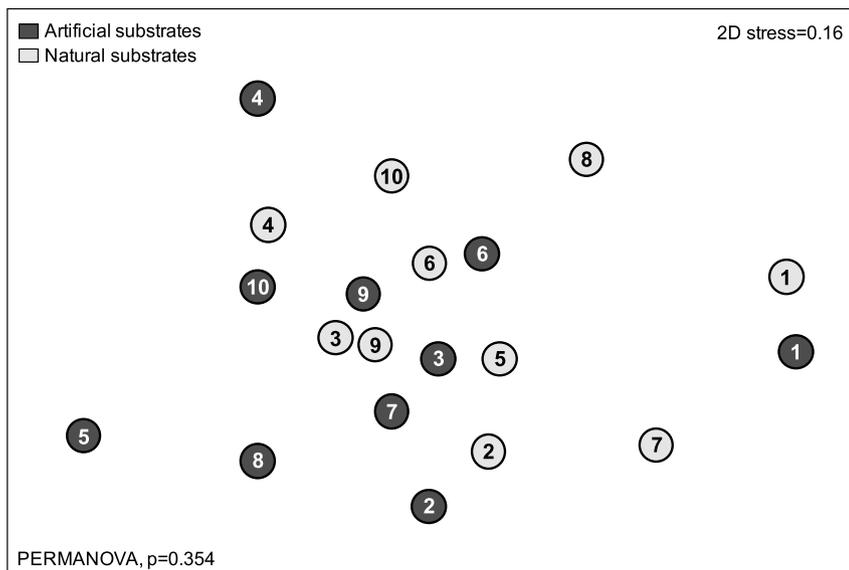


Fig. 5. Non-metric multidimensional scaling (MDS) based on Bray-Curtis distance similarity matrix calculated from square-root transformed abundances of all species found in artificial (dark) and natural (light) substrates. Numbers within circles indicate locations as specified in Table 1. P value provided by permutational analysis of variance to test for differences between artificial and natural substrates. See text for additional details.

Artificial reefs built with concrete blocks seem to increase both fish species and fish biomass (Pickering and Whitmarsh, 1997) as compared to artificial reefs built with pipes or natural reefs (Brock and Norris, 1989). Compared to natural reefs, the smaller size of artificial reefs can also explain higher species densities due to increase reef perimeter/area ratio (Jessee et al., 1985; DeMartini et al., 1989; Bohnsack et al., 1994). Most evidence for enhanced biodiversity (in a broad sense) by artificial reefs stem from fish data (Svane and Petersen, 2001), but increased invertebrate and algal populations have also been reported (Hunter and Sayer, 2009; Granneman and Steele, 2015). Whether the increased abundance, biomass, or diversity (in a broad sense) found in artificial reefs is due to increased production in the artificial structure or to attraction from surrounding environments, i.e., the production vs attraction debate (Pickering and Whitmarsh, 1997), remains unresolved.

Yet marine artificial structures can be deployed with no ecological/conservational goals in mind, for example, to provide shelter for boats as the breakwaters investigated in our study. These type of structures can show trends that diverge from those found in artificial reefs, with decreased biodiversity (in a broad sense) on artificial structures (Chapman, 2003; Airoidi et al., 2015). Our results provided evidence that the effect of artificial substrates varied as a function of the variable and species (or species group) investigated. Three set of data supported evidence for increased performance of artificial over natural substrates in our study. First, average NAR (*Natural-Artificial Ratio*) for high mobility species was negative, providing evidence for larger abundance of high mobility species in artificial than in natural substrates. Because NAR was calculated for every species in our study, the negative average values suggest that the larger abundance of high mobility species found in artificial substrates was a general pattern driven by many species. In fact, 80% of the high occupancy and 45% the low occupancy species with high mobility were more abundant in artificial substrates (as opposed to only 20% and 30% that were more abundant in natural substrates). Second, total and average abundance of high occupancy species were higher in artificial than in natural substrates. Third, the number of exclusive high mobility species with high occupancy found in artificial substrates doubled those found in natural substrates. Our results might suggest that the success of these species stem from their capacity to inhabit a variety of habitats (high occupancy) and to occupy new habitats as they become available (high mobility). All high mobility species in our study were demersal fish, so our study supports for the increased fish abundance and biomass found in many artificial reefs (Chapman, 2003), often deployed with specific conservation goals (as opposed to the coastal protection goals of the breakwaters investigated in our study). Increased fish abundance is a sought-after effect that can bring benefits to multiple stakeholders, including recreational and commercial fishing (Whitmarsh et al., 2008) or diving industry (van Treeck and Schuhmacher, 1999; Crabbe and McClanahan, 2006; Kirkbride-Smith et al., 2013), among others. Given that only high mobility species showed increased performance in the artificial substrates, our results could support for a stronger attraction than production effect in the attraction vs production debate (Pickering and Whitmarsh, 1997).

Our data showed stronger evidence for decreased performance of artificial over natural substrates, which was driven by low occupancy species with medium and low mobility. In our study, medium mobility species included multiple invertebrates and cryptic fish species. Adult organisms of these species are clearly more attached to the substrate than demersal fish and have a somehow reduced mobility. In our study, low mobility species included any sessile organism permanently attached to the substrate and, therefore, with highly restricted (i.e., nil) mobility. Other studies have also reported decreased artificial reef performance associated with sessile species, i.e., higher coral richness and diversity in natural habitats than in artificial reefs (Perkol-Finkel and Benayahu, 2004; Perkol-Finkel et al., 2005, 2006; Burt et al., 2009). Our data also showed that artificial substrates had lower numbers of low occupancy benthic and sessile species that were observed

exclusively in either the natural or the artificial substrate, giving additional evidence for the decreased performance of artificial substrates in species richness. Yet, abundance of sessile species may be higher in artificial than natural reefs (Hunter and Sayer, 2009; Granneman and Steele, 2015). Even more, artificial reefs can be less diverse but, at the same time, hold higher abundance than natural reefs (Burt et al., 2009). We found the opposite, i.e., larger total abundance per species and larger average NAR of low occupancy benthic and sessile species on natural reefs, providing evidence for higher species density in natural than in artificial substrates. Because only medium and low mobility species with low occupancy showed decreased performance in the artificial substrates, these results could support for a weaker production than attraction effect in the attraction vs production debate (Pickering and Whitmarsh, 1997). If our data can be interpreted within this debate, our study might provide greater support for the attraction (improved performance of demersal fish, i.e., associated with the attraction effect) over the production effect (reduced performance of sessile species, i.e., associated with production effect) of the debate. Information on the size distribution of species in both substrate types (not analyzed in our study) could help shed more light into this unresolved debate.

Overall, and beyond the specific results, our findings suggest that artificial substrates missed an important component of biodiversity, the least widely distributed benthic and sessile species. Despite their scarcity, these species were 40% of the total number of species in our study, representing a significant part of the biodiversity of the rocky littoral bottoms. Yet, because the species missing in our artificial substrates were the least apparent species in the community, artificial substrates gave an illusion of natural-like substrates driven by the most conspicuous species. In fact, and for all variables analyzed in our study, natural and artificial substrates failed to differ statistically unless we considered species occupancy and mobility. These species traits were, therefore, critical to find differences between natural and artificial substrates and provided evidence for the big impact that common species have at the community level, both statistically and at an observational, landscape scale. The large influence of common species at the community level exceeds biodiversity implications *per se*, linking biodiversity with ecosystem functioning (Grime, 1998). While common species are responsible for immediate effects, the filter and founder effects of the not-so-common species may become apparent at longer time scales and cannot be neglected (Grime, 1998).

Long-term data on the composition and abundance of species inhabiting artificial reefs is scarce, particularly with proper comparisons with natural reefs. In a 15-year study of artificial reefs off Rio de Janeiro, fish species richness, abundance, and biomass increased up to the 6–7th year to decrease thereafter although, unfortunately, no data is available from adjacent natural reefs (Neves dos Santos and Zalmon, 2015). Other studies have comparisons with natural reefs, but the artificial reefs have been few years underwater. Fish populations in young artificial reefs seem to be larger than in natural reefs (Bohnsack et al., 1994; Clark and Edwards, 1999; Chapman and Clynick, 2006) although fish assemblages may (Bohnsack et al., 1994; Clark and Edwards, 1999) or may not (Tupper and Hunte, 1998) differ. Data for mollusks showed an opposite pattern with lower diversity, richness, and evenness but larger number of specimens and dominance in artificial than natural reefs (Badalamenti et al., 2002). However, their natural and artificial reefs were associated with clear and turbid waters, which could act as a confounding factor (Badalamenti et al., 2002). Besides fish, Chapman and Clynick (2006) also quantified the algal and sessile invertebrate populations on their natural and artificial reefs, which were both similar.

At the other side of the age spectrum, data from a single 119-year old shipwreck and the adjacent reef where it sunk showed that natural-like communities developed only where the structure of the wreck matched the reef structure (Perkol-Finkel et al., 2006). Despite being underwater for over a century, wreck sections that differed structurally from natural reefs also differed ecologically (Perkol-Finkel et al., 2006).

Likewise, sessile communities in natural reefs differed with those from breakwaters of varying age, even after 31 years underwater (Burt et al., 2011). Similarity between natural and breakwater communities increased with time (Burt et al., 2011), which could be interpreted as an example of directional replacement of species. In fact, turf algae dominated breakwaters until 1.5 years, followed by a peak in bivalves on the 3.5 to 5.5-year-old reefs, and then coral cover gradually increased with reef age (Burt et al., 2011). These transitions from short-lived, fast-growing, opportunistic species to long-lived, slow-growing, competitively superior species agrees with the directional replacement of species in classic succession although it does not guarantee stable communities equivalent to those found in surrounded natural reefs (Svane and Petersen, 2001). Other studies have shown that artificial reef communities may take over a decade to resemble those in natural reefs (Asetline-Neilson et al., 1999; Abelson and Shlesinger, 2002; Perkol-Finkel and Beneyahu, 2004, 2007), but the resulting community may not be natural-like (Perkol-Finkel et al., 2006).

Our study is a snapshot comparison of multiple artificial substrates and their adjacent natural counterparts. For each location, natural and artificial substrates were equivalent in terms of orientation, wave exposure, depth, and slope. The artificial substrates we investigated differed in ecological conditions and spanned from 0 to 54 years underwater. We observed no major, community-level temporal trend in the presence and abundance of species. In the 20 reefs studied, we quantified presence and abundance of a total of 107 species. Detailed analyses at the species level or species-specific patterns along the 50-year timespan of our study are beyond the scope of this study. Our goal was to test whether communities inhabiting artificial substrates were equivalent to those found in natural substrates of the same area. As discussed previously, there are multitude examples with varying results often leading to contrasting conclusions. Our approach focused on many species to maximize ecological patterns over species specific responses, paired every artificial substrate with its adjacent natural reef to minimize community differences due to distinct geographic and environmental conditions, and used artificial substrates with varying numbers of years underwater to test for temporal trends in community organization. Overall, i.e., without considering species mobility and occupancy in our models, we found no statistical differences in diversity (broadly defined) between artificial and natural substrates. They seemed to be equivalent. These results were driven by the strong influence of common species, which minimized the large differences in low occupancy species with medium and low mobility. These benthic and sessile species were 40% of the species in our study and they were significantly less represented, both in terms of species number and abundance, in artificial substrates. Inclusion of species mobility and occupancy was therefore critical to describe the biodiversity loss associated with the artificial communities. Contrary to our expectations, age played no significant role to explain differences between natural and artificial substrates. Our results suggest that, regardless of directional replacement of species, communities developing in artificial substrates need not match their natural counterparts, as previously reported (Perkol-Finkel et al., 2006). This output agrees with the ecological succession following non-catastrophic disturbances, despite artificial substrates do offer a denuded substrate for primary succession (Platt and Connell, 2003). Given the current proliferation of artificial structures in our shallow marine environments, we might be building up a large biodiversity loss in shallow water marine communities around the globe. This unintentional loss is hard to detect as it seems to target the least conspicuous and less investigated benthic and sessile species. Fish species, the main target of many studies, seem to thrive in artificial substrates both in terms of number and abundance of species. Since communities inhabiting artificial substrates deviate from natural communities, artificial structures could lead to an increase of regional diversity (Connell and Glasby, 1999). Our results suggest otherwise that artificial substrates are not surrogates for natural communities (Burt et al., 2011). Understanding the strengths and weaknesses of artificial

structures will sure lead to a more effective use of these habitats. Should we aim to minimize biodiversity loss and promote its conservation, reliance on artificial substrates as surrogates of natural reefs looks dubious. Strategies that lessen habitat destruction combined with alternative protection and restoration measures may provide more efficient mechanisms for biodiversity conservation (Abelson et al., 2016; Geist and Hawkins, 2016; Kollmann et al., 2016).

Acknowledgments

We sincerely appreciate the unconditional support of Carlos Ceballos, from the Club Actividades Subacuáticas BIOSUB (www.biosub.es), and The Hotel Rural Casa Amarilla (www.fincacasamarilla.com) to our field activities. We also thank the Reef Life Survey Spain diver community for their help during field surveys and special thanks to Daniel Hernández for his contribution in the field work. This work was supported by the Spanish Ministry of Economy grant MARINERES [grant number CGL2013-49122-C3-1-R]. We deeply appreciate the constructive comments from Dr. Louise Firth and other anonymous reviewers that helped improve the quality of our study.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.marenvres.2018.06.010>.

References

- Abelson, A., Nelson, P.A., Edgar, G.J., Shashar, N., Reed, D.C., Belmaker, J., Krause, G., Beck, M.W., Brokovich, E., France, R., Gaines, S.D., 2016. Expanding marine protected areas to include degraded coral reefs. *Conserv. Biol.* 30, 1182–1191. <http://dx.doi.org/10.1111/cobi.12722>.
- Abelson, A., Shlesinger, Y., 2002. Comparison of the development of coral and fish communities on rock-aggregated artificial reefs in Eilat, Red Sea. *ICES J. Mar. Sci.* 59, S122–S126. <http://dx.doi.org/10.1006/jmsc.2002.1210>.
- Airoldi, L., Beck, M., 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanogr. Mar. Biol. Annu. Rev.* 45, 345–405. <http://dx.doi.org/10.1201/9781420050943.ch7>.
- Airoldi, L., Bulleri, F., 2011. Anthropogenic disturbance can determine the magnitude of opportunistic species responses on pendleton artificial reefs. *PLoS One* 6, e22985. <http://dx.doi.org/10.1371/journal.pone.0022985>.
- Airoldi, L., Turon, X., Perkol-Finkel, S., Rius, M., 2015. Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Divers. Distrib.* 21, 755–768.
- Asetline-Neilson, D.A., Bernstein, B.B., Palmer-Zwahlen, M.L., Riege, L.E., Smith, R.W., 1999. Comparisons of turf communities from pendleton artificial reef, torrey pines artificial reef, and a natural reef using multivariate techniques. *Bull. Mar. Sci.* 65, 37–57.
- Badalamenti, F., Chemello, R., D'Anna, G., Henriquez Ramos, P., Riggio, S., 2002. Are artificial reefs comparable to neighbouring natural rocky areas? A mollusc case study in the Gulf of Castellammare (NW Sicily). *ICES J. Mar. Sci.* 59, S127–S131. <http://dx.doi.org/10.1006/jmsc.2002.1265>.
- Baine, M., 2001. Artificial reefs: a review of their design, application, management and performance. *Ocean Coast Manag.* 44, 241–259.
- Barnabé, G., Barnabé-Quet, R., 2000. *Ecology and Management of Coastal Waters: the Aquatic Environment*. Springer, London.
- Bishop, M.J., Mayer-Pinto, M., Airoldi, L., Firth, L.B., Morris, R.L., Loke, L.H., Hawkins, S.J., Naylor, L.A., Coleman, R.A., Chee, S.Y., Dafforn, K.A., 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. *J. Exp. Mar. Biol. Ecol.* 492, 7–30.
- Bohnsack, J.A., Harper, D.E., McClellan, D.B., Hulsbeck, M., 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off Southeastern Florida, U.S.A. *Bull. Mar. Sci.* 55, 796–823.
- Brock, R.E., Norris, J.E., 1989. An Analysis of the Efficacy of Four Artificial Reef Designs in Tropical Waters. *Bull. Mar. Sci.* 44 (2), 934–941.
- Bryant, D., Rodenburg, E., Cox, T., Nielsen, D., 1995. *Coastlines at Risk: an index of Potential Development-related Threats to Coastal Ecosystems*, WRI Indicator Brief. World Resources Institute, Washington, USA.
- Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *J. Appl. Ecol.* 47, 26–35. <http://dx.doi.org/10.1111/j.1365-2664.2009.01751.x>.
- Burt, J., Bartholomew, A., Sale, P.F., 2011. Benthic development on large-scale engineered reefs: A comparison of communities among breakwaters of different age and natural reefs. *Ecol. Eng.* 37, 191–198. <http://dx.doi.org/10.1016/J.ECOLENG.2010.09.004>.
- Burt, J., Bartholomew, A., Usseglio, P., Bauman, A., Sale, P.F., 2009. Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates?

- Coral Reefs 28, 663–675. <http://dx.doi.org/10.1007/s00338-009-0500-1>.
- Carr, M.H., Hixon, M.A., 1997. Artificial Reefs: The Importance of Comparisons with Natural Reefs. *Fisheries* 22 (4), 28–33.
- Chapman, M.G., 2003. Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. *Mar. Ecol. Prog. Ser.* 264, 21–29.
- Chapman, M.G., Clynick, B.G., 2006. Experiments testing the use of waste material in estuaries as habitat for subtidal organisms. *J. Exp. Mar. Biol. Ecol.* 338, 164–178. <http://dx.doi.org/10.1016/j.jembe.2006.06.018>.
- Chee, S.Y., Othman, A.G., Sim, Y.K., Adam, A.N.M., Firth, L.B., 2017. Land reclamation and artificial islands: Walking the tightrope between development and conservation. *Glo. Ecol. Conser* 12, 80–95.
- Clark, S., Edwards, A.J., 1999. An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 9, 5–21.
- Clynick, B.G., Chapman, M.G., Underwood, A.J., 2008. Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. *Austral. Ecol.* 33, 140–150. <http://dx.doi.org/10.1111/j.1442-9993.2007.01802.x>.
- Connell, S., Glasby, T., 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Mar. Environ. Res.* 47, 373–387. [http://dx.doi.org/10.1016/S0141-1136\(98\)00126-3](http://dx.doi.org/10.1016/S0141-1136(98)00126-3).
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260. <http://dx.doi.org/10.1038/387253a0>.
- Costanza, R., Chichakly, K., Dale, V., Farber, S., Finnigan, D., Grigg, K., Heckbert, S., Kubiszewski, I., Lee, H., Liu, S., Magnuszewski, P., Maynard, S., McDonald, N., Mills, R., Ogilvy, S., Pert, P.L., Renz, J., Wainger, L., Young, M., Richard Ziegler, C., 2014. Simulation games that integrate research, entertainment, and learning around ecosystem services. *Ecosyst. Serv.* 10, 195–201. <http://dx.doi.org/10.1016/j.ecoser.2014.10.001>.
- Crabbe, M., McClanahan, T.R., 2006. A Biosocioeconomic Evaluation of Shipwrecks Used for Fishery and Dive Tourism Enhancement in Kenya. *West. Indian Ocean J. Mar. Sci.* 5 (1), 35–53.
- DeMartini, E.E., Roberts, D.A., Anderson, T.W., 1989. Contrasting patterns of fish density and abundance at an artificial coral reef and a cobble-bottom kelp forest. *Bull. Mar. Sci.* 44, 881–892.
- Duarte, C.M., Pitt, K.A., Lucas, C.H., Purcell, J.E., Uye, S.I., Robinson, K., Brotz, L., Decker, M.B., Sutherland, K.R., Malej, A., Madin, L., 2012. Is global ocean sprawl a cause of jellyfish blooms? *Front. Ecol. Environ.* 11, 91–97.
- Dugan, J.E., Airoidi, L., Chapman, M.G., Walker, S.J., Schlacher, T., 2011. Estuarine and coastal structures: environmental effects, a focus on shore and nearshore structures. In: Wolanski, E., McLusky, D. (Eds.), *Treatise on Estuarine and Coastal Science*. Academic Press, Waltham, Massachusetts, pp. 17–41.
- Edgar, G.J., Stuart-Smith, R.D., 2014. Systematic global assessment of reef fish communities by the Reef Life Survey program. *Sci. Data* 1, 140007. <http://dx.doi.org/10.1038/sdata.2014.7>.
- Firth, L.B., Knights, A.M., Bridger, D., Evans, A., Mieskowska, N., Moore, P.J., O'Connor, N.E., Sheehan, E.V., Thompson, R.C., Hawkins, S.J., 2016. Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanogr. Mar. Biol.* 54, 193–269.
- Geist, J., Hawkins, S.J., 2016. Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 26, 942–962. <http://dx.doi.org/10.1002/aqc.2702>.
- Glasby, T., Connell, S., 2001. Orientation and position of substrata have large effects on epibiotic assemblages. *Mar. Ecol. Prog. Ser.* 214, 127–135. <http://dx.doi.org/10.3354/meps214127>.
- Gothland, M., Dauvin, J.C., Denis, L., Dufossé, F., Jobert, S., Ovaert, J., Pezy, J.P., Tous, A., Spilmont, N., 2014. Biological traits explain the distribution and colonisation ability of the invasive shore crab *Hemigrapsus takanoi*. *Estuar. Coast Shelf Sci.* 142, 41–49. <http://dx.doi.org/10.1016/j.ecss.2014.03.012>.
- Granneman, J.E., Steele, M.A., 2015. Effects of reef attributes on fish assemblage similarity between artificial and natural reefs. *ICES J. Mar. Sci.* 72, 2385–2397. <http://dx.doi.org/10.1093/icesjms/fsv094>.
- Gray, J.S., 1997. Marine Biodiversity: patterns, threats and conservation needs. *Biodivers. Conserv.* 6, 153–175.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910. <http://dx.doi.org/10.1046/j.1365-2745.1998.00306.x>.
- Halpern, B.S., Selkoe, K.A., Micheli, F., Kappel, C.V., 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conserv. Biol.* 21, 1301–1315. <http://dx.doi.org/10.1111/j.1523-1739.2007.00752.x>.
- Heery, E.C., Bishop, M.J., Critchley, L.P., Bugnot, A.B., Airoidi, L., Mayer-Pinto, M., Sheehan, E.V., Coleman, R.A., Loke, L.H., Johnston, E.L., Komyakova, V., 2017. Identifying the consequences of ocean sprawl for sedimentary habitats. *J. Exp. Mar. Biol. Ecol.* 492, 31–48.
- Hunter, W.R., Sayer, M.J., 2009. The comparative effects of habitat complexity on faunal assemblages of northern temperate artificial and natural reefs. *ICES J. Mar. Sci.* 66, 691–698. <http://dx.doi.org/10.1093/icesjms/fsp058>.
- Jessee, W.N., Carpenter, A.L., Carter, J.W., 1985. Distribution patterns and density estimates of fishes on a southern California artificial reef with comparisons to natural kelp-reef habitats. *Bull. Mar. Sci.* 13, 214–226.
- Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84, 2007–2020. <http://dx.doi.org/10.1890/01-0622>.
- Kirkbride-Smith, A.E., Wheeler, P.M., Johnson, M.L., 2013. The relationship between diver experience levels and perceptions of attractiveness of artificial reefs - examination of a potential management tool. *PLoS One* 8, e68899. <http://dx.doi.org/10.1371/journal.pone.0068899>.
- Kohler, K.E., Gill, S.M., 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput. Geosci.* 32, 1259–1269. <http://dx.doi.org/10.1016/j.cageo.2005.11.009>.
- Kollmann, J., Meyer, S.T., Bateman, R., Conradi, T., Gossner, M.M., de Souza Mendonça, M., Fernandes, G.W., Hermann, J.M., Koch, C., Müller, S.C., Oki, Y., Overbeck, G.E., Paterno, G.B., Rosenfield, M.F., Toma, T.S.P., Weisser, W.W., 2016. Integrating ecosystem functions into restoration ecology—recent advances and future directions. *Restor. Ecol.* 24, 722–730. <http://dx.doi.org/10.1111/rec.12422>.
- Lin, A., Shen, S., Wang, J., Yan, B., 2008. Reproduction diversity of *Euteromorpha prolifera*. *J. Integr. Plant Biol.* 50, 622–629. <http://dx.doi.org/10.1111/j.1744-7909.2008.00647.x>.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207. <http://dx.doi.org/10.1890/02-3090>.
- Menge, J., 1976. *Effect of Herbivores on Community Structure of the New England Rocky Intertidal Region: Distribution, Abundance and Diversity of Algae*. Dissertation. Harvard University.
- Miller, M.W., Valdivia, A., Kramer, K.L., Mason, B., Williams, D.E., Johnston, L., 2009. Alternate benthic assemblages on reef restoration structures and cascading effects on coral settlement. *Mar. Ecol. Prog. Ser.* 387, 147–156.
- Neumann, B., Vafeidis, A.T., Zimmermann, J., Nicholls, R.J., 2015. Future Coastal Population Growth and Exposure to Sea-Level Rise and Coastal Flooding - A Global Assessment. *PLoS One* 10 (3), e0118571. <http://dx.doi.org/10.1371/journal.pone.0118571>.
- Neves dos Santos, L., Zalmon, I.R., 2015. Long-term changes of fish assemblages associated with artificial reefs off the northern coast of Rio de Janeiro, Brazil. *J. Appl. Ichthyol* 31, 15–23. <http://dx.doi.org/10.1111/jai.12947>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R.B., Simpson, G., Solymos, P., Henry, M., Stevens Szoecs, E., Wagner, H., 2016. *Vegan: Community Ecology Package*. R Package version 2.4-1. <https://CRAN.R-project.org/package=vegan>.
- Perkol-Finkel, S., Benayahu, Y., 2004. Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. *Coral Reefs* 23, 195–205. <http://dx.doi.org/10.1007/s00338-004-0384-z>.
- Perkol-Finkel, S., Benayahu, Y., 2005. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. *Mar. Environ. Res.* 59, 79–99.
- Perkol-Finkel, S., Shashar, N., Barneah, O., Ben-David-Zaslav, R., Oren, U., Reichart, T., Yacobovitch, T., Yahel, G., Yahel, R., Benayahu, Y., 2005. Fouling reefal communities on artificial reefs: Does age matter? *Biofouling* 21, 127–140. <http://dx.doi.org/10.1080/08927010500133451>.
- Perkol-Finkel, S., Shashar, N., Benayahu, Y., 2006. Can artificial reefs mimic natural reef communities? The roles of structural features and age. *Mar. Environ. Res.* 61, 121–135. <http://dx.doi.org/10.1016/j.marenvres.2005.08.001>.
- Perkol-Finkel, S., Benayahu, Y., 2007. Differential recruitment of benthic communities on neighboring artificial and natural reefs. *J. Exp. Mar. Biol. Ecol.* 340, 25–39.
- Pickering, H., Whitmarsh, D., 1997. Artificial reefs and fisheries exploitation: a review of the 'attraction versus production' debate, the influence of design and its significance for policy. *Fish. Res.* 31, 39–59.
- Platt, W.J., Connell, J.H., 2003. Natural disturbances and directional replacement of species. *Ecol. Monogr.* 73, 507–522. <http://dx.doi.org/10.1890/01-0552>.
- Ponti, M., Fava, F., Angela Perlini, R., Giovanardi, Otello, Abbiati, M., 2015. Benthic assemblages on artificial reefs in the northwestern Adriatic Sea: Does structure type and age matter? *Mar. Environ. Res.* 104, 10–19.
- R Development Core Team, 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.Rproject.org/>.
- Ray, G., McCormick-Ray, M., 2009. Biodiversity of coastal-realm waters. In: *Oceans and Aquatic Ecosystems*. Oxford.
- Rilov, G., Benayahu, Y., 2000. Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. *Mar. Biol.* 136, 931–942. <http://dx.doi.org/10.1007/s002279900250>.
- Rooker, J.R., Dokken, Q.R., Pattengill, C.V., Holt, G.J., 1997. Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs* 16, 83–92. <http://dx.doi.org/10.1007/s003380050062>.
- Ross, S.W., Rhode, M., Viada, S.T., Mather, R., 2016. Fish species associated with shipwreck and natural hard-bottom habitats from the middle to outer continental shelf of the Middle Atlantic Bight near Norfolk Canyon. *Fish. Bull.* 114, 45–57. <http://dx.doi.org/10.7755/FB.114.1.4>.
- Santos, L.A.H., dos Ribeiro, F.V., Creed, J.C., 2013. Antagonism between invasive pest corals *Tubastraea* spp. and the native reef-builder *Mussismilia hispida* in the south-west Atlantic. *J. Exp. Mar. Biol. Ecol.* 449, 69–76. <http://dx.doi.org/10.1016/j.jembe.2013.08.017>.
- Sih, A., Jonsson, B., Luikart, G., 2000. Habitat loss: ecological, evolutionary and genetic consequences. *Trends Ecol. Evol.* 15, 132–134.
- Strain, E.M., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R.L., Bugnot, A.B., Dafforn, K.A., Heery, E., Firth, L.B., Brooks, P., Bishop, M.J., 2017. Eco-engineering urban infrastructure for marine and coastal biodiversity: which interventions have the greatest ecological benefit? *J. Appl. Ecol.* 55, 426–441.
- Svane, I., Petersen, J.K., 2001. On the problems of epibioses, fouling and artificial reefs, a review. *Mar. Ecol.* 22, 169–188. <http://dx.doi.org/10.1046/j.1439-0485.2001.01729.x>.
- Tilman, D., 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, USA.

- Tupper, M., Hunte, W., 1998. Predictability of fish assemblages on artificial and natural reefs in Barbados. *Bull. Mar. Sci.* 62, 919–935.
- van Treeck, P., Schuhmacher, H., 1999. Mass diving tourism – a new dimension calls for new management approaches. *Mar. Pollut. Bull.* 37, 499–504. [http://dx.doi.org/10.1016/S0025-326X\(99\)00077-6](http://dx.doi.org/10.1016/S0025-326X(99)00077-6).
- Whitmarsh, D., Santos, M.N., Ramos, J., Monteiro, C.C., 2008. Marine habitat modification through artificial reefs off the Algarve (southern Portugal): An economic analysis of the fisheries and the prospects for management. *Ocean Coast Manag.* 51, 463–468. <http://dx.doi.org/10.1016/J.OCECOAMAN.2008.04.004>.
- Whittaker, R.H., 1965. Dominance and Diversity in Land Plant Communities. *Science* 80, 250–260. <http://dx.doi.org/10.2307/1715420>.