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UNDERSTANDING THE IMPACT OF COASTAL DEFENCE STRUCTURES ON MARINE BIOTA. EFFECTS AT LOCAL, REGIONAL AND TROPHIC LEVEL.

Evaluación del impacto de las estructuras de defensa costera sobre la biota marina. Efectos a nivel local, regional y trófico.

PhD Thesis Francisco Sedano Vera 2020

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Universidad de Sevilla

EVALUACIÓN DEL IMPACTO DE LAS ESTRUCTURAS DE DEFENSA COSTERA SOBRE LA BIOTA MARINA. EFECTOS A NIVEL LOCAL, REGIONAL Y TRÓFICO.

UNDERSTANDING THE IMPACT OF COASTAL DEFENCE STRUCTURES ON MARINE BIOTA. EFFECTS AT LOCAL, REGIONAL AND TROPHIC LEVEL.

Tesis presentada para optar al título de Doctor con mención internacional por la Universidad de Sevilla.

Francisco Sedano Vera

Sevilla, septiembre de 2020

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INFORMAN:

Que esta Memoria de Investigación, titulada "*Evaluación del impacto de las estructuras de defensa costera sobre la biota marina. Efectos a nivel local, regional y trófico*", fue realizada por Francisco Sedano Vera bajo su dirección, en el Departamento de Zoología de la Universidad de Sevilla. Considerando que reúne las condiciones necesarias para constituir un trabajo de Tesis Doctoral, autorizan su defensa ante los miembros del Tribunal para optar al título de Doctor con Mención Internacional.

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RESUMEN

El escenario actual de cambio global (ej. aumento del nivel del mar y de los eventos climáticos extremos) y el incremento de la población humana en zonas costeras (con el consecuente aumento en la explotación de recursos costeros) está provocando la introducción de numerosas estructuras artificiales en el medio marino costero. Dichas estructuras proporcionan diferentes servicios como la defensa de la costa o la producción de energía, a expensas de la pérdida de hábitat natural, disminución de la biodiversidad y reducción del valor ecológico de las comunidades marinas entre muchos otros impactos.

En la presente tesis hemos estudiado diversas comunidades bentónicas asociadas a distintas estructuras de defensa costera con la finalidad de incrementar el conocimiento de sus impactos sobre dichas comunidades naturales y contribuir al desarrollo de medidas de ecoingeniería. Nos enfocamos principalmente en el Mar de Alborán y la Bahía de Algeciras, incluyendo tres enfoques: 1) el estudio de la biota bentónica a nivel local, 2) el estudio de la biota bentónica a nivel regional y 3) un estudio trófico a nivel de comunidad y de individuo. A nivel local, los resultados obtenidos nos han permitido identificar factores abióticos y bióticos que determinan la biota sésil, macro- y meiobentónica. A nivel regional hemos podido reconocer patrones en el impacto de estas estructuras, identificar qué estructuras presentan mayor o menor valor ecológico, así como valorar los desafíos a los que se enfrenta el campo de la ingeniería ecológica. Finalmente, hemos descrito potenciales impactos a nivel trófico en una comunidad que a menudo juega papeles importantes en las redes tróficas (los anfípodos) y una especie clave del intermareal (la lapa *Patella caerulea*). Concluimos que las estructuras artificiales están generando una pérdida de biodiversidad a nivel local y regional, determinada por factores abióticos como la composición del sustrato o la rugosidad. Las escolleras de roca natural parecen ofrecer un valor ecológico superior al resto de estructuras artificiales. No obstante, es complicado predecir el impacto de un tipo de estructura concreta, dificultando el establecimiento de medidas de ecoingeniería a nivel global.

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ABSTRACT

The current scenario of global change (e.g. sea level rise and increase of climatic extreme events) and the increase of human population in coastal areas (with the concomitant increase in coastal use) is leading to the introduction of numerous man-made structures into the coastal environment. Those artificial structures provide different services such as coastal protection or energy generation, at the expenses of habitat and biodiversity loss and the reduction of marine communities' ecological value.

This thesis studies diverse benthic communities associated to different coastal defence structures with the aim of increasing knowledge of their impact on these communities and contributing to the development of ecoengineering applications. We have focused on the Alboran Sea and Algeciras Bay, including three approaches: 1) the study of benthic biota at local level, 2) the study of benthic biota at regional level and 3) a trophic evaluation at individual and community level. At local level, the obtained results have allowed us to identify abiotic and biotic factors that structure the sessile, macro- and meiobenthic communities. At regional level, we have recognised some patterns in the impact of these structures, identified which of them possess more ecological value, and highlighted the challenges that ecoengineering faces. Finally, we have described the potential trophic impact on a community that usually plays important roles in the food webs (the amphipod community) and a key intertidal species (the limpet *Patella caerulea*). We conclude that artificial structures are generating biodiversity loss at local and regional levels, determined by abiotic factors such as substrate composition and roughness. Rip-raps made of natural rock seem to have greater ecological value over the rest of artificial structures. However, it is hard to predict the impact of a certain structure, therefore hindering the application of global ecoengineering measures.

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Introducción general

En los últimos años hemos visto un gran auge en el sector urbanístico a nivel mundial. En poco más de cien años, la velocidad de urbanización se ha cuadruplicado y desde el año 1950 la población mundial ha crecido más de un 50 % (Fig. 1). Aunque a una velocidad menor en comparación con el periodo anterior (1950 – actualidad), en los años venideros la tendencia sigue al alza, estimándose una subida desde los 7.7 mil millones actuales hasta 9.7 mil millones en 2050 (UN DESA, 2019). Alrededor del 60% de la población se concentra en zonas costeras (Perkol-Finkel et al., 2018) y se espera que las tasas de crecimiento en esta zona sigan aumentando hasta el año 2050 (Merkens et al., 2016). Esto es debido a que la costa favorece ciertas actividades como el transporte, la explotación de recursos, el desarrollo de industrias o actividades turísticas. El escenario es muy similar en España, la cual también ha experimentado un gran crecimiento poblacional desde 1950 (Fig. 2). Esto ha provocado un gran aumento en la urbanización costera, incluyendo la introducción de numerosas estructuras para la defensa de la costa ante la subida del nivel del mar o eventos climáticos extremos entre otros. Dichas construcciones pueden provocar grandes alteraciones en la costa natural e incluso su destrucción, considerándose una de las principales causas de la pérdida de hábitats poco profundos (Airoldi y Beck

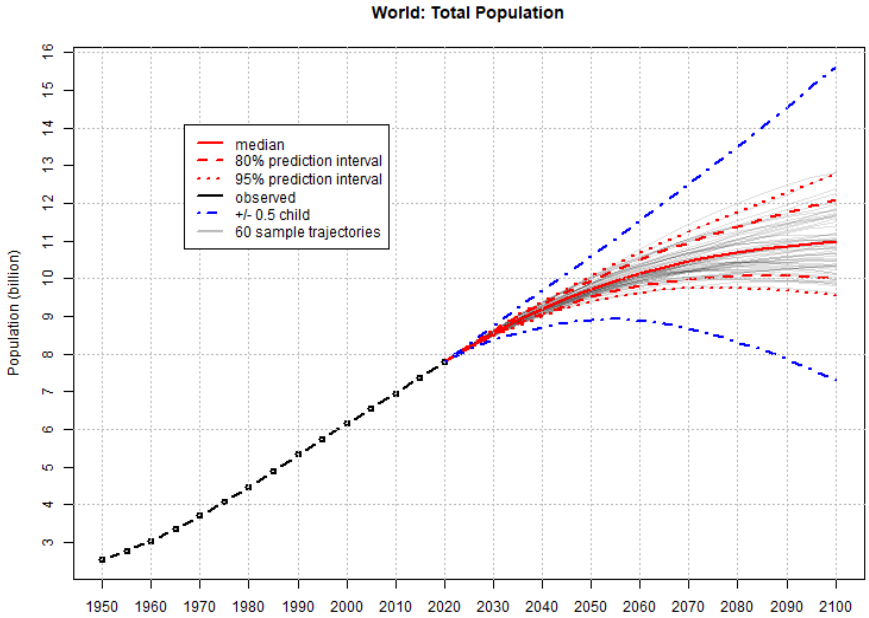

Fig. 1. Crecimiento poblacional observado y estimaciones para el año 2100. Billion: mil millones. Fuente: United Nation, DESA. Population Division. *World Population Prospects 2019. https://population.un.org/wpp*

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2007; Bulleri and Chapman, 2010). Ello conlleva una pérdida de servicios ecosistémicos, que se acentúa con la sobreexplotación de recursos costeros (Agardy y Alder, 2005), cuya demanda aumenta con el mencionado incremento en la población costera (Fig. 3).

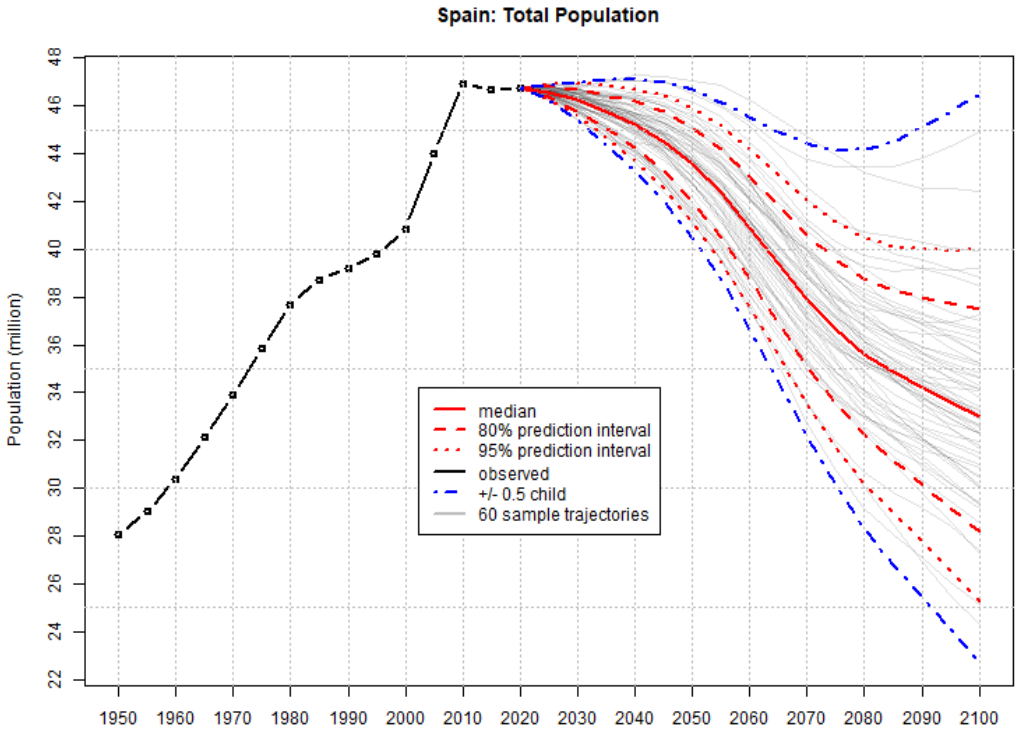

Fig. 2. Crecimiento poblacional observado y estimaciones para el año 2100 en España. Fuente: United Nation, DESA. Population Division. *World Population Prospects 2019. https://population.un.org/wpp*

Los beneficios para el bienestar humano derivados de los servicios ecosistémicos son a menudo menos tangibles que otros intereses económicos más inmediatos (Kansky y Knight, 2014), realzando un conflicto de intereses que pone de manifiesto la importancia de enfocar decisiones medioambientales desde un punto de vista multidisciplinar. Tradicionalmente, en el diseño de estructuras artificiales se contemplan principal o únicamente aspectos físicos como la durabilidad o la disipación del oleaje. El material de construcción más utilizado es el hormigón, y su utilización está tan extendida que en el mundo de la construcción se le denomina al siglo XXI '*el siglo del hormigón en los océanos*' (Mehta, 1991). El cemento Portland

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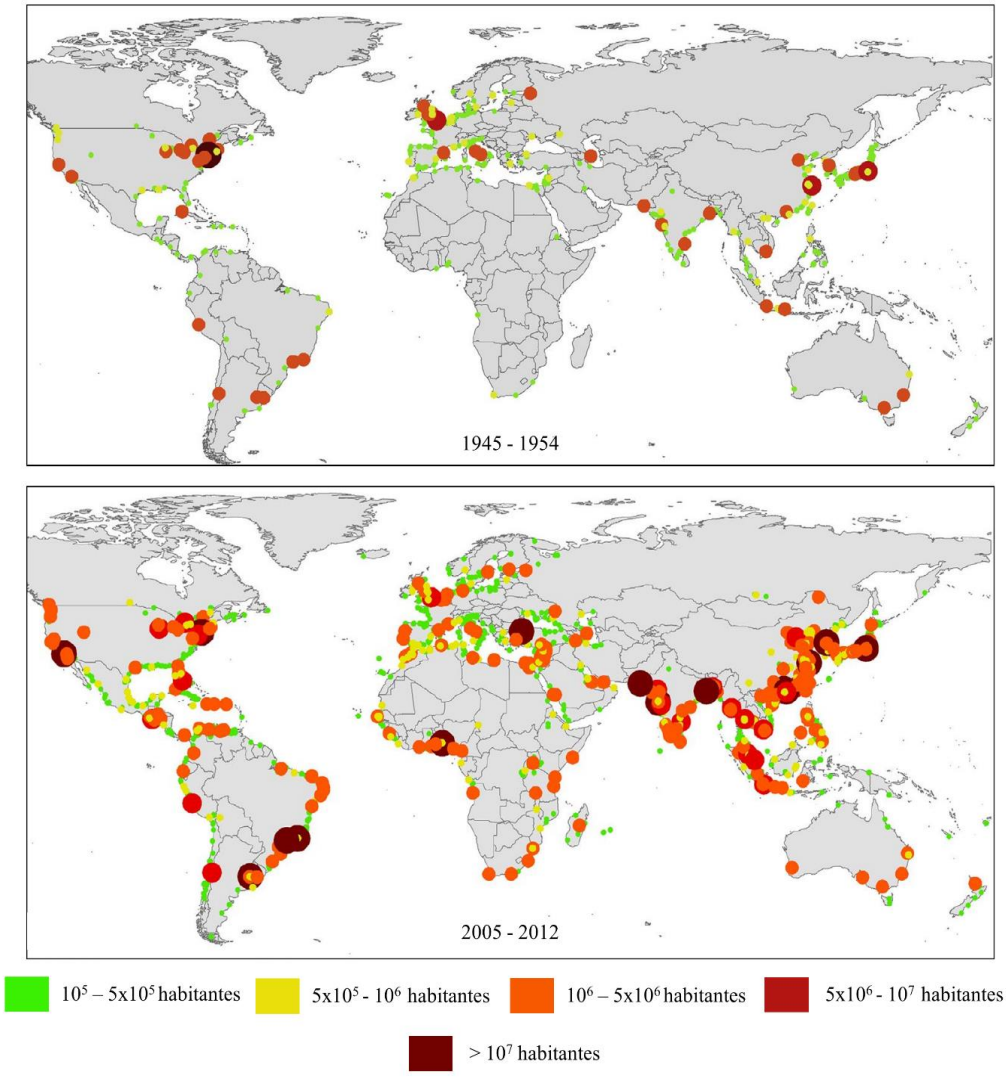

Fig. 3. Representación del aumento poblacional en zonas costeras. Modificado de Barragán et al. (2015).

(principal adhesivo del hormigón) provoca alcalinidades entorno a pH 13 en la superficie de las estructuras de hormigón (Becker et al., 2020) y presenta componentes que son tóxicos para la vida marina (Lukens y Selber, 2004). Además, las estructuras artificiales de hormigón suelen tener superficies lisas y muy inclinadas (franja intermareal reducida) (Loke y Todd, 2016; Moreira et al., 2006). Todo ello provoca que las comunidades que se asientan en este tipo de estructuras sean diferentes (comunidades artificiales) y menos biodiversas en comparación con las asentadas en la roca natural cercana (Bulleri y Chapman 2010; Firth et al., 2016). Debido a ello, con el objetivo de reducir estas diferencias entre las comunidades artificiales y naturales, surge recientemente el campo de la ingeniería ecológica. En este campo, ingenieros, ecólogos

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y *stakeholders* buscan una acción coordinada que promueva el desarrollo urbanístico satisfaciendo ciertos requerimientos medioambientales (Mamo et al., 2018), beneficiando de este modo tanto a la sociedad como al medioambiente.

A medida que se intensifica la urbanización costera, aumenta la presión sobre las constructoras para que incorporen diseños ecológicos (ej. microhábitats, nuevos materiales). Sin embargo, la mayoría de las acciones de ecoingeniería se han llevado a cabo como proyectos piloto, hay pocas directrices para un uso práctico a nivel de usuario (O'Shaughnessy et al., 2019) y hay pocas evidencias de que los diseños desarrollados tengan aplicaciones a nivel global, ya que se desconoce si se obtendrán los mismos resultados bajo condiciones ambientales diferentes. En definitiva, se necesitan más evidencias antes de que los diseños de ecoingeniería se usen con asiduidad (Evans et al., 2019). En este contexto desarrollamos la presente tesis con el **objetivo general** de incrementar el conocimiento sobre los impactos provocados por estructuras de defensa costeras en las comunidades marinas poco profundas del Mar Mediterráneo, con un enfoque particular en el Mar de Alborán y la Bahía de Algeciras. Los datos aquí presentados ayudarán a entender y predecir mejor los efectos de la construcción de estructuras de defensa costera y, por lo tanto, contribuirán al desarrollo de medidas de ecoingeniería destinadas a mitigar dichos impactos.

De la larga serie de impactos que produce la construcción de defensas costeras (Fig. 4), detallamos en los distintos capítulos de esta tesis la pérdida de biodiversidad a nivel local y regional, la pérdida de flora autóctona, los cambios a nivel trófico y los efectos cascada que afectan a niveles de organización superiores. Hemos dividido el trabajo en tres grandes capítulos, cada uno de ellos albergando dos publicaciones específicas y cuyos objetivos e hipótesis presentamos a continuación:

1. **Capítulo 1**: Debido a que la literatura actual raramente incluye la fauna asociada en las comparaciones entre estructuras artificiales y el sustrato natural, nuestro objetivo fue caracterizar dichas comunidades tanto a nivel de especie (usando los anfípodos como modelo) como a nivel de grandes grupos (usando la comunidad asociada al completo), así como identificar los principales factores que las estructuran. Además, enfocamos su estudio a nivel local para evitar el ruido que puedan crear distintas condiciones ambientales y gradientes geográficos.

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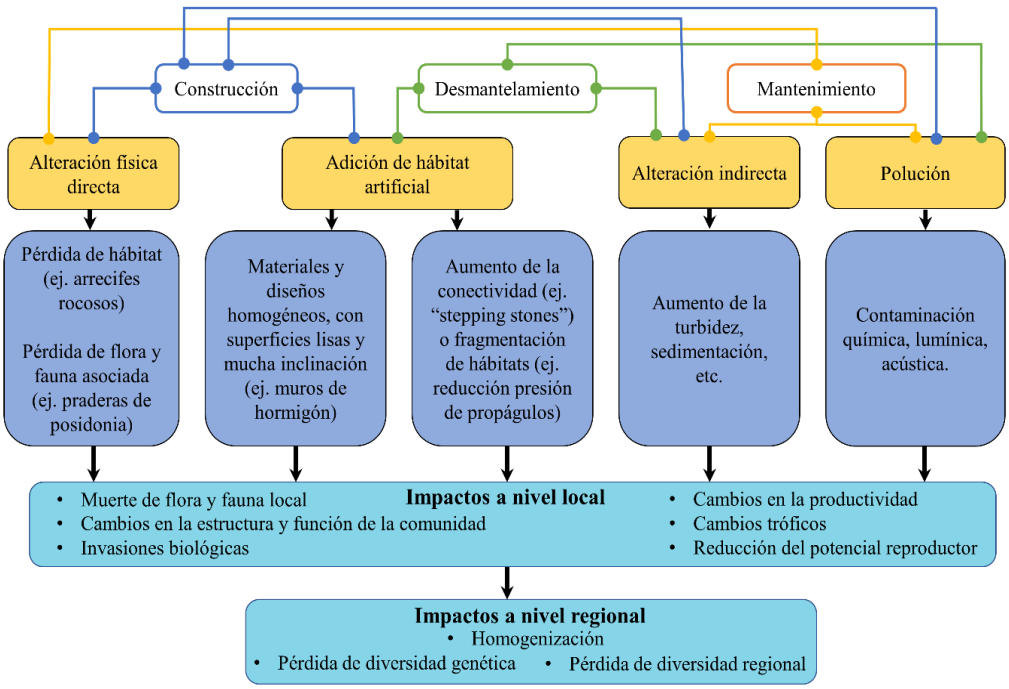

Fig. 4. Modificaciones en el hábitat (cajas naranjas) producidas por las tres fases de ingeniería (*Construcción*, *Mantenimiento* y *Desmantelamiento*). Se incluyen ejemplos de impactos provocados (cajas azules) a nivel local y regional (cajas cian). Fuente: Dafforn et al. (2015).

1.1. En la primera publicación hemos caracterizado cuatro tipos de estructuras artificiales con el objetivo de identificar cuál alberga una comunidad más similar a la de los sustratos rocosos naturales adyacentes. Dicha caracterización incluyó la descripción abiótica de las estructuras y biótica de la comunidad sésil y vágil (macro- y meiofauna) a nivel de grandes grupos con la finalidad de identificar posibles efectos cascada entre distintos niveles de la comunidad. Nuestras hipótesis fueron:

1. Debido a la distinta naturaleza abiótica, la diversidad y estructura de la comunidad de las distintas estructuras artificiales diferirán entre sí y en comparación con el sustrato natural adyacente. Además, las estructuras hormigonadas (acrópodos, cubos y dique vertical) se diferenciarán en mayor medida en comparación con la escollera (estructura artificial de roca natural). Consideramos que la composición y la complejidad estructural afectarán en mayor medida a la comunidad sésil.

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2. Teniendo en cuenta que un aumento de la complejidad estructural a nivel intermareal se relaciona con un aumento de la diversidad, hipotetizamos que las estructuras con mayor microrugosidad tendrán mayor número de taxones que las más lisas.

1.2. El objetivo de la segunda publicación fue confirmar que los patrones observados a nivel de grandes grupos en el capítulo anterior se mantienen a nivel de especie utilizando los anfípodos como modelo, poniendo al mismo tiempo en valor la utilidad de este grupo en el establecimiento de diferencias ecológicas entre tipos de estructuras. Hipotetizamos que la comunidad de anfípodos diferirá entre estructuras y en comparación con el sustrato natural adyacente. Dichas diferencias vendrán determinadas por la naturaleza abiótica del sustrato primario (la estructura artificial en sí), así como por la del sustrato secundario (la comunidad sésil).

2. **Capítulo 2**: Uno de los mayores desafíos de la ingeniería ecológica se encuentra en el establecimiento de diseños o medidas que sean aplicables a nivel global o regional. Es por ello que en el segundo capítulo nos enfocamos en estudiar los impactos de las estructuras artificiales de defensa costera a nivel regional con el objetivo de establecer si su 'comportamiento' es predecible a lo largo de una escala geográfica amplia. Para ello, hemos estudiado dos regiones del Mar Mediterráneo, el Mar de Alborán y la Isla de Creta (Grecia).

2.1. En la primera publicación (enviada a la revista) del segundo capítulo hemos caracterizado la biota intermareal del Mar de Alborán con el objetivo de identificar si la pérdida de biodiversidad asociada a distintas estructuras artificiales se conserva a lo largo de un gradiente geográfico. Nuestras hipótesis fueron:

1. La riqueza intermareal será menor en las estructuras artificiales que en los sustratos naturales más cercanos y este patrón se observará a lo largo del Mar de Alborán independientemente del tipo de estructura.

2. La estructura taxonómica diferirá entre estructuras artificiales y en comparación con el sustrato natural más cercano, siendo los diques verticales los de menor valor ecológico.

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3. Esperamos que los patrones se vean influenciados por la escala espacial del estudio.

2.2. En la segunda publicación hemos caracterizado la biota submareal poco profunda asociada a escolleras a lo largo de la Isla de Creta (Grecia) con la finalidad de profundizar en el conocimiento de esta estructura, ya que tanto nuestros datos como los de otros investigadores coinciden en que este tipo de estructura artificial ofrece mayor valor ecológico que otras estructuras de hormigón (ej. diques verticales). En concreto, nuestro objetivo fue la caracterización de la biota bentónica desde un punto de vista taxonómico y funcional (refiriéndonos a su complejidad tridimensional). Nuestras hipótesis fueron:

1. La estructura de la comunidad y la diversidad diferirá entre las escolleras y el sustrato natural cercano independientemente de la localidad u orientación (Norte/Sur) a lo largo de la isla.

2. Los sustratos naturales tendrán una comunidad más desarrollada desde el punto de vista estructural, albergando mayor cantidad de algas con porte ramificado.

3. **Capítulo 3**: Poco se conoce sobre el impacto que tienen las estructuras artificiales en la estructura trófica de una comunidad o el nicho trófico de un individuo. Es por ello que en este capítulo hemos estudiado la estructura trófica (usando los anfípodos como modelo) y el nicho trófico (usando la lapa *Patella caerulea*) con el objetivo de evaluar si las estructuras artificiales afectan a los mismos.

3.1. En la primera publicación del tercer capítulo hemos caracterizado la estructura trófica y taxonómica de la comunidad de anfípodos asociada al alga *Ellisolandia elongata* en distintas estructuras artificiales a lo largo del Mar de Alborán con el objetivo de evaluar los efectos de éstas sobre la estructura trófica, la abundancia y composición de especies a lo largo de un gradiente geográfico amplio. Nuestras hipótesis fueron:

1. Las estructuras artificiales serán menos diversas y tendrán menores abundancias en comparación con los sustratos naturales adyacentes y por lo tanto tendrán una comunidad estructurada de forma diferente.

2. Las escolleras (estructura artificial de roca natural) serán más similares a los sustratos naturales en comparación con el resto de estructuras artificiales de hormigón.

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3. La estructura trófica (porcentaje de carnívoros, herbívoros, detritívoros y omnívoros) diferirá entre las estructuras artificiales y los sustratos naturales adyacentes.

3.2. En la segunda publicación del tercer capítulo hemos estudiado el nicho trófico (usando el ratio isotópico $\delta^{13}C$ y $\delta^{15}N$) de la lapa *Patella caerulea* en distintas estructuras artificiales a lo largo del Mar de Alborán con el objetivo de identificar posibles cambios en la dieta de esta lapa y por lo tanto evaluar su consideración en la futura gestión de estos animales. De acuerdo con estudios previos, hipotetizamos que las lapas explotarán un nicho trófico diferente en función del tipo de sustrato (artificial vs natural) y de los factores ambientales de la localidad.

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CHAPTER 1: Do different coastal defence structures harbour different marine biota? Lessons at local scale in Algeciras Bay.

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1.1 The role of substrate composition and roughness in structuring sessile, macro- and meiofaunal communities

General hypothesis: Substrate roughness and composition will be the main drivers of the differences (in diversity and community structure) among artificial substrates and in comparison with the natural rock. These two factors will mainly influence the sessile community, possibly inducing cascading effects on higher levels.

1.2 The role of substrate composition and roughness in structuring amphipod communities

General hypothesis: Amphipod assemblages will differ among artificial substrates and in comparison with natural ones. Those differences (community structure and diversity) will be related with the features of the primary (artificial structures) and the secondary (sessile community) substrates.

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CHAPTER 1.1

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1.1 The role of substrate composition and roughness in structuring sessile, macro- and meiofaunal communities

Adapted from: Sedano, F., Navarro-Barranco, C., Guerra-García, J. M., Espinosa, F. (2020). Understanding the effects of coastal defence structures on marine biota: The role of substrate composition and roughness in structuring sessile, macro-and meiofaunal communities. Marine Pollution Bulletin, 157, 111334. https://doi.org/10.1016/j.marpolbul.2020.111334

Abstract

The increasing deployment of artificial structures into the marine environment is creating new hard substrates that differ from natural ones in physical and biological aspects. However, studies of macrofaunal and meiofaunal communities associated with artificial structures are very limited. Seawalls, cubes, acropods and rip-raps in Algeciras Bay (southern Spain) were each compared with the nearest natural hard substrate and their community structure was related to substrate roughness, composition, carbonates content, crystallinity and age, using db-RDA. The results showed clear differences between substrates for the three community levels (sessile, macro- and meiofauna). Overall, rip-raps were the most similar to natural substrates. Under similar environmental conditions, substrate roughness, composition (only for sessile) and age of the structures seemed to play important roles in structuring those communities. They especially affected the sessile community, initiating strong cascading effects that were detectable at high taxonomic level in the associated fauna.

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Introduction

Nowadays, urban infrastructure is significantly increasing along the coast and many natural habitats are being replaced by artificial ones. This creates a strong need for eco-engineering under rigorous experimental frameworks to provide useful information and guidance for managers (Chapman et al., 2018). Marine coastal infrastructures differ from natural hard substrates in several aspects: composition (Coombes et al., 2015), habitat complexity (Loke and Todd, 2016), inclination (Moreira et al., 2006) and even grazing pressure (Ferrario et al., 2016). In some scenarios, they are exposed to different light regimes, hydrodynamics or sedimentation rates (Relini et al., 1994). All these variables have great influence on the settlement and development of benthic communities. Therefore, artificial structures in marine environments cannot be considered surrogates of natural hard substrates (Firth et al., 2016). While most of the studies have focused only on sessile communities (Burt et al., 2009; Cacabelos et al., 2016; Coombes et al., 2015; Moschella et al., 2005), Moura et al. (2008) stated that the vagile fauna should also be considered in the functioning of artificial reefs. However, only few studies have taken the vagile macrofauna (down to 0.5 mm) into account (Carvalho et al., 2013; Lai et al., 2018) and some have even neglected part of the community due to the sampling methodology (e.g. visual counts, photoquadrats) (Bulleri et al., 2005; Cha et al., 2013; Ostalé-Valriberas et al., 2018) or simply because they were not targeted (Moreira et al., 2007; Wehkamp and Fischer, 2013a). Furthermore, meiofaunal communities have also been poorly documented in these kinds of studies (Atilla et al., 2003). Overall, communities on the primary and secondary substrates should be considered when determining their divergence among different artificial structures (People, 2006).

The assessment of habitat quality requires accurate estimates (Beaumont et al., 2007) such as functional approaches (Tillin et al., 2008) or the study of sessile taxa sensitive to disturbances, particularly interesting due to their inability to avoid perturbations (Fa et al., 2002). In some studies, pragmatism (e.g. easy methods and use of high-taxonomic groups) is a priority for labour-saving purposes (e.g. Saiz-Salinas and Urkiaga-Alberdi, 1999) at the expense of accuracy (Beaumont et al., 2007). However, the omission of other community levels

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such as the associated mobile macrofauna may result in biased conclusions when assessing the benthic community (Moura et al., 2008). In fact, it is known that some artificial structures have negative effects on vagile invertebrates (Chapman, 2003), even affecting prey for fish of commercial importance (Cordell et al., 2017). Even so, the literature studying vagile macrofaunal and meiofaunal communities associated to hard infrastructures is very limited (but see Carvalho et al., 2013; Cha et al., 2013). Most of the research has focused on mobile communities associated to soft bottoms affected by coastal infrastructures (Dugan et al., 2011; Martin et al., 2005; Semprucci et al., 2017) or in mobile megafauna (e.g. limpets, starfish, urchins, fish) (Granneman and Steele, 2015; Pereira et al., 2017).

Some studies have demonstrated that differences between natural and artificial substrates at regional scales are hard to predict (Simpson et al., 2017) or can mask the relevance of factors intrinsic to artificial structures (Gacia et al., 2007). In addition, distinctive patterns of colonization can happen as a matter of the interaction of both large- and small-scale processes (Guarnieri et al., 2009). To avoid the interference of external factors over the substrates' features, the different substrates assessed in the present study were adjacent to each other and subjected to similar environmental conditions.

Artificial structures made of concrete (such as cubes or tetrapods) are generally considered to poorly represent the benthic community of nearby natural hard substrates (Ido and Shimrit, 2015). Cubes and tetrapods can have large structural complexity (Dugan et al., 2011) that can increase fish diversity (Wehkamp and Fischer, 2013b) or offer habitat for threatened invertebrates (García-Gómez et al., 2015). However, their smooth surface affects invertebrate larvae settlement (Koehl, 2007), leading to lower diversity values (Moschella et al., 2005). The use of smooth cubes is also not recommended for the settlement of the limpet *Patella ferruginea* (Rivera-Ingraham et al., 2011b), the most endangered invertebrate of the Mediterranean Sea. Similarly, quarried boulders (as the rip-raps of this study), are also reported to have lower biodiversity values (Gacia et al., 2007; Vaselli et al., 2008). However, due to higher microscale roughness and the fact that they are constructed with natural rocks (Liversage and Chapman,

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2018), they can harbour epibenthic communities more similar to natural ones (Gacia et al., 2007; Pister, 2009).

This study aimed to identify which artificial structures are better surrogates of hard natural habitats comparing three different community levels (i.e. sessile taxa and vagile macro- and meiofauna). The main drivers of differences among structures were identified and discussed, arising relevant information for the field of ecological engineering. More specifically, we hypothesized that:

1. Given the fact that different hard substrates lead to different communities (Bulleri and Chapman, 2010; Perkins et al., 2015) and that materials of construction (Ido and Shimrit, 2015) and complexity (Coombes et al., 2015; Sempere-Valverde et al., 2018) play important roles in their development, we hypothesized that community structure and diversity measures would differ among substrates. Also, concrete-based structures (seawall, cube and acropod) would be more similar among them than in comparison with natural rockbased substrates (rip-rap and natural rock). Furthermore, both composition and complexity would drive those differences more strongly over the sessile compartment.
2. Taking into account that higher microscale roughness and the addition of complexity is related to increasing taxa richness in the intertidal environment (Evans et al., 2016; Firth et al., 2014a), we hypothesized that structures with higher microscale roughness would have higher number of taxa at the three community levels studied.

Furthermore, we approached the study of macro- and meiofauna levels using mixed coarse taxonomic resolution (Chapman et al., 2005) to support this procedure when facing taxonomically challenging groups in the assessment of artificial structures. The results will be of interest for management authorities that pursue the inclusion of simple but reliable procedures into monitoring programs.

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Materials and methods

Study area and environmental data

Algeciras Bay is located in the North coast of the Strait of Gibraltar. This Strait is a marine biodiversity hotspot with highly diverse and well-structured marine communities (García-Gómez et al., 2003) due to the confluence of two biogeographical realms (Mediterranean and North Atlantic) (Costello et al., 2017). Its biodiversity and ecology have been the focus of numerous studies in the last decades (Guerra-García et al., 2009). Algeciras Bay is an important industrial area, with chemical factories, refineries, thermal power plants, iron works, paper mills and shipyards, along with a major port (Conradi et al., 1997), which makes this bay a suitable area for studying the effects of anthropogenic disturbances. Algeciras Harbour is in the West side of the Bay (Fig. 1). Its shipping activities have increased since its construction, surpassing in 2017 100 mT of freight, becoming the fifth biggest harbour in Europe (*www.ec.europa.eu/eurostat/*).

Our study area comprises four different coastal defence structures (seawall, cubes, acropods and rip-raps) that surround the harbour, and the nearest natural rocky shore as control habitat. All substrates (artificial and natural) are located within approximately 1 km. According to previous studies, all the habitats sampled showed similar annual averages of dissolved organic matter, silting, hydrodynamics, suspended solids and temperature (Carballo et al., 1996). This allowed us to explore substrate influence on biotic communities avoiding other confounding environmental effects.

Biotic analyses

In January 2017, each substrate (four artificial and the natural control, Fig. 1) was sampled allocating three random sites within it. At each site, three 20 × 20 cm quadrats were scraped and preserved in 96% alcohol until laboratory analyses. Therefore, the experimental design used in the statistical analyses had two factors: 'Habitat' (Ha), a fixed factor with five levels (*Natural*, *Rip-rap*, *Acropod*, *Cube* and *Seawall*) and 'Site' (St), a random factor with three levels (*Site 1*, *Site 2*, *Site 3*) nested in Ha. Samples were taken over vertical surfaces of each

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substrate during low tide at low intertidal zone (5–30 cm over the lowest tidal level). In the laboratory, all sessile fauna and flora were volumetrically quantified and identified to the lowest possible taxonomic resolution. Some taxa (*Spirobranchus* sp./*Dendropoma* sp. and *Gelidium* sp./*Caulacanthus* sp.) were quantified together and referred to as *Spirobranchus* sp./*Dendropoma* sp. reef and *Gelidium* sp./*Caulacanthus* sp. turf in the results, given the difficulty of measuring them individually. Each sample was sieved through a 0.5 mm mesh in order to obtain associated macrofauna and through a 34 μm mesh in order to retain meiofauna. Macro- and meiofauna were sorted into "High-Taxonomic Groups" (HTGs) (Timms et al., 2013). This "low" taxonomic resolution has been frequently used to assess differences in the structure of benthic communities (see Otero-Ferrer et al., 2019).

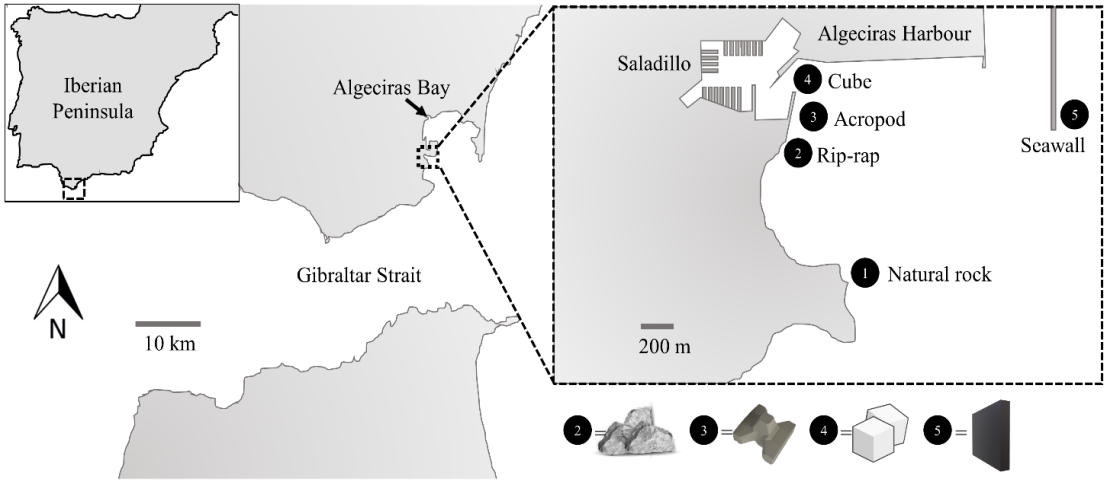

Fig. 1. Location of Algeciras Bay in the Strait of Gibraltar showing the five sampled habitats (1–5).

Since meiofaunal abundances were much over > 2000 individuals per sample, samples were resuspended with a circular movement in a known volume and subsamples of 3 ml were taken for analysis (Danovaro et al., 2003). Abundances of each identified taxon were counted and, based on these data, the number of taxa (S) and Shannon-Wiener diversity (H′) were calculated. To test for differences in S and H′ between substrates, we applied two-way ANOVA when there was homogeneity of variances (i.e. for sessile community) and generalized linear mixed models (GLMMs) when there was heteroscedasticity. For every analysis the same above-mentioned design was used. Homogeneity of variances was confirmed using Cochran's test. When ANOVA detected significant differences for a given factor, the source of difference was identified by applying the Student–Newman–Keuls (SNK) test. For the associated communities

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(macro- and meiofauna), univariate tests were performed using GLMMs including the effect of scraping volume (covariate) in the models. A number of taxa (counts) were fitted to Poisson distribution while Gaussian distribution was used for Shannon's diversity. The absence of overdispersion of residuals was confirmed with Shapiro-Wilk tests. When no variance was detected among sites, random effects ('Site' factor) were not included in the model and the significance level was lowered to $p < 0.01$ to reduce Type I error. Two-way ANOVAs were carried out with GMAV5 software (Underwood et al., 2002), while GLMMs were conducted with Rstudio v.1.2.5001.

PERMANOVA was run to evaluate differences in community structure based on a Bray-Curtis similarity matrix derived from square root transformed data. Non-metric multidimensional scaling (nMDS) was used to visualize patterns in community structure between substrates. To account for the variance in vagile taxa abundances and composition dependent on the volume of sessile scrapes, the total volume of each scrape was used as covariate in the statistical analyses. Bray-Curtis dissimilarity between substrates (natural vs each of the artificial ones) was also calculated with SIMPER (SIMilarity PERcentages) using standardized (by scraped volume) abundance data (except for sessile community) and square root transformation. Analyses were carried out using PRIMER v.6 + PERMANOVA package (Clarke and Gorley, 2006).

Abiotic analysis

Lithologic nature of each substrate was also characterized. Three chips from each substrate were powdered in the laboratory using a ball mill with stainless steel balls as grinding media. The elemental composition and calcination percentage of each sample was quantified by Xray fluorescence (XRF) using an AXIOS spectrometer. Mineralogic absorption spectra were

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detected by X-ray diffraction (XRD) using a powder diffractometer (Bruker D8 Advance) equipped with a high temperature chamber (Anton Paar XRK 900) and a fast response/high sensitivity detector (Bruker Vantec 1) with radial Soller slits (full methodology can be accessed in Valverde et al., 2015). Afterwards, XRF and XRD data were interpreted to quantify the crystallinity and lithology composition of each sample using DRIFAC.EVA.4.1 program. Differences in mineralogic content between substrates were graphically represented using nMDS based on a Euclidean Distance similarity matrix of untransformed data.

Additionally, wave exposure was quantified at each habitat based on a fetch model index developed by Howes et al. (1994). Fetch models have been successfully used to predict marine community patterns (e.g. Ros et al., 2016) by providing quantitative estimates of wave exposure using a combination of two indices: maximum fetch and modified effective fetch. Maximum fetch is defined as the maximum fetch distance in km measured from the point of interest. When a vector does not find and obstacle (i.e. open ocean occurs), a value of 1000 km is conventionally used. Effective fetch (Fe) is calculated from the equation: $Fe = [\Sigma(\cos \Theta i) \times Fi] / \Sigma \cos \Theta i$, where Θi is the angle between the shore-normal and the directions 0°, 45° to the left and 45° to the right, and Fi is the fetch distance in km along the relevant vector. Combining the values obtained for each index, wave exposure class of each habitat was determined based on the classification proposed by Howes et al. (1994).

We carried out a constrained ordination approach to assess how well the biological data relate to different abiotic variables that characterize the different substrates. We considered calcination percentage (carbonates content), roughness (macro- and microscale), crystallinity, age and elemental composition (only elements with a relevant concentration over 3%: silicon, calcium and magnesium; full composition in Supplementary Table 1). Age of the different artificial structures was quantified based on the date of construction. Since it is difficult to infer the age of natural substrates, for analytic purposes, we chose the oldest possible date in the same order of magnitude than the oldest artificial structure. Macroscale roughness was calculated over 15 m length transects. Three transects were selected at each substrate and a flexible meter was laid directly over it, trying to conform as closely as possible to all contours

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of the bare substrate. Regarding microscale roughness, three 15 cm profile gauges with 0.5 mm pins were pushed onto the bare rock to record the surface of each substrate (Frost et al., 2005). The resulting profiles were photographed, and the images were digitally processed with Adobec Photoshop to obtain two coloured images (Fig. 2A). The length of the contour of the profile was obtained with ImageJ software. In both cases (macro- and microscale), substrate roughness was calculated as in Rivera-Ingraham et al. (2011a, 2011b) using the equation by Blanchard and Bourget (1999): Roughness = Tr / Ts, where Tr is the contour measured between two points and Ts the linear distance between those points.

A Principal Component Analysis (PCA) ordination, performed on normalized data, was used to display the relationship between substrates according to elemental composition, calcination percentage, macro- and microscale roughness, crystallinity and age. To explore relationships between abiotic and biotic (sessile, associated vagile macrofauna and meiofauna) data, we used distance-based Redundancy Analyses (dbRDA). dbRDA was chosen over Canonical Correspondence Analyses (CCA) since data fitted a linear species response. Linearity was deducted as in Ter Braak and Smilauer (1998) according to the first axis length in Detrended Correspondence Analysis (DCA) (< 3, linear;>4, unimodal). Prior to analyses, multicollinearity between abiotic factors was tested using Draftsman plots based on Spearman correlation. Only one abiotic factor was used in the analyses when there were high pairs of correlation. If the constrained ordination still portrayed collinearity between abiotic factors, the variable most affected was eliminated attending to Variance Inflation Factor (VIF) in order to avoid misinterpretation of data due to unstable canonical coefficients (Ter Braak, 1988). Collinearity was neglected when VIF < 10 according to Dormann et al. (2013). dbRDA was run using square root transformed biological matrix paired with standardized abiotic matrix. In addition, significance levels ($p < 0.05$) were calculated under 1000 random permutations. The relationship between biotic data and abiotic variables were portrayed using dbRDA biplots. DCA and dbRDA analyses were carried out

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using RStudioc Version 1.1.453. PCA and Draftsman Plot were carried out using PRIMER v.6 + PERMANOVA package (Clarke and Gorley, 2006).

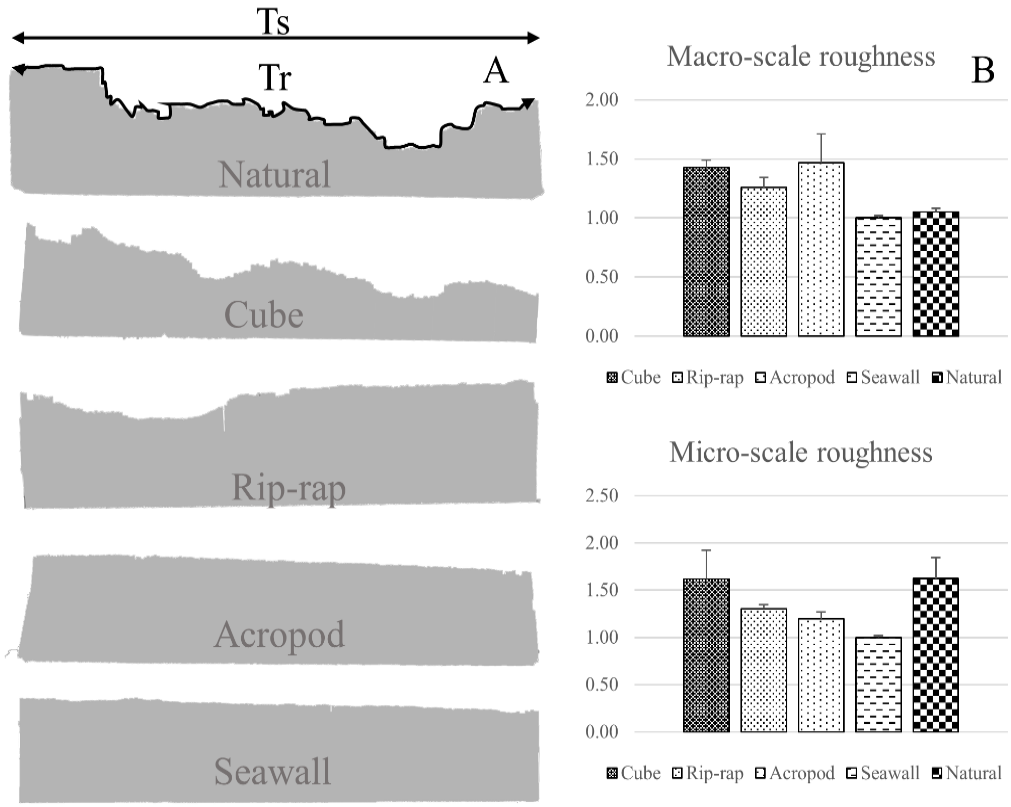

Fig. 2. A: Sample images of profiles measured at the five different substrates to obtain microscale roughness using the formula: Roughness = Tr / Ts, where Tr is the total length of the contour and Ts is the linear distance between two points. B: Histograms for average macro- and microscale roughness. Bars represent standard deviations.

Results

Characterization of each structure

To characterize the various substrates sampled, different abiotic measurements were taken into account (Table 1). Although wave exposure (measured as Fetch index) slightly differed between substrates, all substrates were qualitatively classified as semiexposed (after Howes et

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al., 1994) (see Table 1). Elemental and mineralogical composition clearly varied among substrates (Fig. 3).

Biotic analyses: how do different community levels vary between substrates?

The sessile community comprised 15 taxa (*Mytilus galloprovincialis*, *Spirobranchus* sp./*Dendropoma* sp. reef, *Calpensia* sp., *Perforatus perforatus*, *Pyura dura*, *Ulva* sp., *Rugulopteryx okamurae*, *Ceramium* sp., *Ellisolandia elongata*, *Gelidium* sp./*Caulacanthus* sp. turf, *Jania rubens*, *Laurencia* sp. and *Lithophyllum incrustans*). Presence and dominance of each taxa differed clearly according to the substrate type (Fig. 4). Natural substrates were characterized by a dominance of the calcareous turf alga *E. elongata* and the scarcity of gregarious species such as *P. perforatus* and *M. galloprovincialis*. Seawalls presented the opposite pattern with a dominance of *P. perforatus* and *M. galloprovincialis* while *E. elongata* was absent.

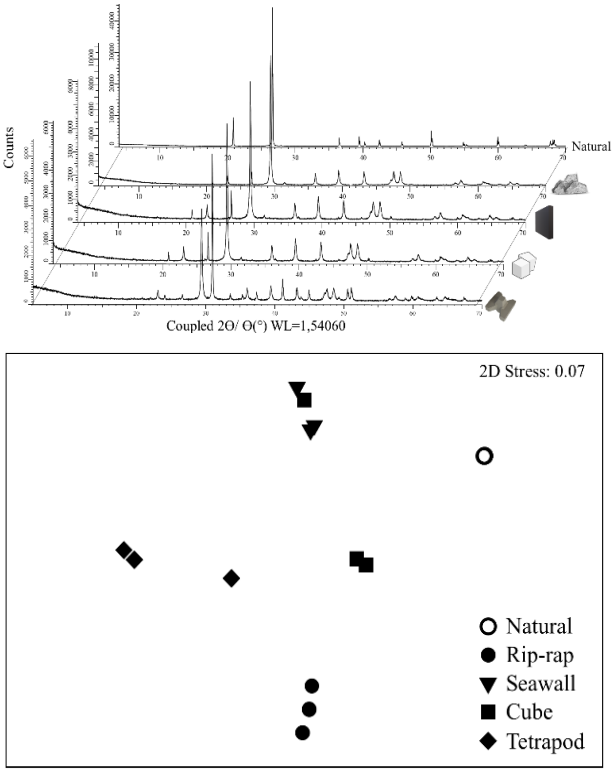

Fig. 3. Up: X-ray diffractograms obtained for one replicate of each substrate. Down: Two dimensional nMDS portraying the differences in mineralogical content between replicates of each substrate (full data in Supplementary Table 2). The three replicates of natural substrate are superimposed due to its homogeneous composition.

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Table 1: Location and descriptors of five different substrates sampled. Macro: macroscale roughness; Micro: microscale roughness; n.a.: not applicable.

	Natural	Rip-rap	Cube	Acropod	Seawall
Latitude	36°06'34.1"N	36°07'01.2"N	36°07'12.1"N	36°07'03.2"N	36°07'00.5"N
Longitude	5°25'55.4"W	5°26'07.9"W	5°26'07.6"W	5°26'07.4"W	5°25'02.4"W
Date of deployment	n.a.	1997	1955	1997	2008
Distance from natural rock	n.a.	0.90 km	1.19 km	0.96 km	1.50 km
Effective fetch (km)	95.79	116.52	74.66	116.52	43.15
Wave exposure class	Semi-exposed	Semi-exposed	Semi-exposed	Semi-exposed	Semi-exposed
Mayor component	Quartz	Calcite	Quartz-Calcite	Dolomite	Magnesium calcite
Macro (average ± SD)	1.05 ± 0.03	1.26 ± 0.09	1.43 ± 0.06	1.47 ± 0.24	1.00 ± 0.01
Micro (average ± SD)	1.62 ± 0.22	1.30 ± 0.04	1.62 ± 0.31	1.20 ± 0.07	1.00 ± 0.01

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The sessile community of rip-raps was also dominated by *E. elongata* while cubes had abundant *P. perforatus* with patches of *E. elongata* and *M. galloprovincialis*. Acropods held the most heterogenous sessile community, characterized by abundant patches of *P. perforatus*, *E. elongata* and *Spirobranchus* sp./*Dendropoma* sp. reef depending on the site (although differences were not statistically significant between sites; data not shown).

As in the nMDS plot (Fig. 4), SIMPER analyses (Table 2) showed that rip-raps supported the least dissimilar sessile communities compared with natural substrates, while seawalls were the most dissimilar. PERMANOVA further confirmed differences in community structure composition, showing significant differences among substrates but not within sites of each substrate (see pair-wise tests in Table 3). In addition, sessile communities on natural substrates were richer compared with each of the artificial substrates. In contrast, due to the high dominance of *E. elongata* (Table 2, Supplementary Table 3), natural and artificial substrates had similar Shannon's diversity values (Fig. 5, Supplementary Table 4).

Regarding associated macrofauna, 16 major taxonomic groups were identified (Cnidaria, Platyhelminthes, Nemertea, Sipuncula, Bivalvia, Gastropoda, Polyplacophora, Annelida, non-Caprellidae Amphipoda, Caprellidae, Decapoda, Isopoda, Tanaidacea, Echinoidea, Pycnogonida and Insecta). Except Caprellidae, Insecta and Polyplacophora (absent from seawalls) and Nemertea (absent from rip-raps), all macrofaunal groups were present in the different substrates. In fact, number of taxa in natural substrates was only marginally higher compare with cubes (Fig. 5, Supplementary Table 4). However, clear differences in taxa abundances were recorded (Fig. 4, Supplementary Table 1). This translated into significant differences in Shannon diversity values, being significantly higher in cubes, acropods and rip-raps. Even with the addition of the covariate (that was highly significant), there were significant differences in communities between natural substrates and acropods, cubes and seawalls, but not with rip-raps (see PERMANOVA in Table 3). Natural substrates were dominated by non-caprellid amphipods together with other peracarids such as isopods, tanaids and caprellids. Gastropods and annelids (mainly polychaetes) were also quite abundant compared with the rest of taxa. Seawalls were dominated by non-caprellid amphipods, isopods and annelids

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(Supplementary Table 1), while the rest of taxa were represented by few individuals. As it can be inferred in the nMDS plot (Fig. 4), cubes, acropods and rip-raps held similar associated macrofaunal communities and abundances, dominated by non-caprellid amphipods, isopods, gastropods, bivalves and annelids. When compared with natural substrates, average similarities were quite high (Table 2), being the macrofaunal communities of rip-raps the most similar to the natural ones.

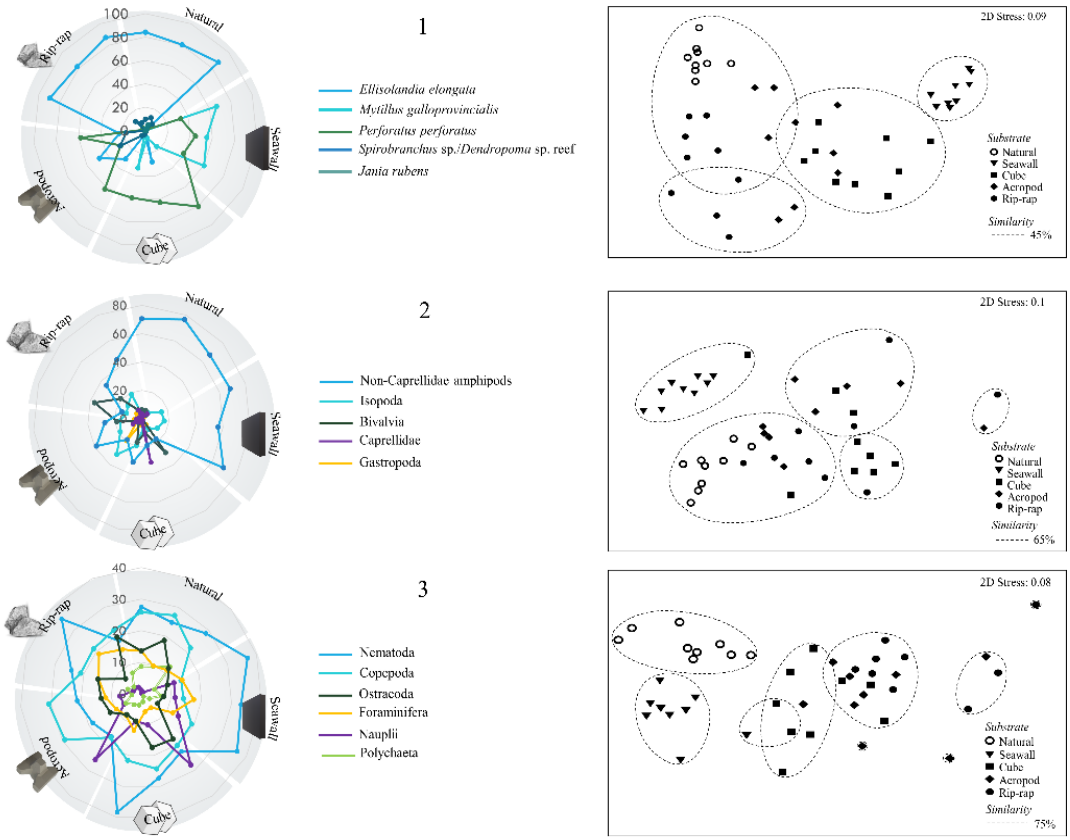

Fig. 4. Left: Average abundance percentage per sites for the three community levels studied (1: sessile, 2: associated macrofauna, 3: associated meiofauna). Taxa with very low representation are not shown. Right: nMDS plots portraying differences at community structure level among substrates.

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Table 2: Results of SIMPER analysis comparing the control habitat (natural rock) with each of the artificial substrates. Data were square root transformed. Associated fauna was standardized using the volume of each scrape. A 90% cut-off for low contributions to dissimilarity has been applied. Diss.: Average dissimilarity; %: Contribution; *S/D* reef: *Spirobranchus* sp./ *Dendropoma* sp. reef; *galloprovin.*: *galloprovincialis*; Non-C Amp.: Non-Caprellidae amphipods.

Sessile community					
Groups ***Natural*** *&* ***Rip-rap***			*Groups* ***Natural*** *&* ***Acropod***		
Average dissimilarity = 74.65%			Average dissimilarity = 77.21%		
Species	Diss.	%	Species	Diss.	%
E. elongata	61.74	82.71	*E. elongata*	51.98	67.33
S/D reef	7.39	9.90	*P. perforatus*	13.5	17.58
			S/D reef	7.44	9.64
Groups ***Natural*** *&* ***Cube***			*Groups* ***Natural*** *&* ***Seawall***		
Average dissimilarity = 93.05%			Average dissimilarity = 99.39%		
Species	Diss.	%	Species	Diss.	%
E. elongata	61.85	66.47	*M. galloprovin.*	40.43	40.68
P. perforatus	15.85	17.04	*P. perforatus*	30.39	30.58
S/D reef	6.93	7.45	*E. elongata*	24.03	24.18
Associated macrofauna					
Groups ***Natural*** *&* ***Rip-rap***			*Groups* ***Natural*** *&* ***Acropod***		
Average dissimilarity = 36.03%			Average dissimilarity = 36.82%		
Species	Diss.	%	Species	Diss.	%
Non-C. Amp.	7.04	19.53	Non-C. Amp	11.13	30.22
Isopoda	6.20	17.20	Isopoda	3.94	10.70
Bivalvia	5.08	14.10	Bivalvia	3.10	8.41
Insecta	3.04	8.43	Gastropoda	2.44	6.64
Caprellidae	2.18	6.04	Pycnogonida	2.25	6.11
Gastropoda	2.16	5.98	Polyplacophora	1.82	4.94
Annelida	2.13	5.90	Tanaidacea	1.76	4.79
Tanaidacea	1.89	5.24	Annelida	1.74	4.72
Polyplacophora	1.73	4.80	Caprellidae	1.65	4.47
Pycnogonida	1.47	4.07	Insecta	1.62	4.40
			Platyhelminthes	1.44	3.92
			Nemertea	1.41	3.84
Groups ***Natural*** *&* ***Cube***			*Groups* ***Natural*** *&* ***Seawall***		
Average dissimilarity = 39.37%			Average dissimilarity = 46.08%		
Species	Diss.	%	Species	Diss.	%
Non-C. Amp.	12.92	32.38	Non-C. Amp.	12.36	26.82
Bivalvia	4.31	10.94	Bivalvia	6.11	13.25
Caprellidae	3.56	9.04	Caprellidae	5.14	11.16
Pycnogonida	2.80	8.43	Gastropoda	4.98	10.80
Gastropoda	2.25	5.73	Pycnogonida	3.45	7.50
Annelida	2.25	5.72	Annelida	2.71	5.89
Tanaidacea	2.13	5.41	Insecta	2.16	4.68
Isopoda	1.93	4.91	Tanaidacea	1.89	4.09
Insecta	1.71	4.34	Isopoda	1.89	4.09
Decapoda	1.07	2.72	Polyplacophora	1.03	2.22

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Associated meiofauna					
Groups ***Natural*** *&* ***Rip-rap***			*Groups* ***Natural*** *&* ***Cube***		
Average dissimilarity = 28.63%			Average dissimilarity = 28.65%		
Species	Diss.	%	Species	Diss.	%
Copepoda	3.27	10.43	Nauplii	4.49	17.43
Ostracoda	3.06	10.67	Nematoda	2.92	10.18
Polychaeta	2.77	9.69	Copepoda	2.81	9.82
Nematoda	2.70	9.42	Polychaeta	2.67	9.32
Foraminifera	2.59	9.06	Ostracoda	2.36	8.24
Mollusca	1.95	6.80	Non-C. Amp.	1.75	6.10
Acari	1.90	6.64	Foraminifera	1.68	5.88
Nauplii	1.78	6.23	Mollusca	1.36	4.76
Non-C. Amp.	1.42	4.96	Kinorhyncha	1.31	4.57
Kinorhyncha	1.27	4.44	Insecta	1.22	4.25
Turbellaria	1.26	4.42	Acari	0.97	3.40
Insecta	1.00	3.48	Oligochaeta	0.89	3.12
Isopoda	0.84	2.94	Caprellidae	0.82	2.87
			Turbellaria	0.72	2.51
Groups ***Natural*** *&* ***Acropod***			*Groups* ***Natural*** *&* ***Seawall***		
Average dissimilarity = 31.07%			Average dissimilarity = 37.49%		
Species	Diss.	%	Species	Diss.	%
Nematoda	3.91	12.58	Copepoda	5.25	14.00
Nauplii	3.75	12.08	Ostracoda	4.44	11.84
Copepoda	3.69	11.89	Polychaeta	3.89	10.39
Polychaeta	3.14	10.10	Nematoda	3.66	9.76
Ostracoda	2.98	9.59	Nauplii	3.00	8.00
Foraminifera	2.37	7.63	Foraminifera	2.49	6.64
Mollusca	1.71	5.51	Mollusca	2.37	6.32
Non-C. Amp.	1.63	5.23	Acari	1.83	4.89
Kinorhyncha	1.43	4.61	Kinorhyncha	1.61	4.27
Acari	1.19	3.84	Insecta	1.49	3.98
Insecta	1.11	3.56	Non-C. Amp.	1.47	3.93
Tanaidacea	1.04	3.35	Nemertea	1.11	2.96
Caprellidae	0.70	2.24	Caprellidae	0.96	2.56
			Tardigrada	0.95	2.52

At meiofaunal level, 19 major taxonomic groups were identified (Foraminifera, Cnidaria, Turbellaria, Nemertea, Nematoda, Kynorhyncha, Tardigrada, Mollusca, Polychaeta, Olygochaeta, Ostracoda, Copepoda, non-Caprellidae Amphipoda, Caprellidae, Isopoda, Tanaidacea, Pycnogonida, Acari and Insecta). PERMANOVA results (Table 3) confirmed that community structure differed between natural and the rest of artificial substrates. These differences relied mainly on different abundances of the dominant groups (nematodes, copepods, polychaetes, ostracods and foraminifers) (Table 2). As for sessile and vagile macrofaunal levels, rip-raps were the least dissimilar structure (Table 2), since they harboured

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very similar nematode/copepod ratios and shared similar abundances of polychaetes, ostracods and foraminifers. In contrast, the presence of kynorhynchs was restricted to natural substrates (except for one replicate of rip-raps). The most dissimilar substrate was the seawall, that compared with the other substrates, held high nematode/copepod ratios (data not shown) and higher abundances of tardigrades, turbellarians and nemertines (exclusively found in seawalls). Number of taxa was significantly higher in natural substrates in comparison with acropods and marginally higher in comparison with cubes and rip-raps (Fig. 5, Supplementary Table 4). There were no differences regarding Shannon's diversity.

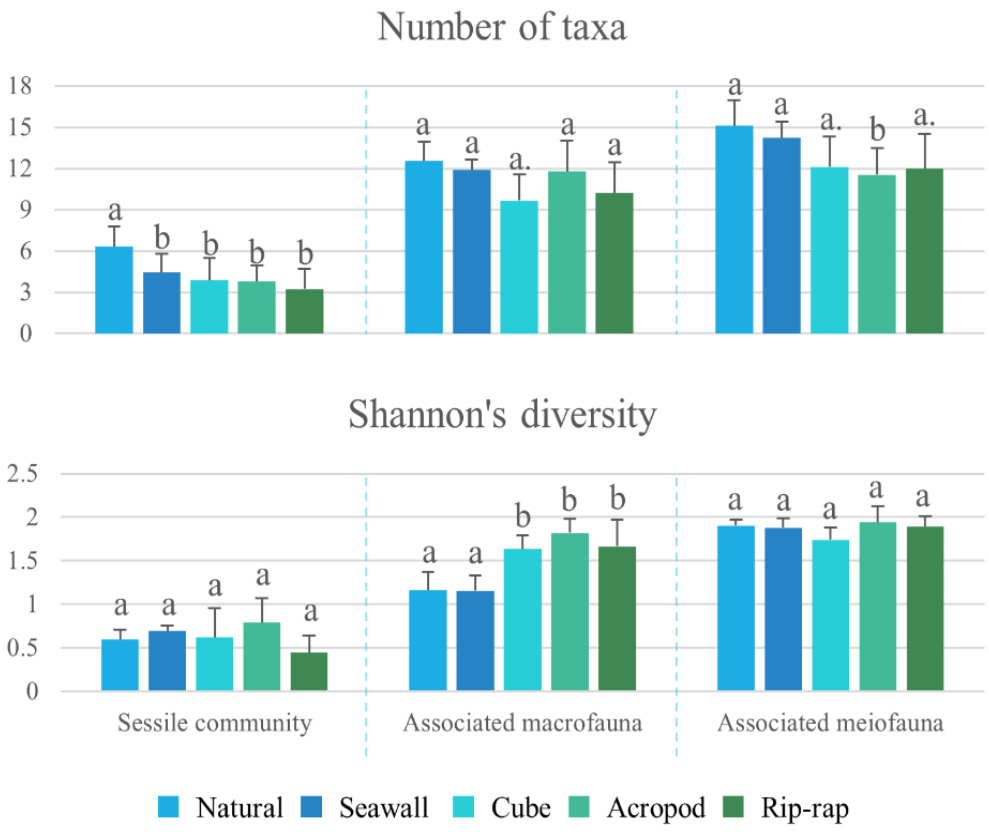

Fig. 5. Average taxa richness (number of taxa / replicate) and Shannon's diversity of the five different substrates at the three community levels studied. Letters 'a' and 'b' represent significant differences ($p < 0.05$), 'a.' represents marginal differences ($p < 0.1$) for the comparison between natural and each of the artificial substrates. Bars indicate standard deviation.

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Abiotic analyses: which abiotic factors play a role in structuring the communities in different substrates?

PCA results (Fig. 6) showed clear differences among substrates according to the abiotic characteristics measured. Axis 1 explained 65.2% of the total variance and correlated with CP (−0.42), silicon (0.42), crystallinity (0.39), age (0.38) and macroscale roughness (0.38); axis 2 explained 16.4% of the total variance and correlated with microscale roughness (0.74; $p < 0.05$) and magnesium (0.53; $p < 0.05$), while axis 3 explained 12.0% of the total variance and correlated with magnesium (0.64; $p < 0.05$), calcium (−0.52; $p < 0.05$) and microscale roughness (−0.35). Natural substrates were clearly separated along axis 1 from the rest of substrates, characterized by very low calcination percentages (indicative of very low concentration of carbonates), high silicon contents (from quartz origin), a greater crystalline structure and macroscale roughness (Fig. 2B), and an older age. Separation among different artificial substrates was also clear along axis 3. Seawalls and acropods had higher magnesium content and lesser microscale roughness as opposed to rip-raps and cubes that had higher calcium content and were more heterogeneous at microscale level.

As seen in the Draftsman's plot (Fig. 6), calcination percentage (CP) was highly correlated with most of the other abiotic variables. In the same way, silicon (Si) was positively correlated with crystallinity (Crystall.) and negatively correlated with calcium (Ca) and CP. These correlations were not surprising since the substrates with higher quartz content bore high percentages of Si and fewer Ca, providing a more crystalline structure and therefore less carbonates content (indicative of low CP). Therefore, CP and Si were eliminated to avoid multi collinearity between predictor variables.

Results of dbRDA (Fig. 7) for the sessile community after the VIF routine (see Materials and methods section) yielded a set of minimum abiotic variables (macro, micro, crystall., age and calcium) that best explained the biotic data. The resulting model was highly significant ($p < 0.001$, Table 4) and accounted for 78.3% of total inertia. According to the marginal effects, only crystallinity was not significantly correlated with the biotic data.

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The sessile community on seawalls appeared to be strongly correlated with the absence of physical attributes (macro- and microscale roughness) and a younger age. Cubes were correlated with a higher Ca content and microscale roughness, and were separated from rip-rap and acropod communities mainly by macroscale roughness and age. Low Ca content, older age and higher macroscale roughness were the main drivers separating the community of natural substrates. In the same way, dbRDA for vagile macrofauna yielded a highly significant model ($p < 0.01$) of abiotic variables that accounted for 70.9% of total inertia. Only the marginal effects of physical attributes (macro- and microscale roughness) and age were significantly correlated with the biotic data. The arrangement of substrates along the axes of dbRDA was very similar to that of the sessile community. In particular, the vagile macrofauna of rip-raps correlated better with the same abiotic factors than natural substrates (age and macroscale roughness).

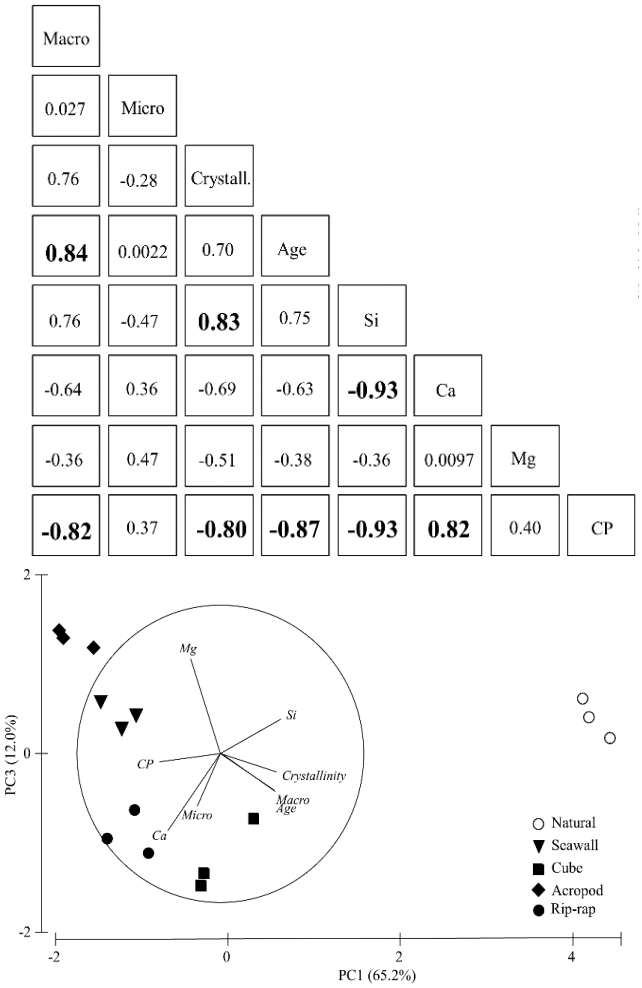

Fig. 6. Up: Draftsman's plot with pairs of correlation between the abiotic variables studied. Numeric values indicate correlation coefficients. Bold numbers represent coefficients higher than 0.80. Down: Principal components analysis (PCA) results for the abiotic variables studied across the different substrates. The percentage of variation explained by axis 1 and 3 is given. Since axis 2 and 3 accounted for very similar percentages of variation explained (16.4% and 12% respectively), we chose to represent axis 3 for graphical convenience. Macro: macroscale roughness; Micro: microscale roughness; Crystall.: crystallinity; CP: calcination percentage.

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Regarding the meiofauna, the model of abiotic variables accounted significantly ($p < 0.01$) for 74.5% of the total inertia, although only the marginal effects of microscale roughness and age were significantly correlated. Cubes, acropods and rip-raps separated along axis 1 for their higher microscale roughness, whereas seawalls and natural substrates did along axis 2 for their younger and older age respectively.

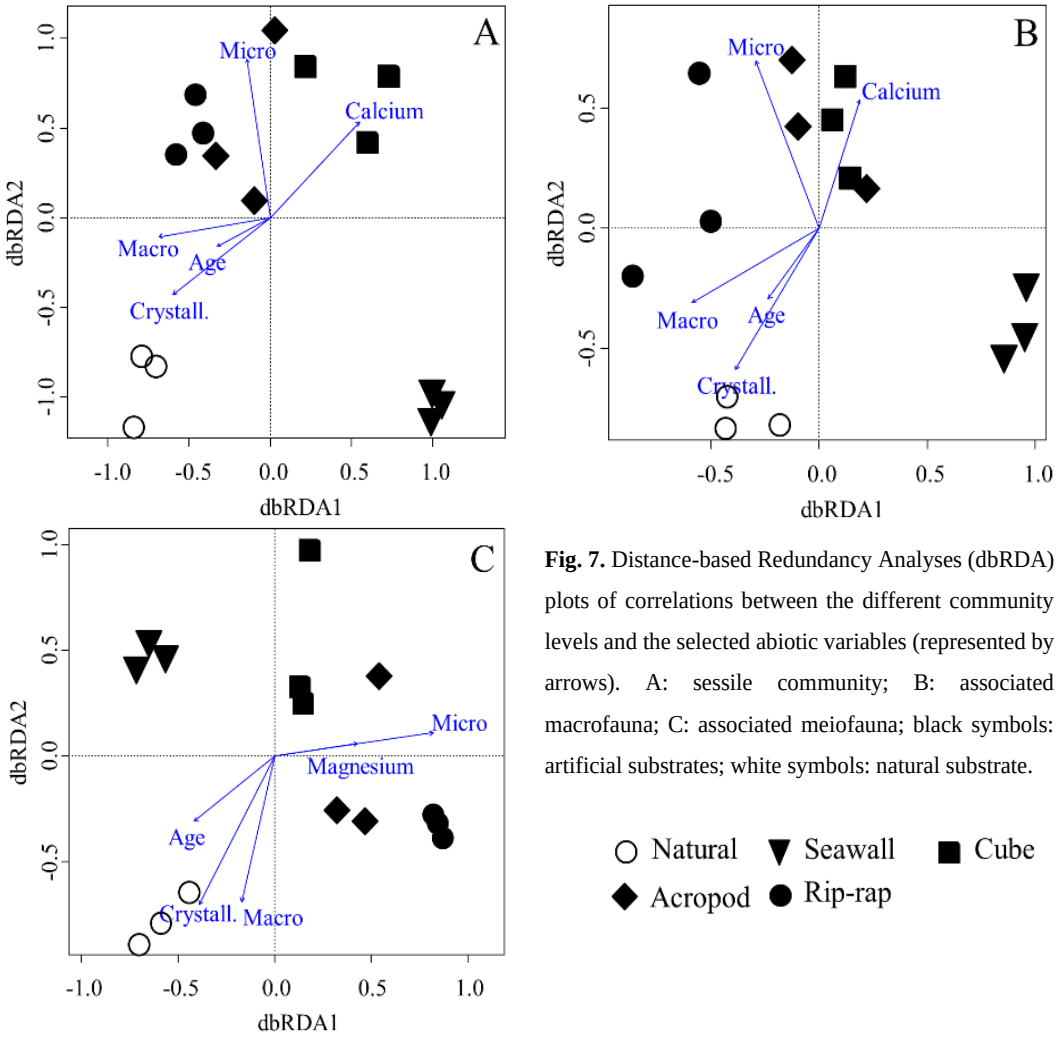

Fig. 7. Distance-based Redundancy Analyses (dbRDA) plots of correlations between the different community levels and the selected abiotic variables (represented by arrows). A: sessile community; B: associated macrofauna; C: associated meiofauna; black symbols: artificial substrates; white symbols: natural substrate.

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Table 3: PERMANOVA results for sessile, associated macro- and meiofauna communities (based on taxa composition and abundances). Pair-wise tests only consider comparisons between natural substrates and each artificial substrate. Ha: Habitat [five levels: N(natural), R(rip-rap), A(acropod), C(cube) and S(seawall)]; Si(Ha): Site; CO: covariate (volume of secondary substrate); df: degrees of freedom; MS: mean square; p: level of significance; ***: $p < 0.001$; n.s.: not significant.

Sessile community					
Source of variation	df	MS	Pseudo-F	Perms.	p
Ha	4	19032	33.676	9896	***
Si(Ha)	10	565.15	0.88467	9881	n.s.
Residual	30	638.83			
Total	44				
Pair-wise tests	Levels of factor (Ha) N≠(R,A,C,S)				
Associated macrofauna					
Source of variation	df	MS	Pseudo-F	Perms.	p
CO	1	10929	19.945	9949	***
Ha	4	3149.3	5.6499	9932	***
Si(Ha)	10	565.37	1.1018	9886	n.s.
Residual	29	513.12			
Total	44				
Pair-wise tests	Levels of factor (Ha) N=R, N≠(A,C,S)				
Associated meiofauna					
Source of variation	df	MS	Pseudo-F	Perms.	p
CO	1	7882.1	27.419	9941	***
Ha	4	3204.7	11.261	9917	***
Si(Ha)	10	282.16	0.94659	9857	n.s.
Residual	29	298.08			
Total	44				
Pair-wise tests	Levels of factor (Ha) N≠(R,A,C,S)				

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Table 4: Permutation test for dbRDA under reduced model for all constrained eigenvalues and the marginal effects of each abiotic variable tested at the three different community levels. Proportion of inertia explained by the model is provided. df: degrees of freedom; sqs: squares; p: level of significance; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; n.s.: not significant.

Sessile community				
	df	% Explained	F	P
Constrained model	5	78.3%	6.498	***
Residual	9			
	df	Sum of sqs.	F	p
Macro	1	0.3745	5.6170	*
Micro	1	0.3721	5.5809	**
Crystall.	1	0.1055	1.5829	n.s.
Age	1	0.6359	9.5387	***
Calcium	1	0.2383	3.5743	*
Residual	9	0.6000		
Associated macrofauna				
	df	% Explained	F	P
Constrained model	5	70.9%	4.3846	**
Residual	9			
	df	Sum of sqs.	F	p
Macro	1	0.1606	6.2060	**
Micro	1	0.0821	3.1722	*
Crystall.	1	0.0337	1.3045	n.s.
Age	1	0.1427	5.5124	**
Calcium	1	0.0322	1.2446	n.s.
Residual	9	0.2329		
Associated meiofauna				
	df	Explained	F	P
Constrained model	5	74.5%	5.2685	**
Residual	9			
	df	Sum of sqs.	F	p
Macro	1	0.0512	2.3058	n.s.
Micro	1	0.2547	11.481	***
Crystall.	1	0.0192	0.8670	n.s.
Age	1	0.1482	6.6789	*
Magnesium	1	0.0319	1.4389	n.s.
Residual	9	0.1997		

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Discussion

Previous studies on sessile and vagile invertebrate communities have shown the poor performance of artificial structures compared with hard natural habitats, regarding community structure and diversity (Bulleri and Chapman, 2004; Evans et al., 2016; Gacia et al., 2007; Moschella et al., 2005; Perkol-Finkel et al., 2006). The abiotic variables measured for each substrate in our study (such as composition, roughness or age) explained high proportions of variance for each community level, indicating their important role in structuring these communities. In fact, a broad range of abiotic factors have been identified as drivers of the ecological differences between natural and artificial substrates. For example, Sempere-Valverde et al. (2018) found that community composition was related to the nature of the substrate. Mercader et al. (2017) highlighted that complex artificial reefs boosted the species richness within a harbour, and Chapman and Underwood (2011) reviewed the importance of inclination. The substrate age has been frequently addressed (Antoniadou et al., 2010; Coombes, 2011; Dong et al., 2016; Ferrario et al., 2016) for its obvious importance for colonizers. The different substrates of our study were located in the same area, exposed not only to similar moderate wave action but also to similar pollution levels. This allowed us to explore the influence of substrates on the biota regardless of the potential effects of environmental and geographical factors.

Substrate complexity correlated significantly with the sessile biota, vagile macrofauna and meiofauna, although only at microscale for the latter. At the intertidal level, substrate heterogeneity (e.g. rock pools and crevices) can increase biodiversity by offering shelter against stressful environmental conditions (e.g. desiccation at low tide) (e.g. Evans et al., 2016; Firth et al., 2014b; Ostalé-Valriberas et al., 2018; Perkins et al., 2015). This usually favours natural habitats compared with the featureless surfaces of coastal defence structures. In addition, higher roughness at the scale of centimetres could improve larvae and spore recruitment (Koehl, 2007; Sempere-Valverde et al., 2018) and increase refuge availability against predators (Loke et al., 2017; Strain et al., 2018a). Despite this, it is known that some species (e.g. *Balanus improvisus*)

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have higher propensity for smooth surfaces (Berntsson et al., 2000), a common condition of concrete structures. Higher abundances of large limpets have been related to smooth surfaces or medium microscale roughness depending on the species (Rivera-Ingraham et al., 2011a; Rivera-Ingraham et al., 2011b), while higher complexity at larger scale could provide shelter for other megafauna grazers such as sea urchins (Dame, 2008) or even invasive crabs (Katsanevakis et al., 2010). According to Miller and Gerstner (2002), our measurements for cubes, rip-raps and natural substrates indicated a high complexity at centimetre scale. Interestingly, at macroscale level, cubes and rip-raps were more heterogeneous than natural substrates. Therefore, higher microscale roughness coupled with lower macroscale heterogeneity might be boosting the occurrence of more sessile taxa in natural substrates through recruitment and competition effects.

Substrate material is another important factor affecting community composition on artificial substrates (Coombes et al., 2015; Sempere- Valverde et al., 2018). Our results showed a clear differentiation of substrates according to mineralogic composition, although calcium (Ca) correlated significantly only with the sessile community. Calcium was present in the artificial substrates mainly as polymorphs of calcium carbonate (calcite, magnesium calcite, aragonite and dolomite) and was almost absent from natural substrates, which were principally composed of quartz (see Supplementary Table 3). Sea water reduces the pH, modifying concrete properties (Ponti et al., 2015) and potentially promoting the dissolution of carbonated minerals and increasing bicarbonate availability around the surface (Mos et al., 2019). Green et al. (2013) related higher percentages of burrowing bivalves to higher aragonite saturation. In fact, we detected the invasive mussel *Myoforceps aristatus* in concrete structures (data not shown). Furthermore, leaching components of cement are known to raise pH levels at the surface of concrete structures (Ido and Shimrit, 2015), fostering alkatolerant and endolithic taxa (Ponti et al., 2015). Our results showed higher biomass of *M. galloprovincialis* and *P. perforatus* in concrete-based substrates compared with rip-raps and natural substrates. This is also in accordance with Guilbeau et al. (2003), whose results demonstrated that high pH cements boosted the attachment of barnacles and with Anderson (1996), who showed that high alkalinity

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at the surface of concrete enhanced oyster settlement. Although mussels and barnacles were present on every concrete structure in this study, seawalls harboured the greater biomass. Even though wave exposure was moderate at every substrate, seawalls lacked porous structures and avoid the waves flowing through, dissipating wave energy less efficiently than boulder like structures (Jung et al., 2012). It is also possible that seawalls were exposed to stronger currents, as it was the only structure not connected to mainland. Therefore, it is probable that a combination of all the above-mentioned factors is boosting the development of filter feeding taxa on the seawall. Contrary to our results, Bavestrello et al. (2000) observed a fewer taxa in rocks with high quartz content and Gacia et al. (2007) did not find differences on the epibiota related to different mineral composition. Moreover, several authors have pointed out that other attributes, such as colour (Dobretsov et al., 2013; Finlay et al., 2008) or porosity (Berntsson et al., 2000), could influence 'larval choice' in settling on different substrates.

Overall, our results support the idea that substrate roughness and composition play important roles in structuring intertidal sessile communities, although we were not able to disentangle this from other variables such as age, that was also significantly correlated. In fact, Nicoletti et al. (2007) distinguished *M. galloprovincialis* (that dominated the youngest structure in this study, i.e. seawalls) as a dominant species during the first years following an artificial reef deployment, although this appeared to be more related to sedimentation processes rather than the artificial structure itself. In addition, the cover of barnacle *Amphibalanus amphitrite* diminishes with age of biofilm (Faimali et al., 2004). On the contrary, Moschella et al. (2005) considered barnacles and mussels as later colonizers of low-crested coastal defence structures. Furthermore, some authors have estimated that it takes from 5 to 20 years for artificial structures to reach climax communities (Coombes, 2011; Hawkins et al., 1983; Pinn et al., 2005), while others suggested that communities on low crested structures never reach climax (Gacia et al., 2007). In some situations, benthic communities are known to change over years (Burt et al., 2011; Ponti et al., 2015) and it has also been proposed that incomplete succession could be a persistent stable state (Ferrario et al., 2016 and references therein). We are yet far from understanding if age plays a critical role or if its effect is overwritten by other factors

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acting at faster scales. Further experimentation using controlled parameters and longer experimental data (Firth et al., 2016) will be needed to fully assess the importance of age.

According to the associated fauna, number of taxa did not differ substantially between natural and artificial substrates. However, due to the absence of highly dominant taxa (in terms of abundance) in cubes, acropods and rip-raps, Shannon's diversity was significantly higher in these structures. Furthermore, similarities increased among substrates compared with the sessile biota. This was probably an artefact of using "High-Taxonomic groups" (HTGs), but also due to the capability of barnacle patches, mussel beds and coralline turfs (the most abundant sessile taxa in our study) of harbouring abundant and diverse associated communities (e.g. Asnaghi et al., 2015; Chintiroglou et al., 2004; Kelaher et al., 2004). Substrate roughness and age were the main drivers affecting the vagile macrofauna. It is possible that substrate roughness affects the occurrence of vagile animals that crawl over the substrate, such as certain gastropods or polyplacophorans. In fact, the latter were absent from the least heterogeneous substrate (seawalls). This is in accordance with Moreira et al. (2007) who found higher abundances of chitons in crevices than on exposed surfaces on seawalls. Increasing shade and roughness on intertidal artificial structures has proven to be one of the most effective measures to improve biodiversity of mobile invertebrates (Strain et al., 2018b). Nonetheless, most of the identified taxa were small macroinvertebrates and meiofauna that need a secondary substrate (sessile) to cling to. The quality and amount of resources provided by sessile host species (such as food, habitat, predator or desiccation refuge) is highly dependent on both morphological and biological features of the secondary substrates (e.g. complexity, epiphytic load, presence of chemical defence or life cycle) (Olafsson, 2016). Since the community structure of the secondary substrate greatly affects the distribution of associated fauna (Kelaher, 2002; Olafsson, 2016; Symstad et al., 2000; Torres et al., 2015), the differences detected herein are thus expected to better respond to the patterns observed for the sessile community. In this sense, the associated communities of artificial structures with greater abundances of mussels and barnacles (the concrete ones) clearly differed from those with higher abundances of coralline algae (rip-rap and natural). Both *M. galloprovincialis* and *E. elongata* provided large volumes

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of secondary substrate but presumably with very different complexity. In line with our results, Palomo et al. (2007) found that isopods and amphipods were the most abundant taxa associated with mussels, and Yakovis et al. (2007) suggested that the cavity-loaded structures of barnacles shaped the associated macrofauna. Amphipods were also dominant at natural habitats but, in our study, abundance of isopods was clearly higher on substrates dominated by *P. perforatus* (seawalls), probably because the habitat they provide fits adults' size and gives refuge against predators and environmental stress. This supports the idea that facilitation processes could be species-specific (Bulleri et al., 2016) and that the vagile fauna can have preferences for some surfaces depending on the characteristics provided by the sessile biota (Moura et al., 2008).

Therefore, the contrasting complexities of different sessile taxa probably determine several differences in the associated communities studied. However, biological features of the secondary substrates also contribute to those differences (Kelaher, 2002). The surface of mussel shells is an appropriate substrate for bacteria and microalgae (Tsuchiya and Nishihira, 2007) which in turn serve as food for mobile taxa (Palomo et al., 2007). It is known that different artificial structures harbour different biofilms (Tan et al., 2015) and that microbial communities associated with the same organism differ depending on the natural or artificial nature of the primary substrate (Marzinelli et al., 2018). Moreover, marine invertebrate larvae can respond to chemical cues produced by biofilms and their associated organisms. For example, encrusting red algae foster the settlement of certain species of gastropods, polychaetes and echinoderms while some bivalves are attracted to filamentous red algae (see Pawlik, 1992 for a review).

Meiofauna is also expected to be influenced by structural complexity and biological interactions. Microhabitats created by biogenic structures are known to determine meiofaunal abundances (Muralikrishnamurty, 1983; Passarelli et al., 2012). Regarding meiofauna, mussel beds and barnacles can have similar functionality than algal turfs (Giere, 2009), which provide shelter from desiccation and predators (Ape et al., 2018; Muralikrishnamurty, 1983). However, our results showed that different sessile taxa favoured the attachment of abundant and rich meiofaunal communities but with significantly different community structure. Ape et al. (2018) also reported differences in intertidal meiofaunal communities associated to macroalgae and

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mussels. They are likely driven by architectural differences between mussels and algae. For example, some taxa (e.g. Peltidiidae and Porcellidiidae copepods) have a depressed body and specialized appendices to attach to the algal canopy (Gibbons, 1991; Giere, 2009). Atilla et al. (2003) also found higher abundances of phytal copepods in algal-covered substrates. In fact, in our study copepods belonging to the Porcellidiidae family were much more abundant in natural substrates, that were mainly covered by algal turfs (Sedano et al., unpublished data). Due to these adaptations, copepods and ostracods are abundant in phytal meiofaunal communities (Giere, 2009). Accordingly, the lowest abundance of ostracods was found on seawalls, where algae were very scarce.

As already mentioned for the macrofauna, biological features may also play important roles in structuring meiofaunal communities. Passarelli et al. (2012) found more developed diatom biofilms on biogenic structures and Sempere-Valverde et al. (2018) related higher primary production and abundances of diatoms to increasing substratum roughness. Diatoms are a food resource for kinorhynchs (Herranz et al., 2014; Nebelsick, 1993 and references therein) and even the main one for shallow water forms (Giere, 2009). In our study, kinorhynchs were restricted to the highly heterogenous and siliceous natural substrates (except for one replicate of rip-raps), which could be related to a greater development of diatoms.

In summary, the physical and biological features of the studied sessile community (secondary substrate) together with the nature of the primary substrate could be influencing their associated fauna, not only through species specific processes but also at larger scales.

Conclusions

Our results showed clear differences between substrates for the three community levels studied (sessile community, vagile macrofauna and meiofauna) and suggest that overall, rip-raps are better surrogates of natural substrates in terms of community structure and taxa composition. Even so, rip-raps have been previously identified as poor surrogates of natural

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habitats in the Mediterranean see (Gacia et al., 2007; Moschella et al., 2005; Sedano et al., 2019) but see Liversage and Chapman (2018) for a review about benefits of incorporating boulder habitats. In general, we showed that artificial structures have lower taxa richness (for the three community levels) compared with the natural rock (although not always significantly). It is known that taxa richness in artificial structures can be increased by mitigating measures (Perkins et al., 2015), such as the creation of rockpools (Ostalé-Valriberas et al., 2018). Therefore, we hypothesized that structures with higher microscale roughness will have higher number of taxa in comparison with smoother ones. However, we found that cubes did not have significantly higher richness in comparison with the other substrates, despite their highest microscale roughness due to strong weathering through time. As already suggested by Perkins et al. (2015), this supports the idea that increasing structural complexity in concrete substrates is not enough to mitigate biodiversity loss. Thus, new ecoengineering actions should compromise between the use of sustainable materials and the addition of complexity.

Although the spatial arrangement of the different structures may affect the obtained results, we showed that physical attributes (micro and macroscale roughness), composition (only for sessile) and age of the structures seem to play important roles in structuring the studied communities under similar environmental conditions. They especially affected the sessile community, initiating strong cascading effects that were detectable at high taxonomic level in the associated fauna. This reinforces the usefulness of both macrofaunal and meiofaunal communities to assess different artificial coastal defence structures in comparison with nearby natural substrates (Sedano et al., 2014). The patterns found by using a mixed coarse taxonomic resolution (Chapman et al., 2005) support the inclusion of fast but reliable procedures in management and monitoring plans (Chatzinikolaou and Arvanitidis, 2016), especially by harbour management authorities and ecoengineers that seek sustainable development goals.

These results are of major importance, since the cascading effects can ultimately affect higher trophic levels such as fish (Cordell et al., 2017) and have economic consequences. Although some direct effects over associated fauna could be expected, the tight relationships of sessile taxa with their associated fauna probably masked those effects. Further

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experimentation sampling the same secondary substrates (or using mimics) in different artificial structures is needed in order to evaluate the effects of artificial structures over associated communities.

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CHAPTER 1.2

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1.2 The role of substrate composition and roughness in structuring amphipod communities

Adapted from: Sedano, F., Navarro-Barranco, C., Guerra-García, J. M., Espinosa, F. (2020). From sessile to vagile: Understanding the importance of epifauna to assess the environmental impacts of coastal defence structures. Estuarine, Coastal and Shelf Science, 235, 106616. https://doi.org/10.1016/j.ecss.2020.106616

Abstract

Ocean sprawl is leading to the introduction of multiple artificial structures into the marine environment. However, the biota on these novel habitats differ from that on natural hard substrates. Amphipods, despite their ecological importance, are usually overlooked when comparing benthic assemblages on artificial and natural hard substrates. So as to assess the effects of artificial structures on amphipod assemblage and to identify the main factors involved, the amphipod assemblage structure was studied in five different substrates (seawalls, cubes, acropods, rip-raps and natural rock). Abiotic measurements of each substrate (complexity, rock composition, and age) were related to the ecological patterns. Complexity measurements seemed to affect the amphipod community structure, highlighting the need to consider physical complexity in eco-engineering actions. Amphipod assemblages were also affected by the secondary substrate (sessile biota), suggesting that artificial structures are indirectly shaping amphipod assemblages by firstly shaping the sessile biota. Future research should study the same secondary substrates across different artificial structures to separate the direct effects (caused by the artificial structures) from the indirect effects (caused by the sessile biota).

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Introduction

The vast proliferation of artificial (man-made) structures in the marine environment in the last decades has attracted the attention of researchers in an attempt to understand and assess the ecological implications of the deployment of artificial substrates (Bulleri and Chapman, 2010; Firth et al., 2016). The potential effects of artificial structures in marine communities have been mainly studied on the basis of the sessile fauna or conspicuous intertidal organisms (Browne and Chapman, 2011; Moreira et al., 2006; Moura et al., 2008). The sessile biota established on artificial structures clearly differ from those found on nearby natural rocky shores, but the potential cascading effects (e.g. facilitation or inhibition of certain vagile species) of these changes on the rest of the community remain largely unknown (Bulleri et al., 2005; Thomsen et al., 2010). These species, acting as secondary substrates, transform bare or simple surfaces into highly structured environments which, in turn, support a wide range of other sessile and mobile species (Bruno and Bertness, 2001; Ólafsson, 2016). Although some taxa can replace the ecological function (e.g. similar trophic groups) of others (e. g Chintiroglou and Antoniadou, 2009 and references therein) it is known that secondary substrates attached to different types of structures can host different macroinvertebrate assemblages (People, 2006).

Epifaunal communities, usually including a great variety of small crustaceans, polychaetes and molluscs, are very important ecologically (e.g. Seed and O'Connor, 1981). However, they are often overlooked because (1) sorting all the epifauna from the samples requires great time and effort, (2) identification of many taxa is still challenging and, therefore, meticulous examination and taxonomical expertise is required to guarantee a correct identification of the species. Thus, few studies on artificial habitats consider these vagile assemblages (Carvalho et al., 2013; Moura et al., 2008). Furthermore, when epifauna is considered, it is common to appeal to "High-Taxonomic groups" (HTGs) (Otero-Ferrer et al., 2019; Timms et al., 2013). Indeed, regarding taxonomic sufficiency, studies considering different levels of taxonomic resolution (species, family, order) often show similar results regarding community distributions and the associated environmental variables (Sánchez-Moyano et al., 2006). However, many

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studies have shown that identification to the species level is mandatory for properly detecting ecological differences in anthropogenic perturbance scenarios (e.g. Guerra-García and García-Gómez, 2005).

Comprising almost ten thousand species worldwide, Amphipod crustaceans are among the most diverse and numerically dominant organisms of benthic assemblages (Dauby et al., 2001; Guerra-García et al., 2011b). They often account for up to 80% of the total mobile epifauna inhabiting macroalgae and other sessile invertebrates, both in natural and artificial habitats (e.g. Fernández-Romero et al., 2017; Gavira-O'Neill et al., 2016; Navarro-Barranco et al., 2018). They are important contributors to benthic production (Mancinelli and Rossi, 2002; Taylor, 1998) and play a relevant role in trophic nets, being an important component of the diets of fish (Doornbos and Twisk, 1987) or other invertebrates like crabs (Kurihara and Okamoto, 1987; Matsumasa and Shiraishi, 1993). Indeed, their potential use as a resource in aquaculture due to their high content in proteins and omega 3 fatty acids is being explored (Baeza-Rojano et al., 2014; Woods, 2009). Amphipods are mainly detritivores and therefore are suitable candidates for Integrated Multitrophic Aquaculture (IMTA) systems (Fernández-González et al., 2018; Guerra-García et al., 2016). Furthermore, amphipods are considered a valuable tool for detection of anthropogenic impacts since they have been successfully used as bioindicators in industrial areas (Conradi et al., 1997), of oil pollution (Gómez-Gesteira and Dauvin, 2000), of TBTs residues (Takeuchi et al., 2001), of trace metal contamination (Guerra-García et al., 2010), of desalination brine discharges (De-la-Ossa-Carretero et al., 2016), and of light pollution (Navarro-Barranco and Hughes, 2015), and therefore included in biotic indexes (e.g. polychaetes/amphipod ratio, Dauvin, 2018). On the other hand, amphipods are frequently associated to fouling communities and are prone to transportation by recreational boating or aquaculture practices; therefore, they are also used as a model in the study of marine invasions (e.g. Ros et al., 2015). However, the potential value of amphipods for assessing the effects of different artificial structures such as seawalls, cubes, acropods and rip-raps, remains unexplored.

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In the present study we selected the amphipod community, using a species level identification approach, as a model to understand the macrofaunal variation between natural and artificial substrates (seawall, cubes, acropods and rip-raps) evaluating how this variety of artificial habitats can modify natural epifaunal communities. Different artificial structures are expected to have different abiotic attributes, which directly or indirectly could affect epifaunal communities. Furthermore, most epifaunal taxa need a secondary substrate (sessile) to attach to, that in turn shapes the composition of the whole epifaunal assemblage (Kelaher, 2002; Ólafsson, 2016; Symstad et al., 2000; Torres et al., 2015). This is dependent on the taxa composition of the sessile component, the quality and amount of resources provided (e.g. food, habitat, refuge against desiccation) and the morphological and biological features of such secondary substrates (e.g. complexity, epiphytic load, presence of chemical defences or life cycle) (Ólafsson, 2016). Thus, potential differences in the epifaunal community among different types of artificial habitats are expected to reflect patterns in taxa composition and/or substrate cover of the sessile community. Therefore, our hypothesis is that amphipod assemblages will differ among artificial substrates and in comparison with natural ones, and that those differences (community structure and diversity) will be related with the features of the primary (artificial structures) and the secondary (sessile community) substrates. Invertebrate assemblage structure at the regional scale has little predictability (Simpson et al., 2017) and regional differences can confound the effects of artificial substrates (Gacia et al., 2007). Consequently, we have selected Algeciras Bay (South Spain) as a study site since this unique location encompasses different types of artificial substrates within an area of 1.5 km, and which are therefore expected to be subjected to similar environmental conditions, thus avoiding potential confounding effects.

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Materials and methods

Study area

Samples were collected in different coastal defence structures of the Algeciras harbour and the nearest natural hard substrate (Fig. 1). The harbour is located on the West side of Algeciras Bay (Strait of Gibraltar, southern Spain) and is one of the biggest harbours in Europe, surpassing 100 mT of freight in 2017 (www.ec.europa.eu/eurostat/). Due to intense shipping activities and the presence of industries such as paper mills, refineries, thermal power plants, iron works, and chemical factories (Conradi et al., 1997), this bay has been the focus of numerous studies (Guerra-García et al., 2010). To avoid heterogenous environmental conditions, we chose substrates located in the surroundings of Algeciras Harbour with a maximum distance of 1.5 km between them. Previous studies in Algeciras Bay have shown similar annual averages of hydrodynamism, suspended solids, silting, organic matter and temperature (Carballo et al., 1996; Naranjo et al., 1996).

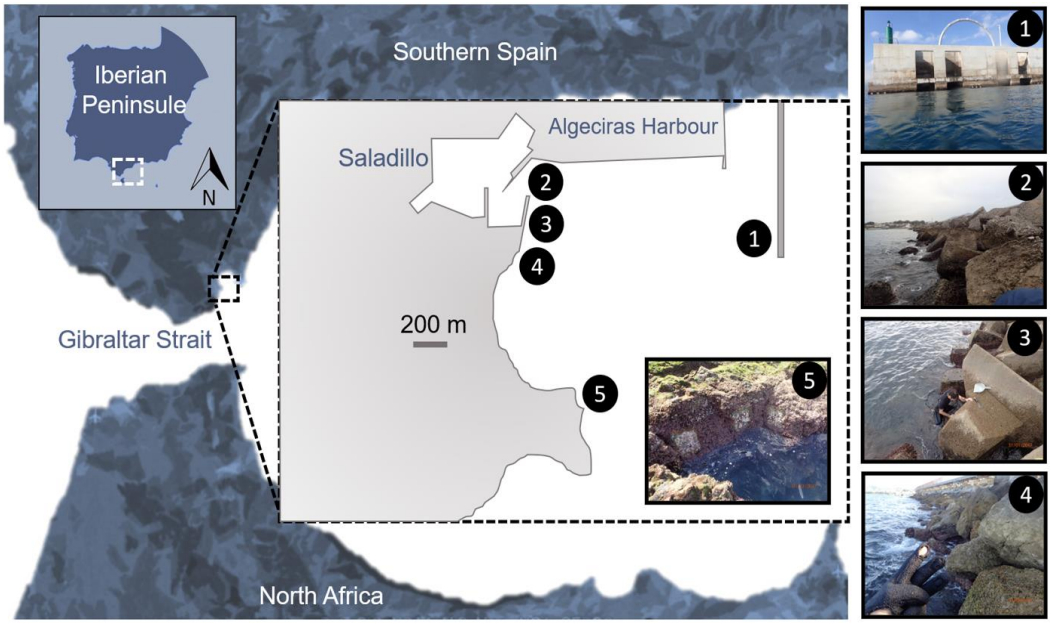

Fig. 1. Location of Algeciras Bay in the Strait of Gibraltar showing the five sampling stations. Seawall, acropod and cubes were concrete-based while the rip-rap was natural rock-based. 1: Seawall; 2: Cube; 3: Acropod; 4: Rip-rap; 5: Natural.

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Abiotic variables

Several variables related to substrate nature were measured for each habitat (natural and artificial) and related to amphipod assemblages' patterns. Three rock samples were taken to study the lithology (mineralogic and elemental composition) and crystallinity of each substrate; this was determined by X-ray fluorescence and X-ray diffraction (full methodology in Valverde et al., 2015). Only elements 3% or higher in concentration (silicon, calcium and magnesium), crystallinity and calcination percentages (CP) (as a measure of carbonate content) were considered in statistical analyses. The age of the different artificial structures was also considered. Age was based on the date of construction. Since it is difficult to infer the age of natural rocky shores, for analytical purposes, we chose the oldest possible date in the same order of magnitude compared to the oldest artificial structure. As a measure of physical substrate complexity, macro- and micro-scale roughness was measured. Macro-scale roughness was calculated over three random 10 m-long transects where a flexible meter was laid directly over the substrate (at the upper intertidal level) conforming as closely as possible to the contour of the bare substrate. Micro-scale roughness was measured using three random 15 cm profile gauges with 0.5 mm pins. The gauge was pushed onto the bare rock (at 5–30 cm over low spring tide) to record the surface (Frost et al., 2005). The resulting profiles were photographed, and the length of the contour was measured using ImageJ software. In both cases (macro- and micro-scale), substrate roughness was calculated as in Rivera-Ingraham et al. (2011) using the equation provided by Blanchard and Bourget (1999): Roughness = Tr / Ts, where Tr is the contour measured between two points and Ts the linear distance between those two points. Furthermore, wave exposure was quantified at each sampling station based on a fetch model index (see methodology in Ros et al., 2016).

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Biological composition

In January 2017, four types of artificial substrates (concrete-based: cube, acropods, and seawall; natural rock-based: rip-rap) and the nearest natural rocky shore (control) were sampled. In each substrate, three random sites (tens of meters apart) were chosen and within each site three 20 x 20 cm quadrats were scraped (i.e. replicates) and preserved in 96% ethanol until laboratory analyses. Two factors were considered in our experimental design: 'Habitat' (Ha), a fixed factor with five levels (Natural, Rip-rap, Acropod, Cube and Seawall) and 'Site' (St), a random factor with three levels (Site 1, Site 2, Site 3) nested in Ha. Samples were taken over vertical surfaces of each substrate during low tide within the lower intertidal zone (5–30 cm over low spring tide). In the laboratory, each replicate was sieved through a 0.5 mm mesh in order to retain the associated macrofauna. Amphipods were sorted and identified to the species level, whenever possible. The sessile taxa present in each replicate were also identified to the lowest possible resolution and their total volume quantified. For each replicate, the number of amphipod taxa (S) and abundance of each taxon was determined. Differences in number of taxa and total abundance of amphipods (number of individuals/1000 ml) among substrates were evaluated using a nested ANOVA on GMAV5 software (Underwood et al., 2002) with the above-mentioned experimental design. When ANOVA detected significant differences for a given factor, the source of the difference was identified by applying the Student–Newman–Keuls (SNK) test (Underwood, 1997). Correlations between sessile taxa volume (displaced volume) and amphipod abundances were calculated using Spearman's correlation coefficient. Nested permutational multivariate analysis of variance (PERMANOVA) was used in order to test the effect of the substrate type on the structure of the amphipod assemblage. PERMANOVA was run on a triangular similarity matrix derived from the values of the Bray-Curtis dissimilarity index on square root transformed amphipod abundance data. PERMANOVA was also conducted with presence/absence data. The total volume of sessile taxa for each replicate was used as covariate in the statistical analyses to account for the variance in amphipod abundance and composition dependent on the volume of

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sessile taxa. Bray-Curtis dissimilarities between natural and each of the artificial substrates were calculated with Similarity Percentages (SIMPER) using standardized (by scraped volume) abundance data and square root transformation. Differences in amphipod assemblages among substrates were graphically portrayed using Cluster analysis performed over a Bray-Curtis similarity matrix of square root transformed data of site-averaged values of each substrate. A similarity profile analysis (SIMPROF) was carried out to identify clusters with significant different assemblage structure ($p < 0.05$). PERMANOVA, SIMPER, Cluster and SIMPROF analyses were carried out using PRIMER v.6þPERMANOVA package (Clarke and Gorley, 2006).

Relationships among abiotic variables and biological assemblages

Distance-based Redundancy Analysis (dbRDA) was used to explore relationships between abiotic data and amphipod assemblages. dbRDA was chosen over Canonical Correspondence Analyses (CCA) since data were linear. Linearity of the data was deducted as in Ter Braak and Smilauer (1998) according to the first axis length in Detrended Correspondence Analysis (DCA) (<3, linear; >4, unimodal). Prior to analyses, multicollinearity between abiotic factors was tested using Draftsman plots based on Spearman correlation (see Fig. 6 in Chapter 1.1 of this Tesis). Only one abiotic factor was used in the analyses when there were pairs of variables showing high correlation values. If the constrained ordination still portrayed collinearity between abiotic factors, the variable most affected was eliminated attending to the Variance Inflation Factor (VIF) in order to avoid misinterpretation of data due to unstable canonical coefficients (Ter Braak, 1988). Collinearity was neglected when VIF <10 according to Dormann et al. (2013). dbRDA was run using the square root transformed biological matrix (amphipod abundances per 1000 ml) paired with a standardized abiotic matrix. In addition, significance levels ($p < 0.05$) were calculated under 1000 random permutations (Manly, 1997). In order to explore the influence of sessile taxa on amphipod assemblage, an additional dbRDA was conducted using the volumes of the different sessile taxa as explanatory variables. The

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relationship between biological assemblages and abiotic variables were portrayed using dbRDA biplots. DCA and dbRDA analyses were carried out using the package "vegan" in RStudio© Version 1.1.453.

Results

Abiotic variables

Fetch index classified each substrate as semi-exposed (Table 1), indicating that exposure to wave action was similar among substrates. Surface complexity was quite different among substrates. Micro-scale roughness was higher in the natural rocky shore, rip-raps and cubes. Rip-raps are constructed with natural rocks and therefore had higher microscale roughness than other smoothed concrete-based artificial structures such as acropods and seawalls. This did not apply for cubes, since weathering through time (they were deployed in 1955) has eroded their surface leading to highly complex surfaces. Macro-scale roughness was higher in boulder-like substrates, i.e. cubes, acropods and rip-raps (Table 1). According to substrate composition, the natural rocky shore was composed mainly of quartz and had very little carbonate content (see calcination percentages in Table 1). In contrast, the aggregates of artificial substrates were rich in carbonate minerals such as calcite and dolomite. Greater carbonate content resulted in higher calcination percentages (CP). In the same way, greater Silicon (Si) content correlated with crystallinity (Draftman's plot with pairs of correlations not shown to simplify). Therefore, CP and Si were not included in dbRDA (see next section) to avoid multi-collinearity between predictor variables.

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Table 1: Descriptors of the five substrates sampled.

	Natural shore	Rip-rap	Cube	Acropod	Seawall
Latitude	36°06'34.1"N	36°07'01.2"N	36°07'12.1"N	36°07'03.2"N	36°07'00.5"N
Longitude	5°25'55.4"W	5°26'07.9"W	5°26'07.6"W	5°26'07.4"W	5°25'02.4"W
Date of deployment	n.a.	1997	1955	1997	2008
Distance from natural rock	n.a.	0.90 km	1.19 km	0.96 km	1.50 km
Effective fetch (km)	95.79	116.52	74.66	116.52	43.15
Wave exposure class	Semi-exposed	Semi-exposed	Semi-exposed	Semi-exposed	Semi-exposed
Macro (average ± SD)	1.05 ± 0.03	1.26 ± 0.09	1.43 ± 0.06	1.47 ± 0.24	1.00 ± 0.01
Micro (average ± SD)	1.62 ± 0.22	1.30 ± 0.04	1.62 ± 0.31	1.20 ± 0.07	1.00 ± 0.01
Major component	Quartz	Calcite	Quartz-Calcite	Dolomite	Magnesium calcite
SiO_2 (average % ± SD)	95.63 ± 1.25	3.88 ± 2.71	31.96 ± 11.28	6.51 ± 1.76	11.34 ± 1.25
MgO (average % ± SD)	0.24 ± 0.10	0.50 ± 0.19	2.48 ± 0.76	14.27 ± 3.06	1.84 ± 0.72
CaO (average % ± SD)	0.02 ± 0.03	52.66 ± 2.23	33.74 ± 7.91	33.14 ± 1.89	45.83 ± 1.85
Calcination Percentage	1.17 ± 0.41	41.56 ± 1.10	29.10 ± 5.20	40.48 ± 1.40	36.62 ± 1.60

n.a. = not applicable, Macro = macro scale roughness, Micro = micro scale roughness.

Sessile flora and fauna and associated amphipods

The secondary substrate scraped (sessile flora and fauna) comprised a total of 15 taxa: *Mytilus galloprovincialis*, *Spirobranchus* sp./*Dendropoma* sp. reef, *Calpensia* sp., *Perforatus perforatus*, *Pyura dura*, *Ulva* sp., *Rugulopteryx okamurae*, *Ceramium* sp., *Ellisolandia elongata*, *Gelidium* sp./ *Caulacanthus* sp. turf, *Jania rubens*, *Laurencia* sp., and *Lithophyllum incrustans*. The natural rocky shore was characterized by a dominance of the calcareous turf alga *E. elongata* and the scarce presence of gregarious species such as *P. perforatus* and *M. galloprovincialis*. Seawalls presented the opposite pattern with a dominance of *P. perforatus* and *M. galloprovincialis* while *E. elongata* was absent. The sessile community of rip-raps was also dominated by *E. elongata* while cubes were characterized by a dominance of *P. perforatus* with patches of *E. elongata* and *M. galloprovincialis*. Acropods held the most heterogenous sessile community, characterized by abundant patches of *P. perforatus*, *E. elongata* and *Spirobranchus* sp./*Dendropoma* sp. reef depending on the site (Fig. 2).

A total of 21,296 individuals were sorted, belonging to twenty-one amphipod species (Table 2), twenty of which were present in the natural rocky substrate. In contrast, several species were absent from artificial substrates and therefore ANOVA showed significantly higher values of species richness in the natural rocky shore (Table 3, Fig. 3). ANOVA also showed significantly

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higher total abundance of amphipods in the natural rocky shore, where the most abundant species were *Stenothoe monoculoides*, *Hyale stebbingi* and *Lembos websteri*. *S. monoculoides* and *H. stebbingi* were also the most abundant species in rip-raps together with *Caprella grandimana* that was, in turn, also abundant in the natural rocky shore. The same species numerically dominated the assemblage on cubes but showed lesser average abundances when compared to rip-raps and the natural rocky shore. In addition, *L. websteri* were absent from cubes which in turn showed the smallest values of species richness across all substrates.

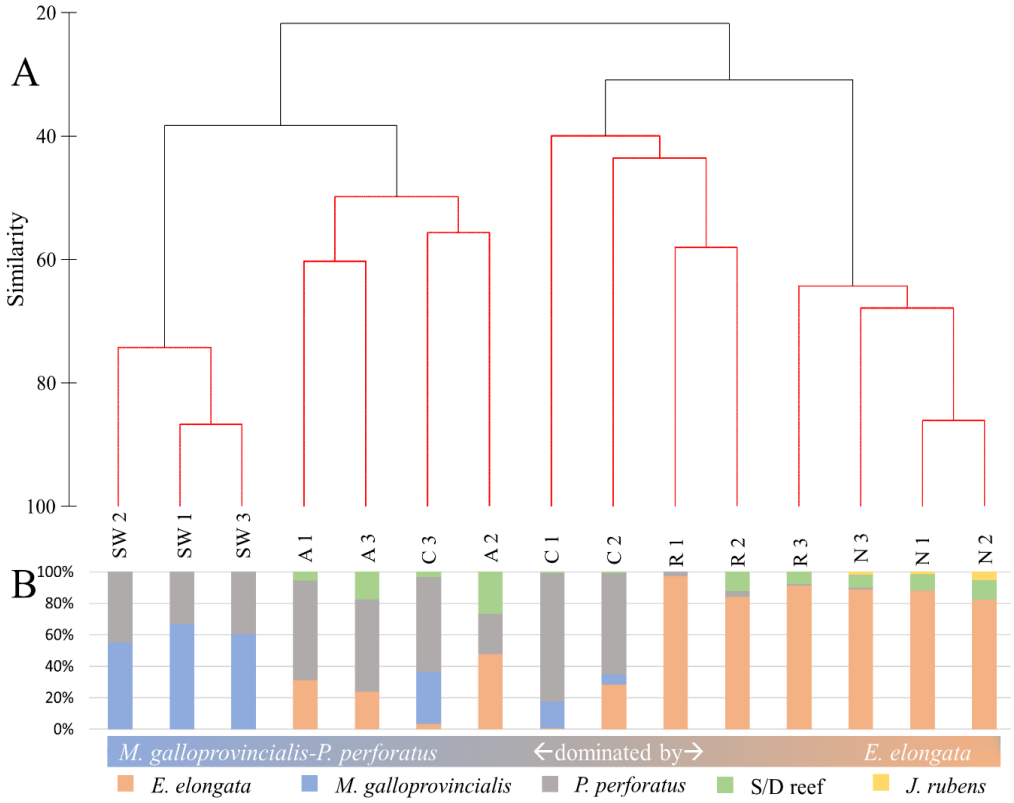

Fig. 2. A: Dendrogram obtained from Cluster analysis showing the classification of sites within each substrate according to the amphipod composition. Red lines represent significant groups based on similarity profile analysis (SIMPROF) test. B: Histogram showing average volume percentages of sessile taxa by site. Taxa showing volumes < 3 ml were not included in the histogram for easiness of interpretation. N: natural rocky shore; SW: seawall; A: acropod; C: cube; R: rip-rap; S/D: *Spirobranchus* sp./*Dendropoma* sp.

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Table 2: Average abundances (individuals/1000 ml ± standard error) of each amphipod species (arranged alphabetically) per site in each substrate. N: natural rocky shore; SW: seawall; C: cube; A: acropod; R: rip-rap; 1-3: replicates.

	N1	N2	N3	SW1	SW2	SW3	C1	C2	C3	A1	A2	A3	R1	R2	R3
Ampithoe ramondi Audouin, 1826	8 ± 5	4 ± 1	8 ± 5	36 ± 11	7 ± 3	18 ± 6	-	-	30 ± 30	-	-	2 ± 2	-	12 ± 12	24 ± 24
A. riedli Krapp-Schickel, 1968	85 ± 45	97 ± 16	58 ± 21	252 ± 76	58 ± 12	185 ± 100	10 ± 10	4 ± 4	100 ± 100	61 ± 61	6 ± 3	15 ± 12	41 ± 27	60 ± 32	380 ± 241
Apocorophium acutum (Chevreux, 1908)	54 ± 6	117 ± 54	257 ± 119	-	-	-	-	13 ± 13	-	-	33 ± 22	-	-	36 ± 21	24 ± 24
Apolochus picadurus (J.L. Barnard, 1962)	2 ± 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caprella grandimana (Mayer, 1882)	323 ± 214	181 ± 107	146 ± 77	-	-	-	22 ± 12	1384 ± 823	72 ± 53	97 ± 51	108 ± 60	147 ± 25	80 ± 58	48 ± 32	867 ± 269
C. penantis Leach, 1814	58 ± 31	32 ± 6	238 ± 131	-	-	-	-	-	-	33 ± 33	71 ± 45	24 ± 20	75 ± 75	54 ± 31	16 ± 16
Colomastix pusilla Grube, 1861	-	-	4 ± 3	-	-	-	-	-	-	8 ± 8	-	2 ± 2	-	-	-
Elasmopus spp.	278 ± 64	224 ± 41	167 ± 69	107 ± 10	59 ± 9	45 ± 5	9 ± 9	40 ± 12	92 ± 82	20 ± 10	175 ± 118	109 ± 38	-	42 ± 16	381 ± 381
Guernea (Guernea) coalita (Norman, 1868)	10 ± 7	2 ± 2	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyale perieri (Lucas, 1849)	57 ± 47	46 ± 31	99 ± 19	192 ± 45	57 ± 23	86 ± 13	91 ± 34	77 ± 41	94 ± 30	517 ± 166	102 ± 51	266 ± 81	149 ± 92	276 ± 85	238 ± 153
H. stebbingi Chevreux, 1888	1765 ± 946	1046 ± 387	89 ± 37	-	2 ± 2	-	367 ± 147	505 ± 263	42 ± 21	58 ± 35	27 ± 22	6 ± 6	667 ± 424	1530 ± 353	1278 ± 615
Jassa marmorata Holmes, 1905	28 ± 12	38 ± 11	296 ± 63	533 ± 167	247 ± 61	550 ± 186	-	60 ± 49	226 ± 207	-	29 ± 21	32 ± 19	82 ± 53	6 ± 6	111 ± 88
J. ocia (Spence Bate, 1862)	7 ± 7	77 ± 56	35 ± 10	4 ± 4	-	-	10 ± 10	-	19 ± 12	51 ± 30	12 ± 7	235 ± 99	-	30 ± 16	61 ± 61
Lembos websteri Spence Bate, 1857	329 ± 21	919 ± 144	261 ± 75	-	-	-	-	-	-	8 ± 8	55 ± 55	56 ± 26	30 ± 30	12 ± 12	173 ± 130
Leucothoe spinicarpa (Abildgaard, 1789)	2 ± 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monocorophium insidiosum (Crawford, 1937)	33 ± 24	23 ± 19	25 ± 19	-	-	-	-	-	-	6 ± 6	4 ± 4	38 ± 20	-	-	-
Podocerus variegatus Leach, 1814	14 ± 10	-	8 ± 8	3 ± 2	-	-	-	4 ± 4	7 ± 7	-	20 ± 10	38 ± 38	15 ± 15	-	-
Quadrimaera inaequipes (A. Costa in Hope, 1851)	-	-	-	-	-	-	-	-	-	-	2 ± 2	2 ± 2	-	-	-
Stenothoe eduardi Krapp-Schickel, 1975	162 ± 23	155 ± 77	368 ± 137	502 ± 125	431 ± 170	429 ± 8	3 ± 3	13 ± 13	93 ± 93	11 ± 11	255 ± 170	47 ± 19	15 ± 15	132 ± 52	323 ± 237
S. monoculoides (Montagu, 1813)	4618 ± 1541	4299 ± 931	3220 ± 1519	-	-	-	72 ± 30	291 ± 18	134 ± 74	178 ± 107	73 ± 61	125 ± 22	428 ± 241	991 ± 345	2226 ± 1579
S. tergestina (Nebeski, 1881)	109 ± 64	57 ± 34	212 ± 111	83 ± 22	124 ± 51	154 ± 32	10 ± 10	7 ± 7	70 ± 70	252 ± 122	116 ± 81	152 ± 77	-	79 ± 62	127 ± 127

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Table 3: Nested ANOVA table of results for species richness and total abundance of amphipods among different substrates. Ha: Habitat [five levels: N (natural rocky shore), R (rip-rap), A (acropod), C (cube) and SW (seawall)]; Si (Ha): Site; df: degrees of freedom; MS: mean square; p: level of significance; **: $p < 0.01$; n.s.: not significant.

Total abundance				
Source of variation	df	MS	F	p
Ha	4	3715	11.09	**
Si (Ha)	10	335	1.24	n.s.
Residual	30	269		
Total	44			
Cochran's test	n.s.			
Transformation	Square root			
SNK tests	Levels of factor 'Ha' N>(A,C,SW,R), SW<R, A=C=SW			
Species Richness				
Source of variation	df	MS	F	p
Ha	4	99.97	14.06	**
Si (Ha)	10	7.11	0.99	n.s.
Residual	30	7.20		
Total	44			
Cochran's test	n.s.			
Transformation	None			
SNK tests	Levels of factor 'Ha' N>(A,C,SW,R), A=C=SW=R			

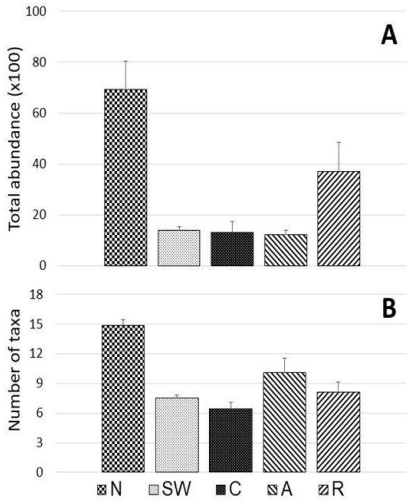

Fig. 3: Total average abundance of amphipods (A) and species richness (B) in the five substrates sampled. Error bars: standard error, N: natural rocky shore; SW: seawall; C: cube; A: acropod; R: rip-rap.

In contrast, seawalls were numerically dominated by *Stenothoe eduardi*, *Jassa marmorata* and *Ampithoe riedli*; on the contrary, species that were abundant in other substrates (e.g. *S. monoculoides* and *C. grandimana*) were completely absent from seawalls. Regarding acropods, *Hyale perieri* was the only species that was clearly more abundant than other taxa. Differences in assemblage structure (species composition and abundances) among substrates were further confirmed by PERMANOVA (Table 4). There were significant differences in the volumes of each replicate. Amphipod assemblage structure significantly differed among substrates except for cubes and acropods (see pair-wise tests in Table 4). Factor "Site" was also significant and pair-wise tests (data not shown) revealed that it was due to a single difference between 'natural site 2' and 'natural site 3' mainly caused by differences in the abundance of dominant species (e.g. *Caprella penantis*, *J. marmorata*, *Stenothoe tergestina*). In fact, factor "Site" was not significant when presence/absence data was considered. Differences were also graphically portrayed by the dendrogram (Fig. 2A), where the different substrates were segregated in four groups (at a similarity level of 40%). Interestingly, the segregation of sites in the dendrogram

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was somehow concordant with the more abundant sessile taxon/taxa in terms of volume at each site (Fig. 2B). In fact, there were high correlation values (Table 5) among some amphipods and certain sessile species, independent of the primary substrate (i. e. habitat): *S. eduardi* and *J. marmorata* correlated with *M. galloprovincialis* and *P. perforatus*, while *S. monoculoides* and *L. websteri* correlated with *E. elongata* and *J. rubens*. On the other hand, other numerically dominant taxa such as *Elasmopus* spp. and *C. grandimana* did not show any preference for the secondary substrate.

Table 4: PERMANOVA table of results for amphipod assemblage (based on taxa composition and abundances). Ha: Habitat [five levels: N (natural rocky shore), R (rip-rap), A (acropod), C (cube) and SW (seawall)]; Si (Ha): Site nested to Habitat; CO: covariate (volume of secondary substrate); df: degrees of freedom; MS: mean square; p: level of significance; *: $p < 0.05$; ***: $p < 0.001$.

Amphipod assemblage				
Source of variation	df	MS	Pseudo-F	p
CO	1	22414	16.412	***
Ha	4	7597	5.2758	***
Si (Ha)	10	1502.6	1.3766	*
Residual	29	1091.6		
Total	44			
Pair-wise tests	Levels of factor Ha: N≠(A,C,SW,R), SW≠(A,C,R), C≠R, A≠R Levels of factor Si (Ha): Only difference detected between 'natural site 2' and 'natural site 3'.			

According to SIMPER analysis (Table 6), rip-raps were the least dissimilar substrate compare to natural ones (48.85% average dissimilarity) while seawalls were the most dissimilar substrate (64.17% average dissimilarity). *Stenothoe monoculoides*, *H. stebbingi* and *L. websteri* were always the species that contributed more to the dissimilarity between the natural and artificial substrates. Results of dbRDA (Fig. 4, Table 7) yielded a model of abiotic variables (macro, micro, crystall., age and magnesium) that significantly explained ($p < 0.01$) 65.7% of the total inertia but according to the marginal effects, only micro-scale roughness was significantly correlated with the amphipod composition. According to dbRDA plots, the vectors of the drivers showed the importance of crystallinity, age and macro scale roughness for the assemblage of the natural rocky shore. Similarly, those were also the principal drivers for the assemblage of seawalls, that had very different amphipod assemblages compared to natural

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ones. The results also represent that the main driver for rip-raps, acropods and cubes was micro-scale roughness.

Table 5: Values of Spearman's correlation coefficient among selected amphipod and sessile species. Only amphipods that had high contributions (> 5.99 %) to dissimilarity between natural and each of the artificial substrates are included. Shaded cells indicate high correlations (> 0.7).

	H. stebbingi	*S. monoculoides*	*S. eduardi*	*J. marmorata*	*Elasmopus* spp.	*L. websteri*	*C. grandimana*
E. elongata	0.364	0.878	0.044	0.173	0.489	0.881	-0.016
M. galloprovincialis	-0.420	-0.360	0.756	0.859	-0.222	-0.270	-0.314
P. perforatus	-0.533	-0.477	0.641	0.744	-0.317	-0.352	-0.310
S/D reef	0.128	0.545	-0.069	-0.336	0.449	0.716	-0.120
J. rubens	0.277	0.703	-0.001	-0.132	0.359	0.966	-0.043

When using the sessile community as a predictor variable, dbRDA results provided a highly significant ($p < 0.001$) model that explained 82.3% of the total inertia (Table 7). Only the marginal effect of *E. elongata* was significantly correlated with the amphipod assemblages. The assemblage on the natural rocky shore was separated from the artificial ones, correlating with *E. elongata*, *J. rubens*, *Ceramium* sp., *Spirobranchus* sp./*Dendropoma* sp. reef, *Laurencia* sp. and *L. incrustans* (Fig. 4). The assemblages of artificial substrates were separated in two main groups along axis 1, with the seawalls' assemblage correlated with *M. galloprovinciallis*, *Ulva* sp. and *R. okamurae*.

Table 6: Results of SIMPER analysis comparing amphipod composition in the natural rocky shore site with each of the four artificial substrates. Only dominant species are included. Av.Diss: Average dissimilarity; SD: standard deviation; Contrib.: contribution to dissimilarity.

Amphipod assemblage					
Groups ***Natural*** *&* ***Rip-rap***			*Groups* ***Natural*** *&* ***Acropod***		
Average dissimilarity = 48.85 %			Average dissimilarity = 58.17 %		
Species	Av.Diss. ± SD	Contrib.%	Species	Av.Diss. ± SD	Contrib.%
S. monoculoides	10.55 ± 1.67	21.60	*S. monoculoides*	16.13 ± 2.78	27.73
H. stebbingi	5.51 ± 1.42	11.27	*H. stebbingi*	7.12 ± 1.44	12.24
L. websteri	3.77 ± 2.47	10.45	*L. websteri*	5.60 ± 1.91	9.62
Elasmopus spp.	3.04 ± 1.48	7.73	*S. eduardi*	3.32 ± 1.60	5.72
Groups ***Natural*** *&* ***Cube***			*Groups* ***Natural*** *&* ***Seawall***		
Average dissimilarity = 64.01 %			Average dissimilarity = 64.17 %		
Species	Av.Diss. ± SD	Contrib.%	Species	Av.Diss. ± SD	Contrib.%
S. monoculoides	16.65 ± 2.29	26.01	*S. monoculoides*	19.59 ± 4.37	30.52
L. websteri	7.41 ± 3.04	11.58	*H. stebbingi*	8.24 ± 1.72	12.84
H. stebbingi	6.20 ± 1.41	9.69	*L. websteri*	7.00 ± 3.16	10.90
C. grandimana	4.27 ± 1.23	6.67	*C. grandimana*	4.24 ± 2.52	6.60
			J. marmorata	3.84 ± 1.78	5.99

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Discussion

Overall, our results support the main hypothesis that this natural rocky intertidal coast harbours a different amphipod assemblage in comparison to the assemblage present on coastal defence structures. Differences were also found among different types of artificial structures (except for the comparison between cubes and acropods). Differences at the community structure level have been widely reported (Firth et al., 2016) for sessile fauna but few studies have taken into account the vagile fauna, and the amphipod assemblage in particular (Moura et al., 2008). The increasing armouring of the coast is replacing important functions (Dugan et al., 2011; Gittman et al., 2016) of natural habitats such as acting as nursery grounds for juvenile fish. Although eco-engineering measures are aiming to restore the conditions sustained by natural habitats (Perkins et al., 2015) providing multifunctional approaches (Dafforn et al., 2015; Strain et al., 2017), new measures should take into account the important role of vagile fauna. Indeed, amphipods and polychaetes constitute an important food source for fish associated with artificial structures (Duffy-Anderson and Able, 2001; Munsch et al., 2015). Cordell et al. (2017) stated that piers held less diverse invertebrate assemblages that in turn affect the availability of fish's prey. This concurs with our results; in fact, artificial substrates held less amphipod taxa and smaller total average abundances compared to the natural rocky shore. Therefore, this could affect the availability of prey depending on the substrate type (Munsch et al., 2015). The natural rocky shore had significantly higher total amphipod abundance that also translated into a higher number of amphipod taxa. In contrast, among artificial substrates, rips-raps showed the highest amphipod abundance, but the number of amphipod taxa was similar in comparison to the other artificial substrates, suggesting that the amphipod assemblage on the artificial structures was more homogenous (Firth et al., 2016) and that the occurrence of new taxa was not dependent on the amphipod abundance. Rip-raps shared with the natural rocky shore 15 out of 20 amphipod taxa identified. As a consequence, rip-raps were the most similar (according to similarity percentages) to the natural rocky shore while the seawall was the least similar.

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Table 7: Permutation test for dbRDA under reduced model for all constrained eigenvalues and the marginal effects of each variable tested. Proportion of the inertia explained by the model is provided. df: degrees of freedom; SS: sum of squares; p: level of significance; *: $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s.: not significant.

Amphipods + Abiotic				
	df	% Explained	F	p
Constrained model	5	65.7%	3.448	**
Residual	9			
	df	SS	F	p
Macro-scale roughness	1	0.2800	1.7191	n.s.
Micro-scale roughness	1	0.8530	5.2381	**
Crystallinity	1	0.1875	1.1514	n.s.
Age	1	0.1954	1.1999	n.s.
Magnesium	1	0.3668	2.2522	n.s.
Residual	9	1.4656		
Amphipods + Biotic (sessile)				
	df	% Explained	F	P
Constrained model	5	82.3%	2.5854	***
Residual	9			
	df	SS	F	p
E. elongata	1	0.3768	2.4924	*
M. galloprovincialis	1	0.3086	2.0415	n.s.
S/D reef	1	0.2860	1.8918	n.s.
J. rubens	1	0.1722	1.1392	n.s.
Ceramium sp.	1	0.1055	0.6978	n.s.
Laurencia sp.	1	0.1601	1.0592	n.s.
L. incrustans	1	0.1149	0.7601	n.s.
Ulva sp.	1	0.1282	0.8479	n.s.
R. okamurae	1	0.1024	0.6775	n.s.
Residual	5	0.7558		

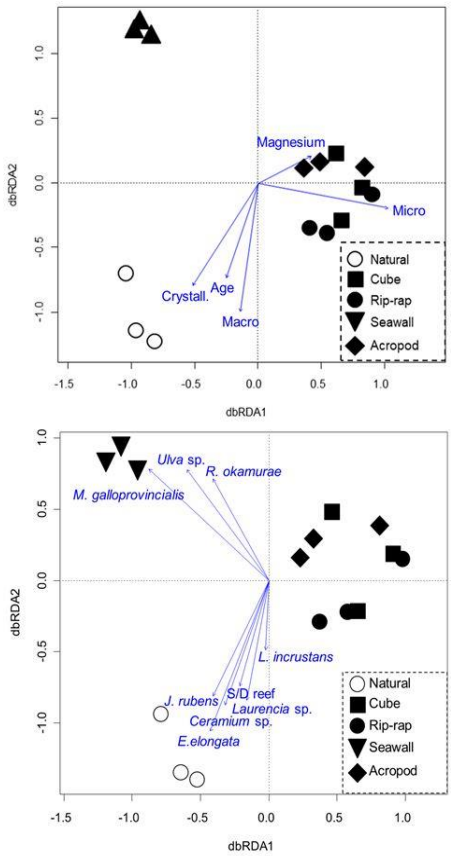

Fig. 4: dbRDA plots of correlations between amphipod assemblage and abiotic data (up) and sessile taxa (down). Dark symbols: artificial substrates; White symbols: natural rocky shore.

Rip-raps have been previously identified as poor surrogates of natural rocky shores (Gacia et al., 2007; Moschella et al., 2005; Sedano et al., 2019) but according to our results, rip-raps seem to perform better than concrete-based substrates (cubes, acropods and seawall). The benefits of incorporating boulder habitats (e.g. rip-raps) have been reviewed by Liversage and Chapman (2018) and furthermore, a meta-analysis by Gittman et al. (2016) showed no differences between rip-raps and natural substrates. The higher similarities between rip-raps and natural habitats may be due to the fact that the former is the only studied artificial substrate built with natural rock. Concrete-based structures are known to raise pH levels and exude toxic components (Ido and Shimrit, 2015) that may stress the associated assemblages, although this

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may be more relevant for sessile species. Within abiotic variables, only micro-scale roughness significantly correlated with the amphipod assemblage. In agreement with our results, a previous experiment focused on ecological engineering revealed the positive response of mobile epibiota (including several families of amphipods) to increasing small-scale complexity of artificial substrates (Lavender et al., 2017). Higher micro-scale roughness can increase refuge availability against stressful environmental conditions and predators (Loke et al., 2017; Strain et al., 2018) giving a competitive advantage to free living or cavity dwelling amphipods. This could be the case of *H. stebbingi*, a species that normally lives tightly associated with algae (Guerra-García et al., 2011a; Izquierdo and Guerra-García, 2011). *Hyale stebbingi* did not correlate with any sessile substrate and was also abundant on cubes, where the phytal substrate was scarce, maybe taking advantage of the highly complex pits and crevices that are colonized by turf algae such as *Ceramium* sp. and *Gelidium* sp. In contrast, *Hyale perieri* was abundant on acropods. *H. perieri* is well adapted to phytal substrates (Scipione, 2011) and can inhabit upper levels of the intertidal that are heavily affected by desiccation (Guerra-García et al., 2011a). It also presents cavity dwelling behaviour and is known to live in association with molluscs (Vader, 1972). Furthermore, this species can reach bigger sizes than *H. stebbingi*, and potentially outcompete the latter in smoothed substrates such as acropods and seawalls. However, further experimental approach would be needed to confirm this hypothesis.

Age, macro-scale roughness and crystallinity were also identified as the main drivers of the assemblages associated with the natural rocky shore and seawalls. The natural rocky shore was rich in quartz and therefore had a more crystalline mineral structure than other substrates, promoting micro-textured surfaces. Berntsson et al. (2000) related micro-textured surfaces with a reduction of 92% in settlement and recruitment of barnacles compared to smooth surfaces. This may explain the scarce presence of barnacles in the natural rocky shore. Along with our results, alkaline cements are known to boost the recruitment of barnacles in concrete structures (Guilbeau et al., 2003) and therefore the absence of cement could explain the scarce presence of barnacles in rip-raps.

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Our results support one of the initial hypotheses: sessile substrates play a key role in the observed differences in amphipod structure between habitats (both natural and artificial). In fact, the dbRDA using the sessile community as an explanatory variable, yielded a highly significant model that accounted for 82.3% of the total inertia suggesting a tight relationship between the secondary substrates and the amphipod assemblages. *Ellisolandia elongata* and *Mytilus galloprovincialis* were the most abundant secondary substrates found in this study. They provided large volumes of habitable substrate for epifauna, but with different surface complexity and therefore different surface area available for colonization (Loke and Todd, 2016). Measurements of the fractal dimensions (D) of *E. elongata* and *Mytillus* beds have provided different results (Kostylev et al., 1997; Commito and Rusignuolo, 2000; Martínez-Laiz et al., 2018). The difference in this morphological measure between *E. elongata* and *M. galloprovincialis* provides different refuge size and different water retention capabilities, therefore, it could be an important factor driving the development of different intertidal amphipod assemblages between substrates.

The most abundant amphipod species in the natural rocky shore was *Stenothoe monoculoides*, a small amphipod well adapted to live on phytal substrates such as *E. elongata* (Izquierdo and Guerra-García, 2011). Its abundance correlated well with *E. elongata* while *S. eduardi* presented the opposite pattern by correlating with *M. galloprovincialis*. *Stenothoe eduardi* is bigger than *S. monoculoides*, is known to inhabit within the cavity of other invertebrates (Krapp-Schickel and Vader, 2015) and is also a good competitor under high sedimentation rates (Lattanzi et al., 2013). Indeed, we observed a higher retention of sediment (personal observation) in the samples with high abundances of filter feeding species (i.e. mussels and barnacles on the seawall). These may have permitted a better adaptation of *S. eduardi* to the environment present on the seawall. Similarly, Yakovis et al. (2007) highlighted how the cavity-loaded structures of barnacles can shape the associated macrofauna. The different habitat distribution showed by *S. monoculoides* and *S. eduardi*, as well as the almost opposite patterns of abundance reported above for *H. stebbingi* and *H. perieri*, points out the relevance of species-level identification. Epifaunal responses to environmental perturbations

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often occur in very complex and specific ways, so that many ecological impacts can be easily overlooked when many different taxa are grouped as simple higher taxonomical units (Maggi et al., 2015; Navarro-Barranco et al., 2019).

In a similar way to *S. eduardi*, abundance of the suspension feeder *J. marmorata* correlated with the abundance of mussels and barnacles. As shown in our results, *J. marmorata* is considered an opportunistic species well adapted to anthropized environments and a very quick colonizer (Beermann and Franke, 2012). The sediment, useful as a binder (Kronenberger et al., 2012), accumulated between the spaces of barnacles and mussels, and the wide surfaces of mussels could provide a suitable substrate for the development of tube-builders, similar to that found by Aikins and Kikuchi (2001) that related higher abundance of tube-builders in broad foliate thalli of algae. Furthermore, the vertical seawalls dissipate wave energy deficiently (Jung et al., 2012) and the construction of tubes may present an advantage over free living species. In contrast, *L. websteri*, another tube-builder, was absent from seawalls and barely present in the other artificial substrates; however, it was very abundant in natural ones, probably due to its low tolerance to stress as it is indicated by its inclusion in the AZTI Marine Biotic Index (AMBI - List of June 2017) (Borja et al., 2000).

Contrarily, some species did not show a close relationship with the secondary substrate and their occurrence in a particular substrate could be more related to other abiotic variables (e.g. the abovementioned case of *Hyale* species) such as substrate roughness or the surrounding environment, rather than the availability of a suitable secondary substrate to attach. In a similar way, Navarro-Barranco et al. (2015) suggested that different sessile invertebrates played equivalent facilitation roles over amphipod assemblages (non-host specialists) indicating that different sessile substrates could have comparable host functions (Bates and DeWreede, 2007; Saarinen et al., 2018). However, Navarro-Barranco et al. (2015) studied subtidal assemblages inhabiting a marine cave under presumably less stressful conditions than those found in our intertidal scenario, where some species presented tight relationships with the sessile taxa, suggesting that the occurrence or dominance on artificial substrates of certain species could be driven by species-specific facilitation processes (Bulleri et al., 2016). Therefore, our results

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could be reflecting the importance of diverse secondary substrates (e.g. with different morphological complexities) in hosting different assemblages under stressful conditions. In accordance to this, Saarinen et al. (2018) found that intertidal communities dominated by foliose algae held a different amphipod assemblage when compared to the controls (eight seaweed species of different functional groups) demonstrating that the identity of the secondary substrate was important under stressful abiotic conditions.

Interestingly, we did not find any non-indigenous species (NIS) in the artificial substrates of the present study. However, other studies conducted inside marinas from nearby areas have reported several NIS inhabiting artificial substrates (e.g. floating pontoons) (Ros et al., 2013a). Fouling transport associated to recreational boating between marinas seems to be an effective vector for the establishment of exotic amphipods within them, but not in the surrounding substrates outside (Ros et al., 2013b). This suggests that exotic amphipods remain concentrated inside the marinas even when there are available artificial substrates to colonize outside.

It is also worth noting that it is not only the distinctiveness of the artificial substrate (or its secondary effects), but also its accessibility that could partially affect the successful establishment of certain species. For example, the caprellids *Caprella grandimana* and *C. penantis* were absent on the seawall, which is the only substrate not connected to mainland. Therefore, their absence could be related to their reduced swimming capability (due to reduction of pleopods) in comparison with other amphipod families (Takeuchi, 1998), as well as the inability of the abovementioned species to be dispersed by rafting or attached to fouling communities. The connectivity of offshore structures may have a relevant role in facilitating the proper colonization by surrounding species. This colonization impediment may lead to comparatively impoverished amphipod assemblages on offshore artificial substrates that could be easily outcompeted by opportunistic species. Sanabria-Fernández et al. (2018) pointed out the relevance of species mobility in the colonization of breakwaters. Biodiversity loss (in comparison with nearby natural habitats) was higher for those species with lower mobility. Therefore, eco-engineering actions directed to facilitate the establishment of native

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assemblages should take into account the deployment location and the different taxa accessibility to it.

Conclusions

In conclusion, according to our results, a number of physical attributes, including micro-scale roughness, seem to be the main factors driving the development of intertidal amphipod assemblages when comparing the performance of artificial habitats to natural rocky shores, and it should be considered in future eco-engineering actions. According to the influence of the secondary substrate, amphipod assemblages associated with artificial structures showing greater abundances of mussels and barnacles (i.e. concrete-made) were clearly different from those on habitats with higher abundances of coralline algae (i.e. rip-raps and natural). Both mussels and coralline algae provided large volumes of available habitat for epifauna but with very different complexity. Therefore, artificial structures are shaping the amphipod assemblage directly through the provision of new habitats and conditions but also indirectly through facilitation effects exerted by the different sessile taxa, which should be taken into account when considering the successful establishment of sustainable structures. Further studies should sample the same secondary substrates (sessile biota) across different artificial substrates in order to separate the direct effects (caused by the artificial substrate) from the indirect effects (caused by the sessile biota). Also, similar experiments should be conducted in different seasons in order to ascertain if the patterns observed are affected by seasonality.

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CHAPTER 2: Is the impact of coastal infrastructure constant at regional level?

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2.1 Coastal armouring produces intertidal biodiversity loss across the Alboran Sea (western Mediterranean Sea)

General hypothesis: Intertidal biodiversity loss will be observed at every artificial structure and locality independently of substrate type across the Alboran Sea. Seawalls will have the lowest ecological value while rip-raps will have the highest. The expected patterns will be influenced by the spatial scale of the study, the environmental gradient presented in the area and the individual local conditions.

2.2 Algae canopy and biodiversity loss on Crete's rip-raps (Greece)

General hypothesis: Biodiversity will be lower on rip-raps in comparison with natural rocky shores across the island independently of locality or orientation (north/south). Community structure and function (in terms of macroalgal structural complexity) will differ between natural and artificial substrates, having the latter an impoverished algal canopy.

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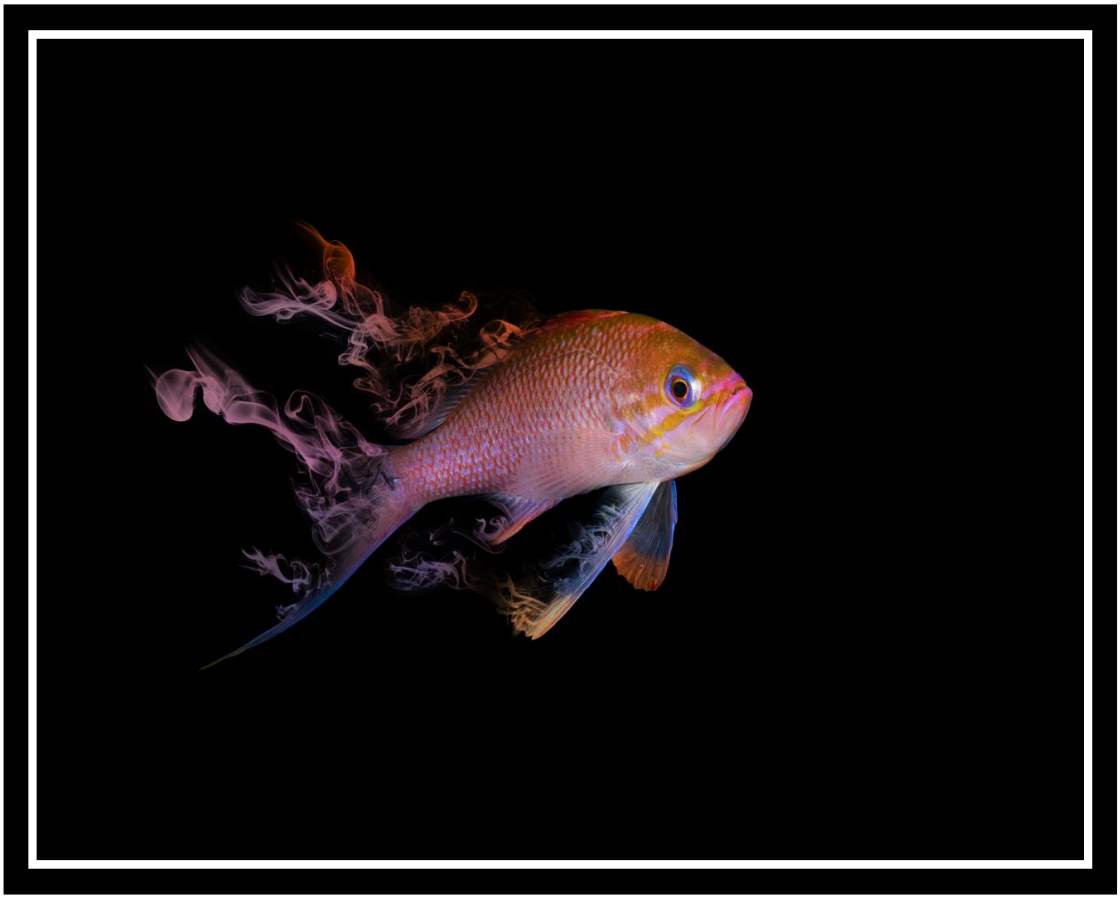
CHAPTER 2.1



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2.1 Coastal armouring produces intertidal biodiversity loss across the Alboran Sea (western Mediterranean Sea)

Adapted from: Sedano, F., Pavón, A., Navarro-Barranco, C., Guerra-García, J.M., Digenis, M., Sempere-Valverde, J., Espinosa, F. (Submitted to journal). Coastal armouring produces intertidal biodiversity loss across the Alboran Sea (western Mediterranean Sea). Ecological Engineering.

Abstract

Intertidal ecosystems are key habitats that are being replaced by artificial hard substrates due to the increment of human activities in coastal areas. These new substrates are generally less biodiverse due to differences in complexity and composition among others. This biodiversity loss is a global phenomenon and has led to the development of mitigating strategies in the framework of eco-engineering. However, mitigating measures, such as new eco-designs, must cope with the high spatial variability of the region where they are applied. Therefore, in order to asses if the biodiversity loss detected at local scales in previous studies could be scaled up to predict patterns at a wider scale, we studied taxa richness and taxonomic structure of intertidal communities across the Alboran Sea (western Mediterranean Sea). We compared four different types of artificial substrates (cubes, rip-raps, seawalls and tetrapods) to assess which produces less impact. Overall, there was a biodiversity loss on artificial substrates across the Alboran Sea. This loss was minimized on boulder-like artificial structures, specially on rip-raps, while it was maximized on seawalls. Nevertheless, the effect of a particular type of artificial structure at a regional scale seems unpredictable, highlighting the challenge that eco-engineering measures face in order to establish global protocols for biodiversity enhancement and the importance of local scale in management programmes.

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Introduction

Intertidal ecosystems are important areas due to their high ecological value and numerous services provided (Branch et al., 2008; Cacabelos et al., 2019) but at the same time they are threatened by climate change and anthropogenic alterations. The sea level rise coupled with the increasing use of coastal areas by a range of human activities (commercial, touristic and recreational) is leading to the destruction, pollution and overexploitation of intertidal ecosystems (Bulleri et al., 2005; Firth et al., 2016a; Helmuth et al., 2006). One of the biggest impacts is the replacement of natural shores or addition of new hard substrates (Gittman et al., 2016). These new substrates are usually concrete defence infrastructures such as seawalls or boulders that currently cover a considerable number of European coasts (Beck and Airoldi, 2007; Ido and Shimrit, 2015). They are generally considered less biodiverse than the natural substrates they replace (see Firth et al., 2016a for a review) due to differences in composition, substrate complexity and surface inclination among others (Coombes et al., 2015; Ido and Shimrit, 2015; Loke et al., 2015; Moreira et al., 2006). Specifically, the lack of complexity and extreme steep inclination of seawalls can limit the number of taxa that recruits or survive on them (Bulleri, 2005). Due to the reduction of intertidal space and higher competition on seawalls, the populations of some limpets have been compromised (Moreira et al., 2006). Lai et al. (2018) suggested that the steep slope of seawalls diminishes the primary productivity potential, limiting the populations of grazers, specially gastropods that feed on turf algae. Seawalls are often more exposed and dissipate wave action less efficiently than boulder habitats, promoting the preferential establishment of certain taxa, such as filter feeding organisms (Sedano et al., 2020a), contributing also to the homogenization of intertidal communities (Firth et al., 2016). For these reasons, seawalls are one of the least ecologically valuable artificial structures, which has attracted the attention of researchers who look for mitigation measures in the framework of eco-engineering (Browne and Chapman, 2011; Loke et al., 2017; Moreira et al., 2007).

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In contrast, boulder habitats can be occupied by more species since they have gentler slopes and higher structural complexity than seawalls (Liversage and Chapman, 2018). For example, the presence of tide pools (Evans et al., 2016; Ostalé-Valriberas et al., 2018) and shady sheltered environments (Sherrard et al., 2016) can favour more diverse communities and even increase the presence of rare or endangered species (García-Gómez et al., 2011) or taxa of commercial importance (Liversage and Chapman, 2018). Consequently, boulder-like artificial structures made of natural rock (rip-raps) have been considered as better surrogates of natural substrates in comparison with other artificial substrates such as concrete cubes or seawalls (Sedano et al., 2020a). Furthermore, the benefits of incorporating boulder habitats in ecological engineering have been reviewed by Liversage and Chapman (2018). However, one of the biggest challenges for coastal managers and environmental policers is the establishment of measures, protocols or ecological designs in this case, that can be applied at great geographical scales in an integrative way (Sanó et al., 2010).

Patterns in nature are intrinsically scale dependent (Terlizzi et al., 2007) and, based on the spatial scale, differences in community structure may be more or less evident (Wiens et al., 1993). This, together with the high spatial variability presented by many taxa, complicates the reliable description of anthropogenic impacts associated with introduced artificial structures (Bishop et al., 2002; Lanham et al., 2018). Therefore, in order to asses if the biodiversity loss associated with artificial substrates detected at local scales in previous studies (Sedano et al., 2020a; 2020b) could be scaled up to predict patterns at a wider scale (Wooton, 2001), we studied the taxa richness ,taxonomic structure (composition of taxa according to their presence/absence) and taxa cover percentages (on vertical exposed surfaces) of intertidal communities across the Alboran Sea (western Mediterranean Sea). Our study included the description of biodiversity patterns on four types of artificial substrates (cubes, rip-raps, seawalls and tetrapods), which were related with abiotic variables of each substrate and their location with the aim of identifying the drivers of biodiversity differences. More specifically, we hypothesized that: 1) Intertidal richness will be lower on artificial substrates in comparison with their nearest natural rocky substrates. This pattern will be observed at every locality

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independently of substrate type across a high spatial scale (i.e., across the Alboran Sea). 2) Taxonomic structure and cover of species will also differ between natural and artificial substrates. We expect that seawalls will have the lowest ecological value and therefore will be the worst surrogates of natural substrates. We also expect that due to their higher complexity and natural composition, rip-raps will be the best surrogates of natural substrates. 3) The expected patterns will be influenced by the spatial scale of the study, the environmental gradient presented in the area and the individual local conditions.

Materials and methods

Biotic and abiotic data collection

In May 2017, we carried out a photographic sampling of four different artificial substrates (three concrete-based: cubes, seawalls and tetrapods, and one natural rock-based: rip-raps) and their nearest natural rocky substrates along the coast of the Alboran Sea (western Mediterranean Sea (Fig. 1, Table 1). Photographs were taken at low intertidal level (5-30 cm over the lowest tidal level).

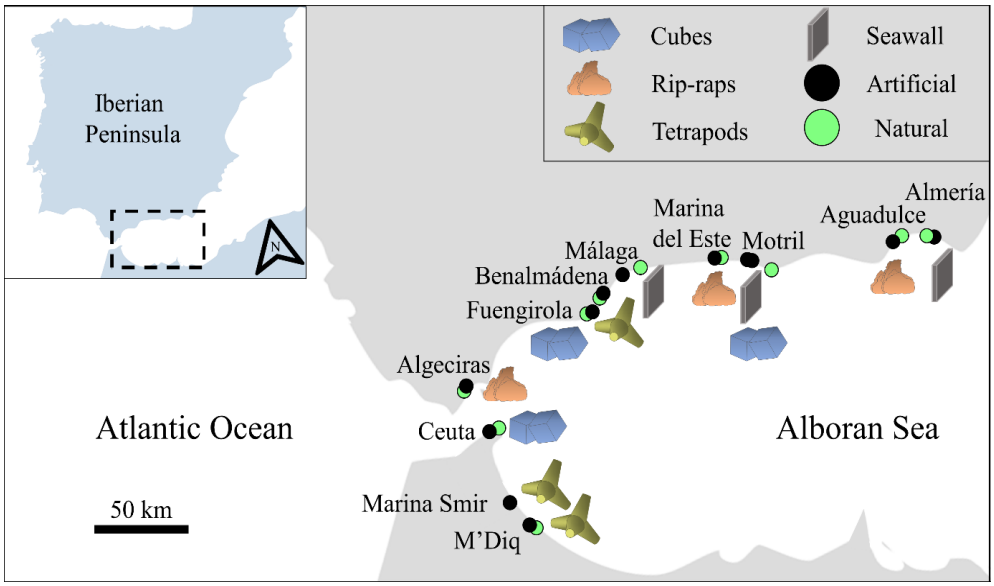

Fig. 1: Sampling map portraying the type of artificial structure sampled at each locality. Note that the closest natural substrate to Marina Smir and M'Diq was the same and that in Motril we sampled two adjacent artificial structures (cubes and seawall).

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Two complementary methodologies were conducted. (i) Taking into account that each kind of substrates can provide different exposure, slope, orientations and microhabitats, global quantitative comparison can be difficult among substrates. Therefore, to properly compare the whole taxonomic structure (taxa composition according to their presence/absence) among substrates (including non-exposed areas, shady places, overhangs, crevices, etc.), we performed three ten-minute transects per substrate at each locality to try to find and photograph as much species as possible. This methodology is an adaptation from the commonly used time transects for bird watching (Hyrenbanch et al., 2007; Van der Meer and Leopold, 1995). In contrast with photoquadrats (used in our second methodology), the use of time transects greatly reduces data collection and post-collection computer analyses of digital photographs (Preskitt et al., 2004), which was a clear advantage for us given the long distance (and the number of replicates) covered in this study. However, using this methodology we could characterised the global intertidal macrobenthic diversity of each substrate, but we could not compare the cover of the different species. (ii) Therefore, to get quantitative data of covers comparable among substrates, we took 15 photoquadrats on vertical exposed faces of each substrate for each locality. The experimental design for each methodology was:

i: Factor Substrate (Su), two levels (artificial, natural), fixed; Factor Locality (Lo), three levels, random and orthogonal with Su. On each substrate, the three 10-minute transects were allocated with tens of metres of separation (20 m to 50 m depending on the length of the substrate).

ii: Factor Substrate (Su), two levels (artificial, natural), fixed; Factor Locality (Lo), three levels, random and orthogonal with Su; and factor Site (Si), three levels, random and nested in Su and Lo. Five 20x20 cm quadrats were photographed at each site. Photos were taken using an Olympus TG4 camera with a Subacqua Helios 1700 focus light. Cover of sessile species was measured by spawning 75 random points using PhotoQuad software (Trygonis and Sini, 2012). Taxa that were present in the photoquadrats but did not fall below a random point were given an arbitrary value of 0.5% cover (Bacchiocchi and Airoldi, 2003; Marzinelli et al., 2011; Ostalé-Valriberas et al., 2018).

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For both methodologies, close-up images were taken to help with species identification, which was done to the lowest possible taxonomic resolution. Along the Alboran Sea, the three localities with cubes were Ceuta (CEU), Fuengirola (FUE) and Motril (MOT); the three with rip-raps were Aguadulce (AGD), Algeciras (ALG) and Marina del Este (MES), the three with seawalls were Almería (ALM), Málaga (MAL) and Motril (MOT), and the three with tetrapods were Benalmádena (BEN), M'Diq (MDQ) and Marina Smir (SMR). The same natural habitat was compared with the cubes and the seawall of Motril, since they were in the same place (Harbour of Motril). Also, the nearest natural rocky shore was the same for the tetrapods of M'Diq and Marina Smir. Therefore, data from both artificial substrates was compared with the same set of data from the same natural rocky shore

The full taxonomic structure (composition of taxa according to their presence/absence, methodology i) as well as the cover percentages of each taxa on the vertical face of each substrate (methodology ii), were related to a set of abiotic variables that included wave exposure, age, roughness, substrate elemental composition, substrate crystallinity and calcination percentages (as a measure of carbonates content). A full description of the abiotic analyses can be found in Sedano et al. (2020a). Briefly, the elemental composition, calcination percentages and crystallinity were quantified (three rock samples by substrate) by Xray fluorescence (XRF). Age of the different artificial substrates was quantified based on the date of construction. Since it is difficult to infer the age of natural substrates, for analytic purposes, we chose the oldest possible date in the same order of magnitude than the oldest artificial substrate. Roughness data included macroscale roughness (order of centimetres) and microscale roughness (order of millimetres). Macroscale roughness was calculated over 15 m length transects. Three transects were selected at each substrate and a flexible meter was laid directly over it, trying to conform as closely as possible to all contours of the bare substrate. Regarding microscale roughness, three 15 cm profile gauges with 0.5 mm pins were pushed onto the bare rock to record the surface of each substrate (Frost et al., 2005). Finally, wave exposure was quantified at each substrate using the modified effective fetch index developed by Howes et al. (1994).

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Table 1.- List of sampling localities ordered from west to east. [+]: Dolomite, calcite and quartz.

Localities	Coordinates (Latitude/Longitude)	Date of deployment	Distance from nearest natural rock (km)	Dominant Mineral
Natural				
M'Diq	35º40'56.87''N/5º18'23.38''W	n.a.	n.a.	Quartz
Marina Smir	35º40'56.87''N/5º18'23.38''W	n.a.	n.a.	Quartz
Ceuta	35º53'50.94''N/5º17'57.46''W	n.a.	n.a.	Quartz
Algeciras	36º06'34.10''N/5º25'55.40''W	n.a.	n.a.	Quartz
Fuengirola	36º30'23.34''N/4º38'21.76''W	n.a.	n.a.	Quartz+Albite
Benalmádena	36º34'47.41''N/4º32'48.25''W	n.a.	n.a.	Quartz
Málaga	36º42'41.73''N/4º19'39.19''W	n.a.	n.a.	Dolomite
Marina del Este	36º43'23.31''N/3º43'35.22''W	n.a.	n.a.	Dolomite
Motril	36º42'10.27''N/3º24'40.06''W	n.a.	n.a.	Quartz
Aguadulce	36º49'11.89''N/2º31'54.64''W	n.a.	n.a.	Dolomite
Almería	36º49'41.48''N/2º29'34.89''W	n.a.	n.a.	Dolomite
Cubes				
Ceuta	35º54'01.03''N/5º19'27.26''W	2004	2.3	Dolomite
Fuengirola	36º32'31.83''N/4º36'51.25''W	1986*	4.6	Dolomite
Motril	36º43'07.38''N/3º31'29.14''W	1986*	10.4	Dolomite+
Rip-raps				
Algeciras	36º07'01.20''N/5º26'07.90''W	1997	0.9	Calcite
Marina del Este	36º43'31.00''N/3º43'32.66''W	1986*	0.3	Calcite
Aguadulce	36º48'58.70''N/2º33'20.98''W	1989*	2.4	Dolomite
Seawalls				
Málaga	36º42'28.57''N/4º24'42.84''W	2003*	7.4	Dolomite
Motril	36º42'59.64''N/3º31'15.12''W	2003*	10.4	Dolomite
Almería	36º49'38.97''N/2º28'55.04''W	2015	0.9	Dolomite
Tetrapods				
Marina Smir	35º45'25.57''N/5º20'28.19''W	2003*	8.8	Quartz+Calcite
M'Diq	35º41'03.12''N/5º18'40.51''W	2009*	0.5	Dolomite+Quartz
Benalmádena	36º35'50.06''N/4º30'28.52''W	1986*	4.0	Dolomite

*Older data estimated according to historical aerial images from Google Earth and http://fototeca.cnig.es; n.a.: not pplicable

Statistical analyses

Number of unique taxa per substrate and shared taxa among substrates was calculated using a Venn diagram (http://bioinformatics.psb.ugent.be/). Differences between artificial and natural substrates in taxa richness found during the ten-minute transects were evaluated using two-way analysis of variance (ANOVA) with the abovementioned experimental design (i). Also, differences in taxa cover percentages of the most abundant taxa (> 20% of average abundance per site) on vertical faces were evaluated using three-way ANOVA with the (ii) design mentioned above. Homogeneity of variances was confirmed using Cochran's test. Data were transformed when there was heterogeneity of variances [square root or log(x+1)]. If the transformation was unsuccessful, analysis was carried out with untransformed data and

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significance level was lowered to $p < 0.01$ to reduce Type I error. When ANOVA detected significant differences for a given factor or interaction, the source of the difference was identified by applying the Student-Newman-Keuls (SNK) test (Underwood, 1997).

We tested the effect of Substrate and Locality on the full taxonomic structure (global macrobenthic diversity, methodology i), as well as on the taxa cover percentages on vertical faces (methodology ii), of each substrate type by using permutational analysis of variance (PERMANOVA). Analyses were run on a triangular similarity matrix derived from the values of the Bray-Curtis similarity on untransformed taxonomic structure data using 9999 permutations. In cases of small numbers of unique permutations (100 or less), p-values were obtained through a Monte Carlo test (Anderson et al., 2008). Non-metric multidimensional scaling (MDS) based on Bray Curtis similarities was used to visually interpret the similarities between substrates and among localities for both, the full taxonomic structure (methodology i) and the cover percentages on vertical faces (methodology ii). MDS was also used to interpret the influence of latitude (from western to eastern Alboran Sea) in structuring the taxonomic structure (presence/absence) of communities across the Alboran Sea. Localities were sorted in four regions as follows: West region (ALG, CEU, MDQ, SMR), Middle West region (BEN, FUE, MAL), Middle East region (MES, MOT) and East region (AGD, ALM). Significant differences for the taxonomic structure among regions were tested using unbalanced PERMANOVA with two factors: Factor Region (Re), a fixed factor with the abovementioned four levels; and Factor Locality (Lo), a random factor nested in Region with eleven levels (each of the studied localities).

Bray-Curtis dissimilarity between substrates (natural vs each of the artificial ones) was also calculated with SIMPER (SIMilarity PERcentages) in order to identify the species that contributed the most to the differences between substrates in both cases (full taxonomic structure and cover percentage on vertical faces).

To relate the abiotic variables measured with the taxonomic structure as well as with the taxa cover on the vertical faces, we carried out a constrained ordination approach. We considered calcination percentage (carbonates content), roughness (macro- and microscale),

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crystallinity, age and elemental composition (only elements with a relevant concentration: silicon, calcium and magnesium; full composition in Supplementary Table 5). We used distance-based Redundancy Analyses (dbRDA) for the taxonomic structure and Canonical Correspondence Analyses (CCA) for the taxa cover percentage on the vertical faces since data fitted a linear and unimodal species response respectively. Linearity was deducted as in Ter Braak and Smilauer (1998) according to the first axis length in Detrended Correspondence Analysis (DCA) (< 3, linear; > 4, unimodal). Prior to analyses, multicollinearity between abiotic factors was tested using Draftsman plots based on Spearman correlation. Only one abiotic factor was used in the analyses when there were high pairs of correlation ($r > 0.80$, Chatzinikolau et al., 2016). If the constrained ordination still portrayed collinearity between abiotic factors, the variable most affected was eliminated attending to Variance Inflation Factor (VIF) in order to avoid misinterpretation of data due to unstable canonical coefficients (Ter Braak, 1988). Collinearity was neglected when VIF < 10 according to Dormann et al. (2013). dbRDA and CCA were run using untransformed biological data paired with standardized abiotic matrix. Significance levels ($p < 0.05$) were calculated under 9999 random permutations.

A Principal Component Analysis (PCA) ordination, performed on normalized data, was used to display the relationship among substrates according to the variables used in the constrained ordination after performing the variables selection (i.e.: Calcium, Magnesium, Crystallinity, Macro- and Microscale roughness, Fetch and Age).

Two-way ANOVAs were carried out with GMAV5 software (Underwood et al., 2002). Draftsman Plot, MDS, PCA, SIMPER and PERMANOVA analyses were carried out using PRIMER v.6 + PERMANOVA package (Clarke and Gorley, 2006). CCA, DCA, dbRDA analyses were carried out using RStudio© Version 1.1.453.

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Results

Taxonomic structure. Results of methodology i

Analysing the species that appeared in each type of substrate (Table 2, Fig. 2), we did not find unique taxa appearing on artificial substrates (except for Ostreidae on the seawall of Málaga). In contrast, there were twenty-five species that uniquely appeared on natural substrates. Out of the seventy-seven identified taxa, we found twenty common taxa that were present on all substrates (not necessarily at every locality) (Table 2). Rip-raps were the substrate that shared more unique taxa with natural substrates (six).

In comparison with their nearest natural substrate, the number of taxa was lower on the cubes, seawalls and tetrapods of every locality (Fig. 3), while the rip-raps of Aguadulce had higher number of taxa. From all of the artificial substrates, the seawalls had the lowest average number of taxa (9.8 ± 2.7), while the rip-raps had the highest (19.6 ± 2.2), doubling the number of taxa on seawalls. Cubes and tetrapods had similar average number of taxa (17.7 ± 5.2 and 17.4 ± 3.1 respectively). Results of the two-way ANOVA comparing taxa richness are included in Supplementary Table 6.

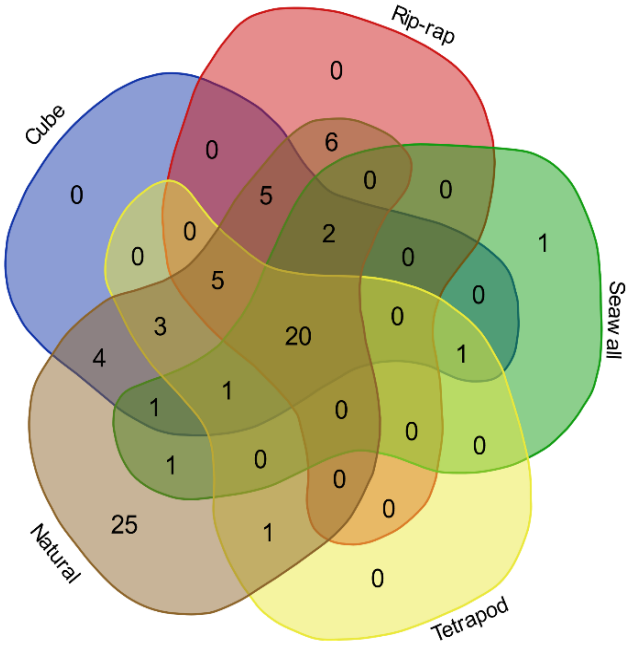

Fig. 2: Venn diagram portraying the number of unique taxa identified at each substrate and the shared taxa among them.

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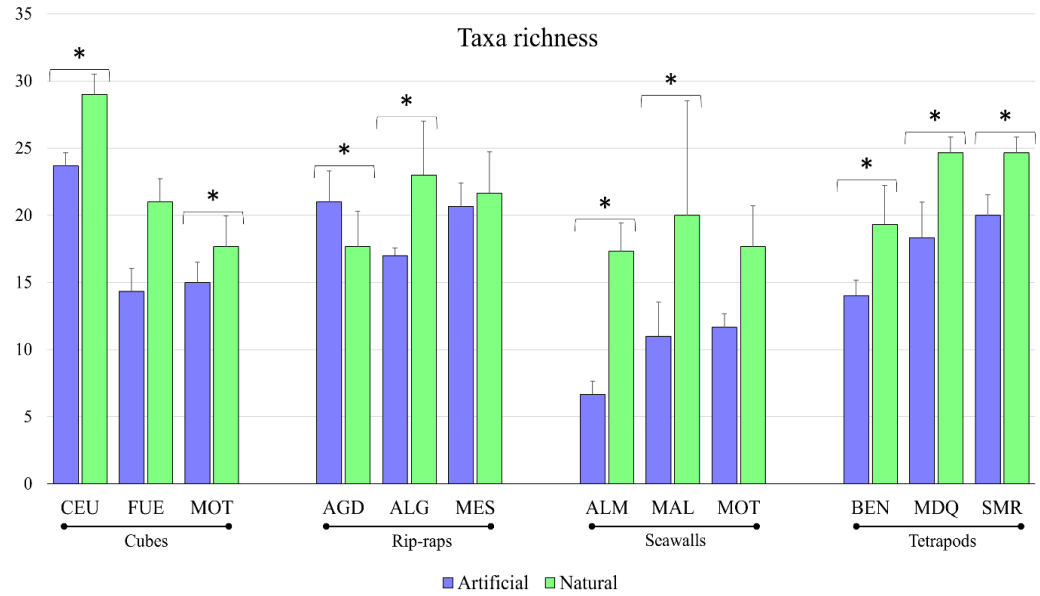

Fig. 3: Number of taxa found on artificial and natural substrates at each locality. Asterisks indicate significant differences detected by two-way ANOVA. CEU: Ceuta, FUE: Fuengirola, MOT: Motril, AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este, ALM: Almería, MAL: Málaga, MOT: Motril, BEN: Benalmádena, MDQ: M'Diq nd SMR: Marina Smir.

Table 2: Frequency of occurrence (%) of every taxa identified at the different substrates. To estimate the frequency of each species in the community, presence/absence data at each substrate per locality were summed (1: presence; 0: absence), ranging from 0 to 3 for each artificial substrates (3 localities sampled: 100%) and from 0 to 10 for natural substrate (10 localities sampled: 100%). Cells shaded in green indicate taxa that uniquely appeared in natural substrates. Cells shaded in blue indicate taxa common to all substrates.

Phyllum	Identified taxa	Rip-rap	Cube	Seawall	Tetrapod	Natural
Cyanobacteria	*Rivularia atra*	0	33	66	0	20
Chlorophyta	*Codium adhaerens*	33	66	0	0	40
	Codium sp.	0	0	0	0	10
	Green filamentous algae	66	66	66	33	90
	Ulva sp.	66	66	0	33	70
	Valonia macrophysa	33	0	0	0	30
Ochrophyta	*Colpomenia sinuosa*	33	33	0	66	30
	Cystoseira spp.	0	33	0	33	70
	Dictyopteris sp.	0	0	0	0	10
	Dictyota cyanoloma	0	33	33	66	0
	Dictyota spp.	0	0	0	33	50
	Fucus spiralis	0	0	0	0	20
	Halopteris spp.	0	0	0	0	10
	Padina pavonica	0	0	0	0	30
	Ralfsia verrucosa	100	100	100	100	100
	Rugulopterix okamurae	0	33	0	0	10
	Sargassum sp.	0	0	0	0	20
Rhodophyta	*Asparagopsis armata*	0	33	0	66	20
	Bangia sp.	33	66	33	33	20

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	Caulacanthus sp.	100	100	66	100	100
	Dichotomic rhodophyta	33	33	0	0	20
	Ellisolandia elongata	100	100	33	100	100
	Encrusting red algae	100	100	33	100	80
	Foliose rhodophyta	0	33	0	0	10
	Gastroclonium sp.	0	0	0	0	40
	Gelidium sp.	100	66	0	0	90
	Hildenbrandia sp.	100	66	33	66	80
	Jania rubens	0	0	0	0	90
	Lithophyllum byssoides	0	33	0	0	10
	Nemalion sp.	33	0	0	0	20
	Pyropia sp.	66	33	0	0	50
	Rhodomelaceae	33	0	0	0	30
	Rissoella verruculosa	0	0	0	0	30
	Turf forming rhodophyta	100	33	33	0	40
Porifera	*Clathrina rubra*	0	0	0	0	10
	Orange sponge	33	66	33	66	10
Cnidaria	*Actinaria* sp.1	0	0	0	0	30
	Actinaria sp.2	0	0	0	0	10
	Actinia equina	100	100	66	100	100
	Aglaophenia pluma	0	0	0	0	20
	Aiptasia mutabilis	0	0	0	0	10
	Anemonia sp.	33	0	0	0	50
	Astroides calycularis	33	33	0	66	30
	Cereus pedunculatus	0	0	0	0	10
Annelida	Serpullidae	0	0	0	0	10
	Spirorbinae	0	0	0	0	30
	Terebellidae	0	0	0	0	10
Mollusca	*Acanthochitona* sp.	3	0	0	0	10
	Cymbula safiana	3	66	33	100	30
	Dendropoma sp.	66	33	33	0	70
	Echinolittorina punctata	66	33	66	66	40
	Fissurellidae	66	66	0	66	60
	Gastrochaena dubia	0	0	0	0	10
	Littorinidae	0	0	33	0	10
	Melarhaphe neritoides	66	33	33	66	40
	Myoforceps aristatus	0	0	0	0	20
	Mytilus sp.	33	66	66	100	80
	Onchidella celtica	0	0	0	0	30
	Ostreidae	0	0	33	0	0
	Patella ferruginea	66	66	33	66	50
	Patella rustica	100	100	66	100	100
	Patella spp.	100	100	100	100	100
	Perna perna	0	0	0	0	20
	Polyplacophora	66	100	0	33	80
	Siphonaria pectinata	100	100	100	100	100
	Stramonita haemastoma	0	66	33	33	20
	Thuridila hopei	0	0	0	0	10
	Trochidae	100	66	100	100	83
	Vermetus triquetrus	33	0	0	0	20
Arthropoda	*Chthamalus stellatus*	100	100	100	100	100
	Eriphia verrucosa	0	0	0	0	20
	Pachygrapsus marmoratus	0	33	0	0	40
	Perforatus perforatus	66	100	100	66	80
	Pollicipes sp.	0	66	0	33	20
Echinodermata	*Arbacia lixula*	66	33	0	0	10
	Paracentrotus lividus	0	0	0	0	10

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PERMANOVA results (Supplementary Table 7) showed significantly different taxonomic structure (presence/absence data) between substrates (interaction SuxLo). According to the pair-wise tests, the taxonomic structure was different between natural and artificial substrates at every locality except three (Marina del Este [Rip-raps], and Motril [Seawalls and Cubes]) (Fig. 4). This was also graphically portrayed in the MDS (Fig. 4), where a clear segregation between artificial and natural substrates is observed for every type of artificial substrate except for the rip-raps, where it is possible to infer some overlapping. In fact, rip-raps had the most similar taxonomic structure in comparison with the natural substrates (see SIMPER in Table 3). The taxonomic structure of the seawalls was the most dissimilar.

Fig. 4: MDS of the taxonomic structure by type of substrate. The dashed boxes contain the results of the pair-wise tests according to PERMANOVA.

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Table 3: Results of SIMPER analysis comparing the taxonomic structure between natural and each of the artificial substrates. To summarize the information, only the first thirteen taxa are included. Av.Diss: Average dissimilarity; SD: standard deviation; Contrib.: contribution to dissimilarity.

Intertidal taxonomic structure					
Groups ***Natural*** *&* ***Rip-rap***			*Groups* ***Natural*** *&* ***Cube***		
Average dissimilarity = 36.80%			Average dissimilarity = 45.75%		
Species	Av.Diss. ± SD	Contrib.%	Species	Av.Diss. ± SD	Contrib.%
J. rubens	1.91 ± 1.82	5.18	Green fil. algae	1.83 ± 1.50	4.00
Trochidae	1.64 ± 1.38	4.47	*Ulva* sp.	1.76 ± 1.35	3.84
Bangia sp.	1.40 ± 1.09	3.81	*J. rubens*	1.64 ± 1.35	3.59
Mytilus sp.	1.39 ± 1.09	3.78	Rhodomelaceae	1.60 ± 1.35	3.50
P. rustica	1.37 ± 1.09	3.72	*Cystoseira* spp.	1.54 ± 1.26	3.36
Pyropia sp.	1.30 ± 1.01	3.52	*C. sinuosa*	1.48 ± 1.17	3.23
Green fil. algae	1.28 ± 1.01	3.48	Trochidae	1.42 ± 1.08	3.10
Dendropoma sp.	1.12 ± 0.88	3.04	*Gelidium* sp.	1.41 ± 1.08	3.08
P. perforatus	1.09 ± 0.88	2.96	*Mytilus* sp.	1.34 ± 1.03	2.92
Hildenbrandia sp.	1.06 ± 0.88	2.88	*C. safiana*	1.30 ± 1.01	2.85
P. ferruginea	0.90 ± 0.75	2.43	Polyplacophora	1.28 ± 0.95	2.81
Rhodomelaceae	0.86 ± 0.69	2.35	*P. perforatus*	1.27 ± 0.95	2.78
Nemalion sp.	0.86 ± 0.69	2.35	*Pyropia sp.*	1.25 ± 0.91	2.73
Groups ***Natural*** *&* ***Tetrapod***			*Groups* ***Natural*** *&* ***Seawall***		
Average dissimilarity = 40.58%			Average dissimilarity = 58.69%		
Species	Av.Diss. ± SD	Contrib.%	Species	Av.Diss. ± SD	Contrib.%
Encrusting red algae	2.01 ± 1.94	4.96	*Caulacanthus* sp.	2.93 ± 1.73	4.99
Cystoseira spp.	1.73 ± 1.38	4.25	*E. elongata*	2.54 ± 1.34	4.33
C. safiana	1.68 ± 1.34	4.13	*Gelidium* sp.	2.45 ± 1.37	4.18
Ulva sp.	1.62 ± 1.28	3.98	*Ulva* sp.	2.43 ± 1.32	4.14
Green fil. algae	1.57 ± 1.28	3.88	Polyplacophora	2.29 ± 1.25	3.90
Dyctiota spp.	1.44 ± 1.19	3.56	Encrusting red algae	2.22 ± 1.25	3.78
E. punctata	1.31 ± 1.02	3.23	*P. rustica*	2.14 ± 1.15	3.64
P. perforatus	1.27 ± 0.99	3.20	*Hildenbrandia* sp.	1.91 ± 1.01	3.25
Hildenbrandia sp.	1.23 ± 0.96	3.12	*Gastroclonium* sp.	1.88 ± 1.08	3.21
C. sinuosa	1.23 ± 0.95	3.04	Trochidae	1.84 ± 0.95	3.13
A. armata	1.23 ± 0.95	3.03	*Mytilus* sp.	1.84 ± 0.95	3.13
A. calycularis	1.23 ± 0.95	3.02	*A. equina*	1.82 ± 0.92	3.10
M. neritoides	1.22 ± 0.95	3.01	*P. perforatus*	1.80 ± 0.93	3.06

Taxa cover in vertical exposed surfaces. Results of methodology ii

We found eight taxa that had an average cover (per site) higher than 20% at least at one locality: *Caulacanthus* sp., *Chthamalus stellatus*, *Cystoseira* spp., *Ellisolandia elongata*, Encrusting red algae, *Lithophyllum byssoides*, *Mytilus galloprovincialis* and *Ralfsia verrucosa* (Fig. 5). There were significant differences in the individual taxa cover between substrates (artificial vs natural). Although these results depended on the locality, there were some constant patterns across the Alboran Sea (see SNK results in Fig 5). Covers of *R. verrucosa* were significantly higher on the artificial substrates of Motril (Cubes and Seawall), Málaga (Seawall), Benalmádena, M'Diq and Marina Smir (Tetrapods). The covers of *C. stellatus* were

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significantly higher on concrete made artificial substrates (cubes of Fuengirola and Motril, seawalls of Almería and Málaga, and tetrapods of M'Diq and Marina Smir), while they were lower on the natural-rock made rip-raps of Aguadulce and Algeciras. On the other hand, canopy algae cover was significantly lower on artificial substrates of some localities. The coralline algae *E. elongata* had significantly lower covers on Ceuta (Cubes), Almería (Seawall), Málaga (Seawall), M'Diq (Tetrapod) and Marina Smir (Tetrapod). The cover of *Cystoseira* spp. was also significantly lower on the cubes of Ceuta, the rip-raps of Marina del Este and the Seawall of Málaga. Interestingly, the cover percentage of the protected coralline algae *L. byssoides* was quite high in the Cubes of Ceuta.

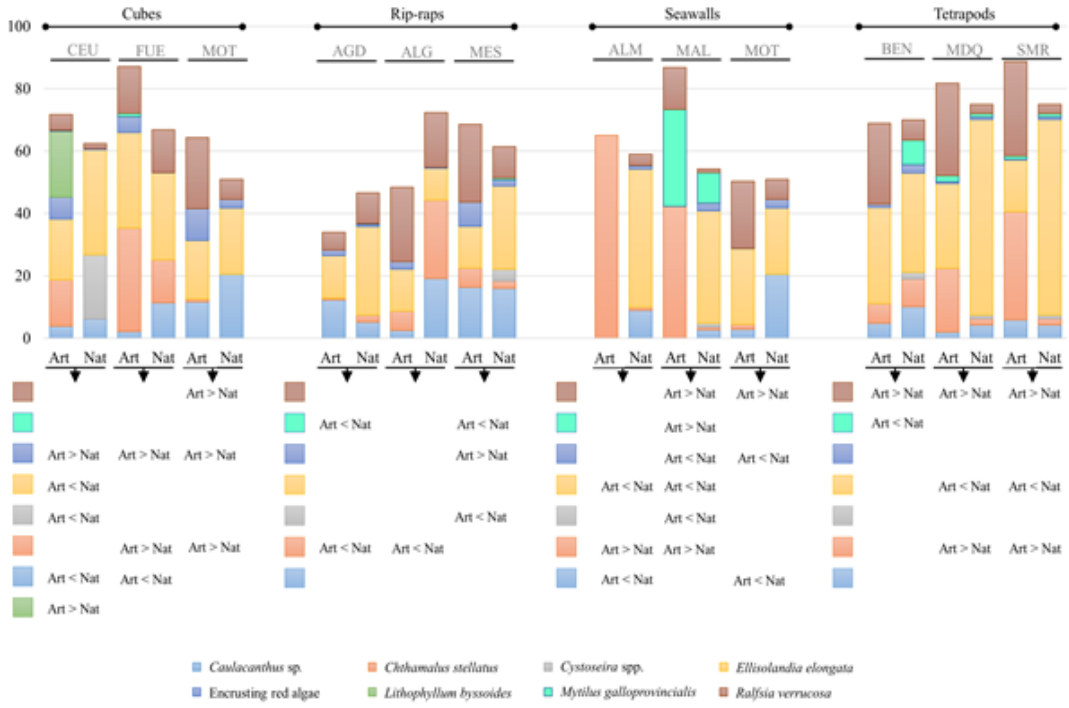

Fig. 5: Taxa cover percentages on vertical surfaces of each substrate. Only taxa with a cover higher than 20% on at least one site are represented. Results of the SNK comparisons according to three-way ANOVA are also given. Art: Artificial; Nat: Natural; CEU: Ceuta; FUE: Fuengirola; MOT: Motril; AGD: Aguadulce; ALG: Algeciras; MES: Marina del Este; ALM: Almería, MAL: Málaga, MOT: Motril; BEN: Benalmádena, MDQ: M'diq; SMR: Marina Smir.

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According to the taxa cover percentage on vertical faces, a clear segregation between artificial and natural substrates was observed except for rip-raps (see MDS in Fig. 6). In fact, PERMANOVA detected significant differences between substrates at every locality and type of artificial structure, with the exception of Aguadulce and Marina del Este's rip-raps (Fig. 6, Supplementary Table 8). These lower dissimilarities between rip-raps and the natural hard substrate were also confirmed by SIMPER (Table 4). Rip-raps had the lowest dissimilarities (61.23%) while seawalls had the highest (74.88%).

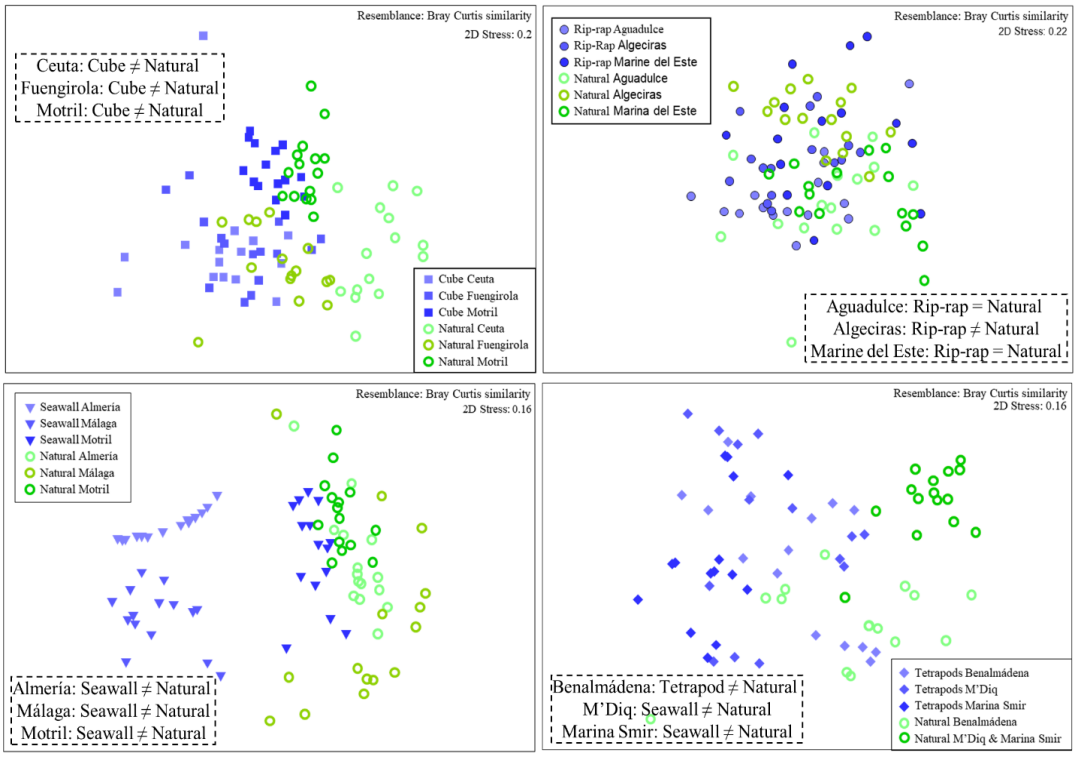

Fig. 6: MDS for the taxa cover percentages on vertical faces. Dashed boxes contain pair-wise results according to PERMANOVA.

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Table 4: Results of SIMPER analysis comparing the taxa cover percentages on vertical faces between natural and each of the artificial substrates. Cut off for low contributions: 90%. Av.Diss: Average dissimilarity; SD: standard deviation; Contrib.: contribution to dissimilarity.

Intertidal vertical faces					
Groups ***Natural*** *&* ***Rip-rap***			*Groups* ***Natural*** *&* ***Cube***		
Average dissimilarity = 61.23%			Average dissimilarity = 63.52%		
Species	Av.Diss. ± SD	Contrib.%	Species	Av.Diss. ± SD	Contrib.%
Empty	11.50 ± 1.35	18.79	*E. elongata*	8.36 ± 1.24	13.16
E. elongata	9.41 ± 1.29	15.38	Empty	8.14 ± 1.32	12.81
R. verrucosa	8.42 ± 1.22	13.75	*C. estellatus*	8.10 ± 0.98	12.75
Caulacanthus sp.	7.21 ± 1.14	11.77	*R. verrucosa*	6.49 ± 1.03	10.21
C. estellatus	5.57 ± 0.77	9.09	*Caulacanthus* sp.	5.64 ± 1.14	8.87
Hildenbrandia sp.	2.29 ± 0.56	3.73	Encrusting red algae	3.36 ± 0.87	5.77
Encrusting red algae	2.19 ± 0.49	3.57	*L. byssoides*	3.52 ± 0.57	5.54
Ulva sp.	1.85 ± 0.41	3.02	*Cystoseira* spp.	3.41 ± 0.50	5.37
Dendropoma sp.	1.84 ± 0.27	3.01	Rhodomelaceae	3.38 ± 0.63	5.32
J. rubens	1.35 ± 0.27	2.21	*Ulva* sp.	3.04 ± 0.55	4.78
Green filamentous	1.28 ± 0.38	2.09	*A. armata*	1.47 ± 0.45	2.31
Patella spp.	1.13 ± 0.93	1.85	*Hildenbrandia* sp.	1.32 ± 0.42	2.08
Rhodomelaceae	0.87 ± 0.37	1.42	*P. perforatus*	1.26 ± 0.27	1.98
Groups ***Natural*** *&* ***Tetrapod***			*Groups* ***Natural*** *&* ***Seawall***		
Average dissimilarity = 64.96%			Average dissimilarity = 74.88%		
Species	Av.Diss. ± SD	Contrib.%	Species	Av.Diss. ± SD	Contrib.%
E. elongata	15.06 ± 1.72	23.19	*C. estellatus*	17.91 ± 1.20	23.29
R. verrucosa	12.67 ± 1.17	19.50	*E. elongata*	14.35 ± 1.51	19.17
C. estellatus	9.77 ± 1.05	15.04	Empty	10.40 ± 1.35	13.89
Empty	6.74 ± 0.95	10.37	*R. verrucosa*	6.14 ± 0.84	8.20
Caulacanthus sp.	3.50 ± 0.98	5.38	*M. galloprovincialis*	5.89 ± 0.71	7.87
A. armata	3.40 ± 1.25	5.24	*Caulacanthus* sp.	5.22 ± 0.93	6.98
P. perna	2.04 ± 0.52	3.14	Rhodomelaceae	2.19 ± 0.32	2.93
M. galloprovincialis	1.87 ± 0.74	2.88	*Dendropoma* sp.	1.76 ± 0.37	2.36
C. sinuosa	1.69 ± 0.55	2.60	*P. perna*	1.64 ± 0.44	2.19
P. perforatus	1.27 ± 0.72	1.96	*Hildenbrandia* sp.	1.41 ± 0.43	1.88
Encrusting red algae	0.90 ± 0.58	1.38	*Ulva* sp.	1.34 ± 0.50	1.78

Intertidal communities and abiotic variables

We also tested how a set of abiotic variables explained, 1) the full taxonomic structure (presence/absence) found all around each substrate and 2) the taxa cover percentage of only the vertical exposed surfaces. The variables used (macro- and microroughness, age, crystallinity, Calcium content [Ca], Magnesium content [Mg] and wave exposure [Fetch index]) clearly segregated artificial from natural substrates and also the seawalls from the rest of artificial substrates (see PCA in Fig. 7). We initially included Al, Fe, K, and Si content and Calcination Percentages but after confirming the collinearity with other variables (Draftman's plot results not shown), we eliminated those variables from subsequent analyses. The age together with Ca and Mg content were the main drivers segregating the substrates along axis 1 (31.3 % of variance explained). Along this axis, many natural substrates are separated from the artificial ones (and some natural ones) due to their older age and/or high Silicon content (i.e. low Mg

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and Ca content). Along axis 2 (20.1 % of variance explained), the main driver was macroscale roughness, segregating clearly the seawalls (that lacked any) from the rest of artificial substrates. Differences in the abiotic nature of cubes, rip-raps and tetrapods were not really evident, since they had a high degree of macroscale roughness and age range.

The resulting model of abiotic variables for the full taxonomic structure explained 26.09% of the variance ($p<0.0001$) (Table 5). According to the marginal effects, Ca and crystallinity were not significantly correlated with the taxonomic structure while macroscale roughness was marginally correlated ($p<0.1$). Microscale roughness, Mg, Fetch and Age were significantly correlated, being the age of the substrates the variable most correlated. In contrast, when pairing the same abiotic data with the cover percentages of taxa developing on the vertical surfaces, the marginal effects showed a significant correlation of all variables (except for Ca that was marginally significant). The resulting model explained 39.49% of the variance. In both cases, the explained variability can be considered low, indicating an influence of other variables (likely environmental variables acting at regional level) not included in the model. In fact, the MDS using factor Latitude (West, Middle West, Middle East, East) clearly sorted the replicates according to their regional position, independently of substrate type (Fig. 8). The PERMANOVA results (Supplementary table 9) showed the significant effect of latitude (Factor Region: Pseudo-$F_{3,71} = 3.25$, $p < 0.001$), differentiating the taxonomic structure of western regions (ALG, CEU, MDQ, SMR) from the middle western (BEN, FUE, MAL) and the eastern ones (MES, MOT, AGD, ALM) (Fig. 8).

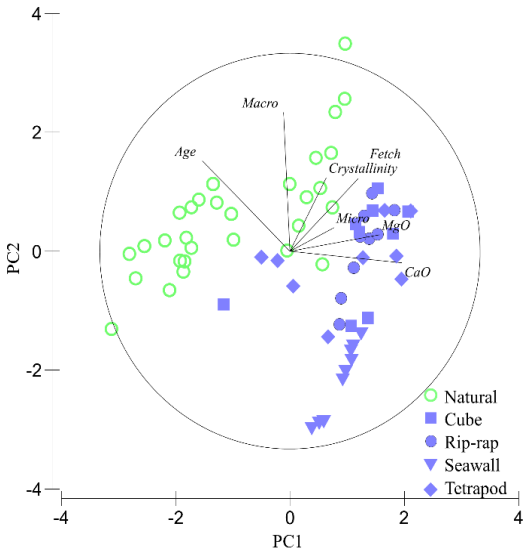

Fig. 7: Principal Component Analysis of the abiotic variables used (after variable selection to avoid collinearity).

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Table 5. Permutation test for dbRDA and CCA for all constrained eigenvalues of taxa cover percentages developing on vertical surfaces and full taxonomic structure respectively. The marginal effects of each abiotic variable tested and the proportion of the inertia explained by the models are also provided. .: p<0.1; *: p<0.05; **: p<0.001; ***: p<0.0001.

Full taxonomic structure				
	Df	% Explained	F	P
Constrained model	7	26.09%	3.228	***
Residual	64			
	Df	Sum of sqs.	F	p
Macro	1	0.1763	1.8866	.
Micro	1	0.2235	2.3914	*
Magnesium	1	0.2585	2.7658	**
Calcium	1	0.1283	1.3729	n.s.
Crystallinity	1	0.1167	1.2482	n.s.
Age	1	0.5213	5.5769	***
Fetch	1	0.2325	2.4870	*
Residual	64	5.9824		
Vertical faces				
	Df	% Explained	F	P
Constrained model	7	39.49%	5.9675	***
Residual	64			
	Df	Sum of sqs.	F	p
Macro	1	0.3046	3.8924	**
Micro	1	0.1919	2.4525	*
Magnesium	1	0.2557	3.2679	**
Calcium	1	0.1509	1.9281	.
Crystallinity	1	0.2336	2.9845	**
Age	1	0.5700	7.2834	***
Fetch	1	0.3246	4.1479	***
Residual	64	5.9824		

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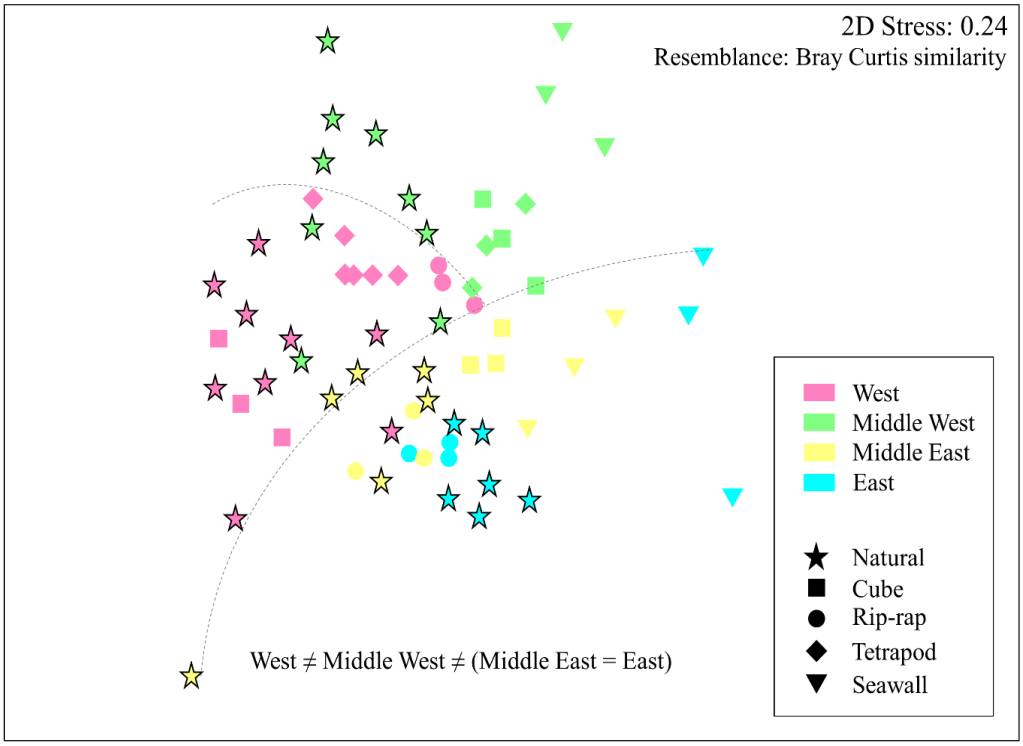

Fig. 8: MDS results portraying the differences between samples according to their latitude (factor Region: four levels). The results of PERMANOVA pair-wise tests are also given.

Discussion

The comparison between natural and artificial substrates usually yields higher biodiversity values for the former ones (Firth et al., 2016b). As we expected, we found concordant results for the natural substrates studied along the Alboran Sea. Within the twenty-five taxa uniquely found on natural substrates, we found different species of algae (9 out of 25) including *Jania rubens*, *Rissoella verruculosa*, *Padina pavonica*, *Halopteris* spp., *Dictyopteris* sp. or *Sargassum* sp.. These species have different growth forms and provide an algal canopy that may be adequate for hosting a broad number of mobile taxa (Navarro-Barranco et al., 2018; Ólafsson, 2016; Saarinen et al., 2018). The stressful intertidal environment can boost the importance of species-specific interactions between sessile taxa and their associated mobile macro- and meiofauna (Bulleri et al., 2016; Sedano et al., 2020a; 2020b). Therefore, the lack of different algae and other sessile taxa with a variety of growth forms may be an important

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factor affecting the diversity of mobile associated communities on artificial substrates. The reduction of phytal taxa on artificial substrates has been previously reported (Ferrario et al., 2016; Sedano et al., 2019) and it has been identified not only as a handicap for the establishment of propagules and larvae (Arenas et al., 2006; Bulleri et al., 2009), but also as a reduction of primary production for supporting higher trophic levels such as fishes (Cheminée et al., 2017; Thiriet et al., 2016).

Apart from macroalgae, within the twenty-five taxa exclusively found in natural substrates, we identified species whose living style does not allow them to be emerged or need a shadowy environment. It is the case of the subtidal grazer *Thuridilla hopei*, the suspension feeder *Aglaophenia pluma*, or other subtidal benthic taxa such as *Cereus pedunculatus*, Terebellidae, Actinaria and *Clathrina rubra*, the latter being well documented to live underneath shallow subtidal boulders (Trowbridge et al., 2018). Logically, we were able to record these taxa only in some intertidal pools and shady overhangs of natural substrates. The presence of intertidal pools provides refuges for intertidal and subtidal species, representing 'islands' of different habitat (Underwood and Skilleter, 1996) scattered within the surrounding rocky surfaces, contributing to the diversity and range of ecological functions of intertidal habitats. This has led to the creation of artificial rock-pools on the usually smooth artificial substrates in order to improve their ecological value (Ostalé-Valriberas et al., 2018). Our results have reinforced the importance of macro- and microhabitats in boosting the biodiversity, being the seawalls (featureless artificial substrates) the substrates with the lowest number of taxa. In fact, *Eriphia verrucosa* and *Onchidella celtica* were exclusively recorded inhabiting the microhabitats (small crevices) of natural substrates (Kent and Hawkins, 2019).

However, we found not only differences in the number or composition, but also in the cover (i.e. abundance) of shared taxa. The results of taxa cover on vertical faces demonstrated that some patterns of occurrence can be generalized along a geographical gradient. For example, the algae *R. verrucosa* was usually higher in artificial substrates while the cover of canopy algae such as *E. elongata* and *Cystoseira* spp. was lower in artificial substrates. We also found higher covers of the barnacle *C. stellatus* on concrete made structures (cubes, seawalls and

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tetrapods). This result is concordant with previous studies that stated that barnacle's abundance can be increased in smooth surfaces and alkaline substrates (Berntsson et al., 2000; Guilbeau et al., 2003), two features that characterize concrete made artificial structures.

Among the twenty common taxa to all substrates, we found ecologically important species for their use as biological indicators or their protection status. For example, the cnidarian *Actinia equina* is included in the AMBI index as a species very sensitive to disturbance (Borja et al., 2000). In addition, the limpets *Cymbula safiana* and *Patella ferruginea* are included in the list of endangered or threatened species (Annex II) of the Barcelona Convention (1996) and the Red Data Book of Andalusian Invertebrates (Barea-Azcón et al. 2008). Interestingly, the frequency of occurrence of these limpets was higher on artificial substrates than on natural ones at some localities, agreeing with previous studies that showed important populations of these species on artificial structures (Espinosa et al., 2018; Rivera-Ingraham et al., 2011). These figures of protection may produce important benefits for a number of co-occurring species, a concept known as 'umbrella species' (Roberge and Angelstam, 2004). Furthermore, other protected species also occurred on most of the artificial substrates. The reef forming mollusc *Dendropoma* sp. was recorded at every substrate except on tetrapods, while the endangered coral *Astroides calycularis* was found at every substrate except seawalls, usually at the lowest intertidal level under overhangs or the ceiling of big boulders, reinforcing again the importance of habitat heterogeneity in the occurrence of more and rare taxa (Aguilera et al., 2014). For all these reasons, it has been pointed out the value of some artificial substrates in the conservation of certain species, even leading to the proposal of establishing some figure of protection for these artificial coastal defence structures (García-Gómez et al., 2015).

All these differences in the occurrence of common and rare taxa were translated into different diversity values as well as a different taxonomic structure between natural and artificial substrates; however, the differences were not consistent at all localities. The taxonomic structure did not differ at three out of twelve localities. For example, the nearest natural rocky substrate from Motril (where we sampled cubes and a seawall) was located in a bay dominated by natural rocky cliffs without gently intertidal slopes and therefore with

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homogeneous intertidal habitats without rock pools, resulting in one of the natural localities with the lowest intertidal biodiversity. In addition, the occurrence of common taxa (*Caulacanthus* sp., *Ellisolandia elongata*, *Ralfsia verrucosa*, *Chthamalus stellatus*) was high in the seawall and cubes. It is also possible, that the seawall benefited from the richer and more complex adjacent cubes, receiving from there a higher propagule pressure and facilitating the recruitment of sessile and mobile species. For these reasons, the test failed to find significant differences in the taxonomic structure between natural and artificial substrates at this locality. A similar scenario was found in Marina del Este, where the taxa richness and taxonomic structure between rip-raps and the natural substrate neither differed. However, the reason here was not the impoverished natural substrates but the rich artificial ones. The rip-raps of Marina del Este are located next to the natural substrates, in an upwelling zone (Cebrián and Ballesteros, 2004; Sedano et al., 2014a, 2014b) and also next to a protected area (Rodríquez et al., 2003), therefore there is presumably a high pressure of propagules. Also, the rip-raps are constructed with natural rocks, in this case dominated by calcium carbonates (dolomite and calcite), the same composition of the natural substrate sampled (dolomite). In addition, the rip-raps had high levels of macro- and microroughness. Altogether, it is likely improving the settlement of 'natural' taxa, such as the orange coral *Astroides calycularis*, the anemone *Actinia equina* or polyplacophorans, as well as promoting a higher occurrence of other common taxa such as limpets and canopy forming algae. This higher degree of similarity between rip-raps and natural substrates was also evident when comparing taxa covers on vertical faces of the substrate, and was previously seen in other studies (Gittman et al., 2016; Sedano et al., 2020a; 2020b), however they are still far from being true surrogates of the natural substrates they replace (Gacia et al., 2007; Sedano et al., 2019). In Aguadulce, they even reached higher taxa richness than the nearest natural substrate. Sometimes, artificial structures are deployed in naturally impoverished systems. For example, to avoid beach erosion (Martin et al., 2005), artificial structures are deployed in sandbanks with low diversity of hard substrates taxa. This situation brings up the question whether we should look for biodiversity enhancement of artificial substrates, even in higher numbers than the surrounding natural habitat no matter

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where they will be deployed. In the last decade, efforts have been made to suggest different eco-engineering designs to enhance biodiversity, functions and services of artificial substrates (O'Shaughnessy et al., 2020), but the enhancement of biodiversity *per se* may not always be beneficial. Eco-engineering designs should be adapted to the local communities where the new substrates are deployed to avoid the establishment of 'artificial' communities (even if they are super rich) and undesired effects such as acting as stepping stones for non-native taxa (Glasby et al., 2007; Salomidi et al., 2013).

The variability explained by the abiotic model was higher over vertical surfaces in comparison with the full taxonomic structure, probably because we provided more information to the model (i.e. taxa abundance), but also because sources of variability introduced by highly heterogenous structures (rock pools, crevices, overhangs…) are also not considered in the vertical surfaces. This, evidences again the importance of substrate heterogeneity in creating variability and therefore harbouring richer communities. However, in both cases (full taxonomic structure and vertical surfaces comparisons) the seawalls presented clearly different taxonomic structure and did not seem to be any more like the vertical faces of boulder structures. This might suggest that the microhabitats surrounding the vertical faces may influence the settlement on this and adjacent areas, as we mentioned previously for the seawall of Motril. For example, some taxa may recruit first in the internal protected surfaces and then migrate to the external ones. There can be also a higher propagule pressure coming from the richer internal environment (Sherrard et al., 2016) and a lesser abiotic stress from sand scouring (Moschella et al., 2005) due to a better wave dissipation in boulder-like structures (Jung et al., 2012; Sherrard et al., 2016). In fact, wave exposure and macroscale roughness seemed to be important drivers of the taxonomic structure found across the Alboran Sea.

Although some of the abiotic factors used in the model seem to be influencing both, the taxonomic structure (methodology i) and the taxa cover percentages (methodology ii) of natural and artificial substrates across the Alboran Sea, the model of abiotic variables did not explain high percentages of variability, indicating that other factors not included in the model may be important drivers of these communities. In a previous study using a very similar set of abiotic

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variables, we found much higher values of variability explained in the structure of communities developing on artificial structures located in the same area (Algeciras Bay) (Sedano et al., 2020a). This suggests that there is high variability in our samples introduced by environmental factors acting at regional scale across the Alboran Sea. Cacabelos et al. (2019) also found a high variability in boulder communities across a range of spatial scales. In fact, we showed how our samples were sorted according to their geographical location (west, mid-west, mid-east, east) independently of substrate type, but still portraying the differences between natural and artificial substrates within the relevant localities. This is in agreement with the eutrophication gradient towards western waters of the Alboran Sea (Cebrián and Ballesteros, 2004; Sedano et al., 2020c) and implies bigger challenges in the management of artificial structures and the design of eco-engineering solutions since they should be applied at local levels.

Conclusion

According to our first hypothesis, we can confirm that there is an intertidal biodiversity loss associated with artificial coastal defence structures, and that this pattern occurs even at high spatial scales (the Alboran Sea region in our case). However, the intertidal biodiversity found on boulder-like artificial structures (cubes, rip-raps and tetrapods) was not negligible. From a conservationist point of view, they harboured some important species such as the endangered orange coral *Astroides calycularis*, or the protected limpets *Cymbula safiana* and *Patella ferruginea*. From this perspective, the rip-raps seemed to be better surrogates of their adjacent natural habitats and the seawalls had the lowest ecological value, confirming our second hypothesis. Nevertheless, the effect of a particular type of artificial structure at a regional scale (i.e. at different localities) seems unpredictable since it may have higher or lower ecological value depending on the local conditions. We confirm this way our third hypothesis and highlight the challenge that eco-engineering measures face in order to establish global protocols

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for biodiversity maintenance or enhancement, and the importance of local scales in management programmes

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CHAPTER 2.2

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2.2 Algae canopy and biodiversity loss on Crete's rip-raps (Greece)

Adapted from: Sedano, F., Florido, M., Rallis, I., Espinosa, F., Gerovasileiou, V. (2019). Comparing sessile benthos on shallow artificial versus natural hard substrates in the Eastern Mediterranean Sea. Mediterranean Marine Science, 20(4), 688-702. https://doi.org/10.12681/mms.17897

Abstract

Artificial structures cover a considerable part of the Mediterranean coasts. In the Aegean Sea, most studies related to artificial structures have focused in vagile fauna on harbours and marinas but little attention has been given to the sessile biota on coastal defense structures. The aim of this work was to describe for the first time the shallow subtidal sessile benthos on coastal defense structures in Crete (Eastern Mediterranean Sea) in order to identify potential differences in comparison to natural rocky substrates, adopting both a taxonomic and functional (i.e. macroalgal structural complexity) approach. Three shallow (1-3 m) localities were studied in the north coast and three in the south coast of the island (six localities in total). At each locality, two types of hard substrate were selected: an artificial coastal defense structure (rip-rap) and the nearest natural rocky substrates. The percent cover of sessile taxa was calculated using random points counts over photoquadrats (20 x 20 cm). The structure of the assemblage differed between artificial and natural habitats. Values of Shannon-Wiener's diversity index and number of taxa were higher in natural substrates. In addition, cover of arborescent macroalgae was lower on artificial substrates. In conclusion, rip-raps do not function as surrogates of natural hard substrates in the study area since their shallow subtidal assemblages differ in terms of community structure, diversity and functionality. The deficient performance of such artificial structures could be attributed to the combined effects of abiotic factors and biotic processes, including substrate nature and roughness as well as differential grazing pressure.

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Introduction

Shoreline urbanization combined with the increase of tourist, recreational and commercial activities, result in the introduction and proliferation of artificial structures in marine coastal habitats worldwide (Bulleri and Chapman, 2010; Dafforn *et al*., 2015; Firth *et al*., 2016a). These structures are mostly linked to coastal defense purposes against sea-level rise, but also to commercial infrastructures, protection against coastal erosion and wave action, extraction of oil (e.g. offshore platforms), energy generation (e.g. wind farms) and aquaculture (Bacchiocchi and Airoldi, 2003; Dafforn *et al*., 2015; Firth *et al*., 2016a and references therein). Recently, some eco-engineering interventions have been carried out with the purpose of increasing or maintaining biodiversity inhabiting such structures (see review by Strain *et al*., 2018). Nevertheless, strict or well-defined ecological criteria and management practices are lacking during the design stage or after installation of these infrastructures (Moschella *et al*., 2005; Firth *et al*., 2014, Dafforn *et al*., 2015). Their impacts have been largely documented, generally concluding that artificial structures do not function *per se* as surrogates of natural habitats (e.g. Bulleri and Chapman, 2010; Perkins *et al*., 2015) due to different habitat complexity (e.g. Perkol-Finkel and Benayahu, 2004; Lam *et al*., 2009; Loke *et al*., 2015; Mercader *et al*., 2017), nature of building materials (e.g. Coombes *et al*., 2015; Sempere-Valverde *et al*., 2018), surface inclination and orientation (e.g. Moreira *et al*., 2006; Chapman and Underwood, 2011) and even differential grazing pressure between artificial and natural habitats (Ferrario *et al*., 2016). Consequently, the importance of ecological characterization of these structures and the incorporation of ecological criteria in their design should not be neglected (Mosquella *et al*., 2005; Perkins *et al*., 2015).

The European coasts have been highly modified by the introduction of artificial structures (Airoldi and Beck, 2007). In the Mediterranean Sea, the ecological study of artificial structures as "hot spots" of biological invasions has been particularly prolific, focusing mainly in marinas (e.g. Ros *et al*., 2014; Ulman *et al*., 2017; Martínez-Laiz *et al*., 2018) or artificial reefs (Fabi *et al*., 2011; López *et al*., 2016). However, only few studies have compared communities of

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natural hard habitats with coastal defense structures (e.g. Gacia *et al*., 2007; García-Gómez *et al*., 2015; Ido and Shimrit, 2015). In the Aegean Sea, most studies related to artificial structures have focused in vagile fauna associated with harbours and marinas (Karalis *et al*., 2003; Chintiroglou *et al*., 2004; Corsini-Foka *et al*., 2015; Ulman *et al*., 2017; Chatzinikolaou *et al*., 2018; Zenetos *et al*., 2018), aquaculture facilities (Fernández-González and Sánchez-Jerez, 2017) and artificial reefs (Sinis *et al*., 2000; Lök *et al*., 2008; Klaoudatos *et al*., 2012). Regarding sessile fauna, a recent study in Saronikos Gulf found higher abundances of the cryptogenic coral *Oculina patagonica* over anthropogenic structures compared with natural habitats (Salomidi *et al*., 2013).

The northern coast of Crete (Eastern Mediterranean Sea, Greece) is greatly affected by urbanization because the largest cities and main tourist infrastructures (e.g. harbours) of the island are located there (e.g. Chatzinikolaou and Arvanitidis, 2016). This has resulted in an increase of maritime traffic and the establishment of various types of coastal defense structures. In spite of this, there is a lack of studies on the impact of these structures on the benthic biota. The aim of this work was to study and compare for the first time the subtidal sessile benthos on coastal defense structures with that of nearby natural rocky substrates around Crete. Our main hypothesis is that the assemblage structure and function (in terms of macroalgal structural complexity) will differ significantly between artificial and natural substrates.

Materials and methods

Study area

Crete (Greece) is located between the Aegean and Libyan Seas in the Eastern Mediterranean Sea, one of the most oligotrophic marine areas (Boetius *et al*., 1996) and among the main hotspots for marine bioinvasions worldwide (Rilov and Galil, 2009). Six localities around Crete

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(Fig. 1) were studied: three in the north (South Aegean Sea) and three in the south (Libyan Sea) coast of the island. Northern localities were Kato Galatas (35.513º N, 23.964° E), Bali (35.413° N, 24.784° E) and Gournes (35.336° N, 25.299° E), while southern localities were Hora Sfakion (31.198º N, 24.136º E), Agia Galini (35.094º N, 24.689° E) and Tsoutsouros (34.150º N, 25.287º E).

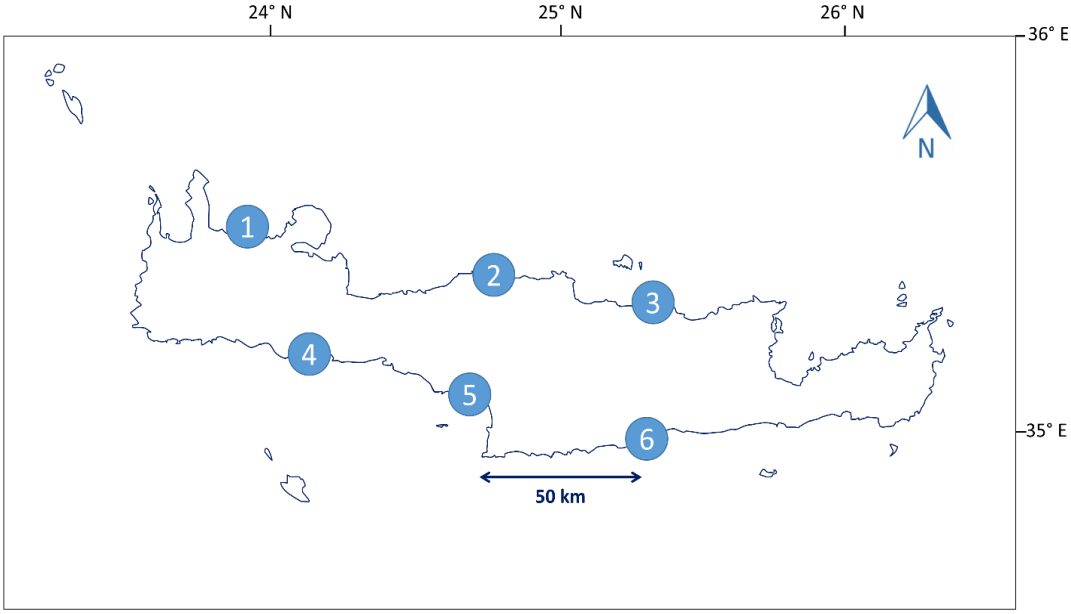

Fig. 1. Sampling localities in Crete Island. 1: Kato Galatas; 2: Bali; 3: Gournes; 4: Hora Sfakion; 5: Agia Galini; 6: Tsoutsouros.

At each locality, two types of hard substrates were sampled in the upper subtidal zone (1-3 m deep): (a) artificial boulder-like coastal defense structures (hereafter “rip-raps”) deployed in marinas more than 10 years ago, and (b) nearby natural rock (Habitat type “1170 Reefs” according to the EU Directive 92/43/EEC). Natural substrates within each locality were predominantly adjacent to rip-raps, except for one locality (Gournes) where the only available natural hard substrate was located approximately 1 km away from the rip-raps. The sampled substrates faced North/North-east in the three northern localities and to South in the southern ones.

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Samples collection and processing

Sampling took place in July 2017. At each locality, three random sites located tens of meters apart, were selected for each substrate type. Within each site, three quadrats were photographed using an Olympus TG4 camera with a Subacqua Helios 1700 focus light. A total of 108 photoquadrats were collected (3 photoquadrats * 3 sites * 2 substrates * 6 localities). Photoquadrats were randomly taken while snorkeling at a depth of 1-3 m by placing a 20 x 20 cm aluminum square frame (Bianchi *et al*., 2004). At each site, the first quadrat was placed at the first available subtidal vertical surface orientated seawards. Subsequent quadrats were placed at the first available surface at least 3 m away or further. Cover of sessile species was measured by spawning 100 random points using PhotoQuad software (Trygonis and Sini, 2012). Sessile taxa that were present in the photoquadrats but did not fall below a random point were given an arbitrary value of 0.5% cover (Bacchiocchi and Airoldi, 2003; Marzinelli *et al*., 2011; Ostalé-Valriberas *et al*., 2018). Qualitative samples of the main benthic taxa present in the photoquadrats were also collected when needed for accurate taxonomic identification in the laboratory.

Statistical analyses

Taxa cover percentages were calculated for each photoquadrat, and based on these data, values of three diversity indices were further determined: number of taxa (S), Shannon-Wiener's diversity (H') and Pielou's evenness (J'). In order to test the null hypothesis of no difference in the aforementioned parameters between substrates and orientations and among localities and sites, multivariate and univariate statistical analyses were applied.

Four-factor permutational multivariate analysis of variance (PERMANOVA) was used to examine the effect of substrate type, orientation, locality and small-scale heterogeneity (sites within locations) on the structure of the sessile assemblage (based on taxa cover percentages). Thus, four factors were considered: 'Substrate' (Su), a fixed factor with two levels (*Natural*,

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Artificial); 'Orientation' (Or), a fixed factor with two levels (*North*, *South*) and crossed with Substrate; 'Locality' (Lo), a random factor nested in Or with three levels for each orientation (North: *Kato Galatas*, *Bali*, *Gournes*; South: *Hora Sfakion*, *Agia Galini*, *Tsoutsouros*); and 'Site' (St), a random factor nested in Su, Or and Lo, with three levels for each locality (*Site 1*, *Site 2*, *Site 3*).

PERMANOVA was run on a triangular similarity matrix derived from Bray-Curtis dissimilarity index of square-root transformed data. In cases of small numbers of unique permutations, P-values were obtained through a Monte Carlo test (Anderson *et al*., 2008). When significant differences for a given factor or interaction of factors were detected, the sources of variation were identified based on Pair-wise comparisons. Additionally, in order to test the dispersion among samples for the fixed factors Su and Or, a permutational analysis of multivariate dispersions (PERMDISP) was used. No action was taken when there was heterogeneity of variances, since PERMANOVA is largely unaffected by heterogeneity in cases of balanced design (Anderson and Walsh, 2013).

Multivariate non-metric multidimensional scaling (MDS) was also used, along with the Bray-Curtis similarity index to visualize patterns in assemblage structure between substrates, orientations and localities. Kruskal's stress coefficient was used to test whether the ordination was reliable (Kruskal and Wish, 1978). The data (taxa cover percentages) were square-root transformed. The contribution of each taxon to the Bray-Curtis similarity within each substrate type was determined with the SIMPER (SIMilarity PERcentages) analysis.

A four-factor analysis of variance (ANOVA) following the abovementioned design was used to examine whether the number of taxa, Shannon-Wiener's diversity and Pielou's evenness differed with substrate type, orientation, locality and sites. Prior to ANOVA, heterogeneity of variance was tested with Cochran's test. Since there was heteroscedasticity, Box-Cox routine was applied in order to estimate the most effective lambda (λ) for Box-Cox transformations ($x_t = (x^{\lambda} - 1) / \lambda$) (Osborne, 2010). Variances remained heterogenous ($p < 0.01$) for number of taxa, and thus, the level of significance was reduced consequently to $p < 0.01$ to reduce type I errors (Underwood, 1997). When ANOVA detected significant differences for a

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given factor, the source of difference was identified by applying the Student–Newman–Keuls (SNK) test (Underwood, 1981, 1997).

Since macroalgae were the main ecosystem-engineering taxon on the studied hard substrates, a two-way ANOVA was used to examine whether there were differences for Su and Or in terms of macroalgal morphological complexity. For this reason, macroalgae were assigned to two morpho-functional groups, i.e. arborescent and non-arborescent taxa. The criterion followed to consider any given alga as arborescent was the capability of growing in the vertical axis forming three-dimensional branched canopies. Multivariate analyses were conducted with PRIMER v.6+PERMANOVA package (Clarke, 1993) and ANOVAs with GMAV5 software (Underwood *et al*., 2002).

Results

A total of 49 taxa were identified, which belonged to 10 major taxonomic groups: Chlorophyta, Ochrophyta, Rhodophyta, Porifera, Cnidaria, Polychaeta, Gastropoda (family Vermetidae), Cirripedia (family Balanidae), Bryozoa, and Ascidiacea. Twenty-three out of 45 taxa identified in natural substrates were macroalgae. Rhodophytes were the dominant phylum with five taxa (*Lithophyllum* spp., *Jania adhaerens*, *Peyssonnelia* spp., *Laurencia obtusa* and *Amphiroa rigida*) contributing by 68.78% to the similarity in natural substrates. On the other hand, in the studied artificial substrates only 16 out of 30 identified taxa were macroalgae, with two taxa (the rhodophyte *Lithophyllum* spp. and the filamentous chlorophyte *Cladophora* spp.) contributing by more than 72% to the Bray-Curtis similarity. Regarding metazoans, 22 taxa were found in natural substrates while only 14 taxa in rip-raps, being noteworthy the absence of cnidarians and the lower diversity of sponges (7 versus 12 taxa) in the latter. Consequently, of the total taxa, 17 were found exclusively on natural substrates while only three on ripraps (Table 1).

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Table 1: Percentage cover for every taxon identified at each locality. Ka: Kato Galatas; Ba: Bali; Go: Gournes; Ho: Hora Sfakion; Ag: Agia Galini; Ts: Tsoutsouros.

	Natural substrate						Artificial substrate (rip-raps)					
	Ka	Ba	Go	Ho	Ag	Ts	Ka	Ba	Go	Ho	Ag	Ts
Phylum Chlorophyta												
Class Ulvophyceae												
Order Bryopsidales												
Family Halimedaceae												
Halimeda tuna (J.Ellis & Solander) J.V.Lamouroux												
Family Udoteaceae												
Flabellia petiolata (Turra) Nizamuddin												
Order Cladophorales												
Family Anadyomenaceae												
Anadyomene stellata (Wulfen) C.Agardh												
Family Cladophoraceae												
Cladophora spp.												
Order Dasycladales												
Family Polyphysaceae												
Acetabularia acetabulum (Linnaeus) P.C. Silva												
Order Siphonocladales												
Family Valoniaceae												
Valonia sp.												
Phylum Ochrophyta												
Class Phaeophyceae												
Order Dictyotales												
Family Dictyotaceae												
Dictyota spp.												
Padina pavonica (Linnaeus) Thivy												
Zonaria sp.												
Order Fucales												
Family Sargassaceae												
Cystoseira spinosa Sauvageau												
Order Sphacelariales												
Family Sphacelariaceae												
Sphacelaria sp.												
Family Stypocaulaceae												
Halopteris scoparia (Linnaeus) Sauvageau												
Phylum Rhodophyta												
Class Florideophyceae												
Order Ceramiales												
Family Rhodomelaceae												
Alsidium helminthochorton (Schwendimann) Kützing												
Laurencia obtusa (Hudson) J.V.Lamouroux												
Order Corallinales												
Family Corallinaceae												
Amphiroa cryptarthrodia Zanardini												
Amphiroa rigida J.V.Lamouroux												
Ellisolandia elongata (J.Ellis & Solander) K.R.Hind & G.W.Saunders												
Hydrolithon farinosum (J.V.Lamouroux) Penrose & Y.M.Chamberlain												
Jania adhaerens J.V.Lamouroux												
Lithophyllum spp.												
Order Nemaliales												
Family Galaxauraceae												
Tricleocarpa fragilis (Linnaeus) Huisman & R.A.Townsend												

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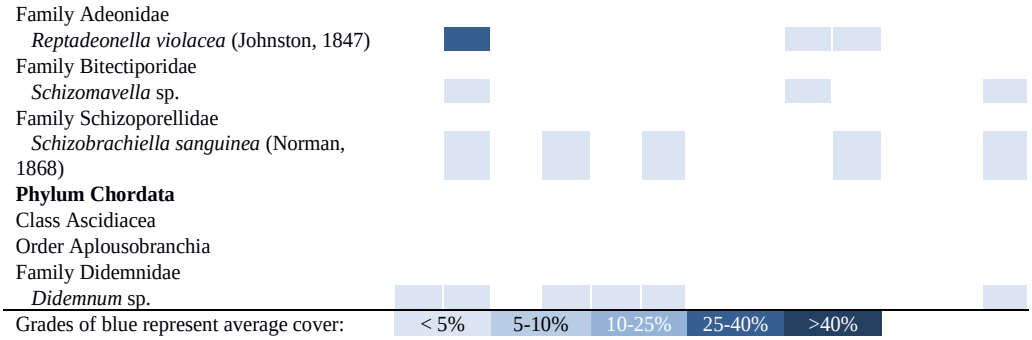

The three dimensional MDS showed a clear ordination of samples according to the habitat type (Fig. 2). Even though there was a high dispersion among samples between substrate types (see PERMDISP in Table 2), PERMANOVA results (Table 2) showed significant differences in assemblage structure between the two substrate types but not between orientations. Moreover, significant differences were observed for locality and two significant interactions between factors were detected, i.e. Su x Or and Su x Lo(Or). Pair-wise comparisons revealed that the interaction Su x Or was significant between substrates within each orientation but not between orientations for each level of substrate. Pair-wise comparisons for Su x Lo(Or) revealed that at each locality the assemblage differed between the two substrates except for Tsoutsouros (Supplementary Table 10). No significant differences were found for small-scale heterogeneity, i.e. among sites for each substrate within any given locality.

The results of the four-factor ANOVA for the three diversity measures are shown in Table 3. There were significant differences in number of taxa for substrate, locality and their interaction Su x Lo(Or). According to the SNK tests, number of taxa was significantly higher in natural substrates, and the interaction Su x Lo(Or) revealed that number of taxa was higher at every locality, although non-significantly at Tsoutsouros (Fig. 3A). With regard to the substrate type, the SNK test showed that number of taxa was significantly higher in natural substrates of Bali compared to Gournes. In the south, natural substrates of Hora Sfakion and Agia Galini had higher number of taxa than Tsoutsouros. No differences were found in the number of taxa in artificial substrates among localities except for Kato Galatas where number of taxa was significantly higher compared to Gournes. Values of H' differed significantly for the substrate factor; SNK tests showed that H' values were higher in natural substrates. Also, a

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significant interaction Su x Lo(Or) was detected for H'. SNK tests (in the same way than for number of taxa) showed that H' values in natural substrates were higher at every locality except for Tsoutsouros (Fig. 3B). Regarding Pielou's evenness, communities over natural substrates were more evenly distributed than on artificial substrates (Fig. 3C). In accordance with SNK tests results, this was explained by the significant differences found only at Bali and Gournes.

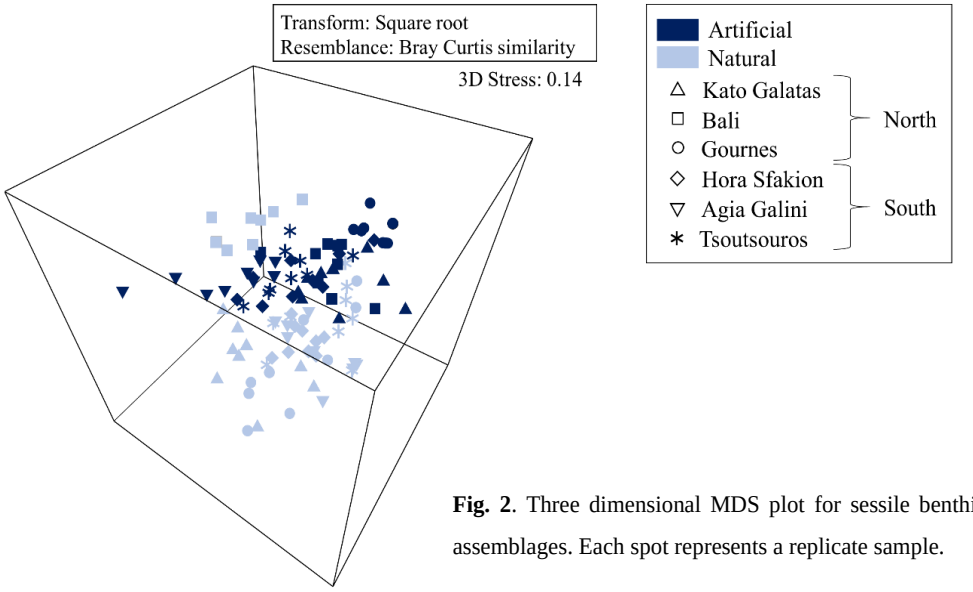

Fig. 2. Three dimensional MDS plot for sessile benthic assemblages. Each spot represents a replicate sample.

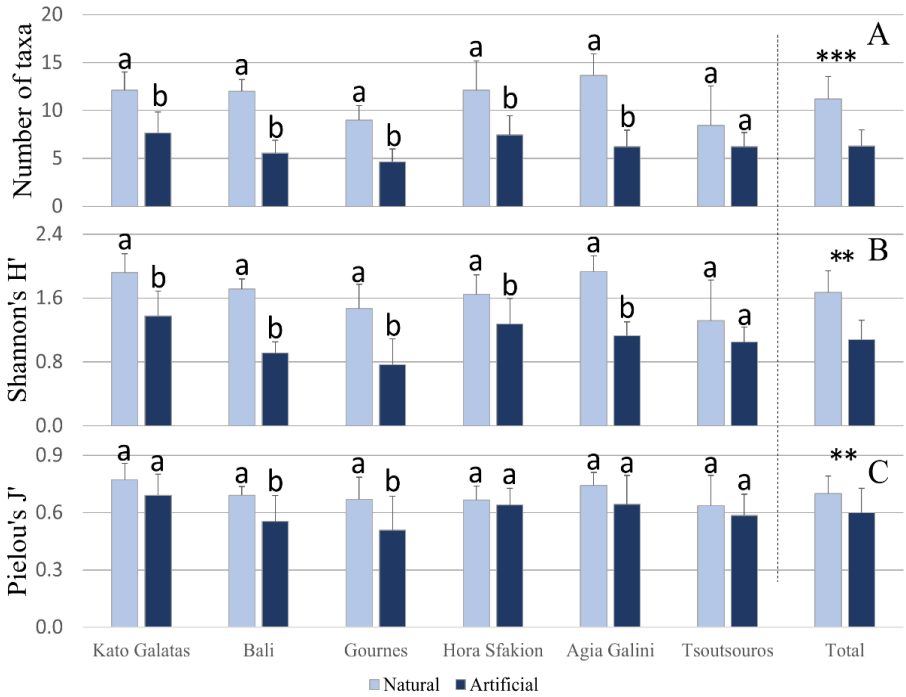

Fig. 3. Average values of A: number of taxa, B: Shannon-Wiener's diversity and C: Pielou's evenness. a, b denotes significant sources of variation detected by SNK in four-factor ANOVA. ** $p < 0.01$; *** $p < 0.001$.

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According to the SIMPER, seven species contributed to 81.12% of the similarity for natural substrates while only three species accounted for 81.78% of the similarity in artificial substrates (Fig. 4).

Ten taxa found in this study were considered as arborescent macroalgae, i.e. *Amphiroa cryptarthrodia*, *A. rigida*, *Cystoseira spinosa*, *Dictyota* spp., *Ellisolandia elongata*, *Ganonema farinosum*, *Halopteris scoparia*, *Jania adhaerens*, *Laurencia obtusa* and *Tricleocarpa fragilis*. Coralline macroalgae of the genus *Lithophyllum* dominated on both artificial and natural substrates (Table 1). Consequently, average cover of non-arborescent algae was higher at every locality compared with arborescent taxa. However, average arborescent macroalgae cover was higher in natural (29.15 % ± 3.58, mean ± SE) than in artificial (12.08 % ± 2.12, mean ± SE) habitats and thus the ratio non-arborescent/arborescent algae was higher on artificial substrates (Fig. 5). ANOVA results confirmed those differences (Table 4).

Table 2: Results of PERMANOVA test with Substrate (Su), Orientation (Or), Locality (Lo) and Site (St) factors for the total assemblage structure (taxa cover percentages) based on Bray-Curtis dissimilarity index of square-root transformed data. MS: mean square; p: level of significance; df: degrees of freedom; n.s.: not significant; * p<0.05; ** p<0.01.

Source of variation	**df**	**MS**	**Pseudo-F**	**p**
Su	1	23104	5.5842	*
Or	1	9908.9	0.94008	n.s.
Lo(Or)	4	10541	10.275	**
Su x Or	1	15281	3.6934	*
Su x Lo(Or)	4	4137.4	4.0331	**
St (Su x Lo(Or))	24	1025.9	1.2002	n.s.
Residual	72	854.75		
Total	107			
PERMDISP	(Su)	F = 4.42 p = 0.045*		
	(Or)	F = 3.03 p = 0.115		
Pair-wise tests	Levels of factor (Or)			
Su x Or	Natural: North = South			
	Artificial: North = South			
	Levels of factor (Su)			
	North: Natural ≠ Artificial			
	South: Natural ≠ Artificial			

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Table 3: Results of the four-factor ANOVA for number of taxa, Shannon-Wiener's diversity and Pielou's evenness. MS: mean square; p: level of significance; df: degrees of freedom; n.s.: not significant; * p<0.05; ** p<0.01; *** p<0.001.

		Number of taxa (S)			Shannon-Wiener diversity (H')			Pielou's evenness (J')		
Source of Variation	**df**	**MS**	**F**	**p**	**MS**	**F**	**p**	**MS**	**F**	**p**
Su	1	36.0901	24.28	***	5.9786	27.25	**	0.5669	25.77	**
Or	1	0.9997	0.49	n.s.	0.0964	0.15	n.s.	0.0045	0.03	n.s.
Lo(Or)	4	2.0266	5.96	**	0.6289	8.84	***	0.1625	3.44	*
St (Su x Lo(Or))	24	0.3402	0.72	n.s.	0.0711	1.16	n.s.	0.0437	1.58	n.s.
Su x Or	1	0.0318	0.02	n.s.	0.2383	1.09	n.s.	0.1039	4.72	n.s.
Su x Lo(Or)	4	1.4864	4.37	**	0.2193	3.08	*	0.1039	0.47	n.s.
Residual	72	0.4705			0.0615			0.0300		
TOTAL	107									
Cochran's test		0.4085			0.0998			0.1281		
		p<0.01			n.s.			n.s.		
Transformation		Box-Cox (λ=0.3555)			Box-Cox (λ=0.2548)			Box-Cox (λ=0.2021)		

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Table 4: ANOVA test with Substrate (Su) and Orientation (Or) factors for arborescent algae cover percentages. Due to heteroscedasticity, level of significance was reduced to p<0.01 to reduce type I error. MS: mean square; p: level of significance; df: degrees of freedom; n.s.: not significant; * p<0.01.

Source of variation	**df**	**MS**	**Pseudo-F**	**p**
Su	1	7862.6134	19.098	*
Or	1	368.5208	0.522	n.s.
Su x Or	1	1629.4468	3.56	n.s.
Residual	104	458.0262		
Total	107			
Cochran-test		p<0.01		

Taxa	Av. Sim. %	Contrib. %
Group Natural	42.93	
1 *Lithophyllum* spp.	16.96	39.50
2 *Jania adhaerens*	4.16	9.68
3 *Peyssonnelia* spp.	3.89	9.06
4 *Cladophora* spp.	2.70	6.30
5 *Cliona viridis*	2.59	6.04
6 *Laurencia obtusa*	2.36	5.50
7 *Amphiroa rigida*	2.17	5.04
		Total = 81.12
Group Artificial	47.66	
I *Lithophyllum* spp.	29.30	61.47
II *Cladophora* spp.	5.47	11.48
III *Cliona viridis*	4.21	8.83
IV *Peyssonnelia* spp.	3.33	7.00
		Total = 88.78

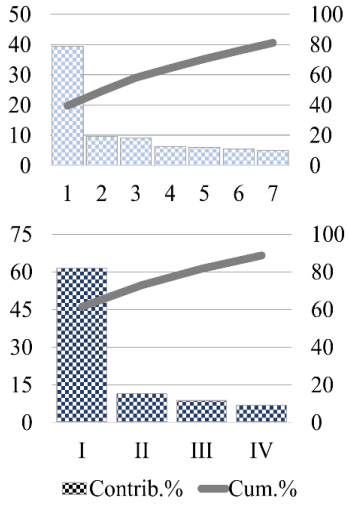

Fig. 4. Results of SIMPER analysis. Taxa that contributed less than 5% to the total similarity are not shown. Histograms represent contributions (bars, left axis) and cumulative contributions (grey line, right axis) for the taxa indicated with natural numbers (Group Natural) or Roman numerals (Group Artificial).

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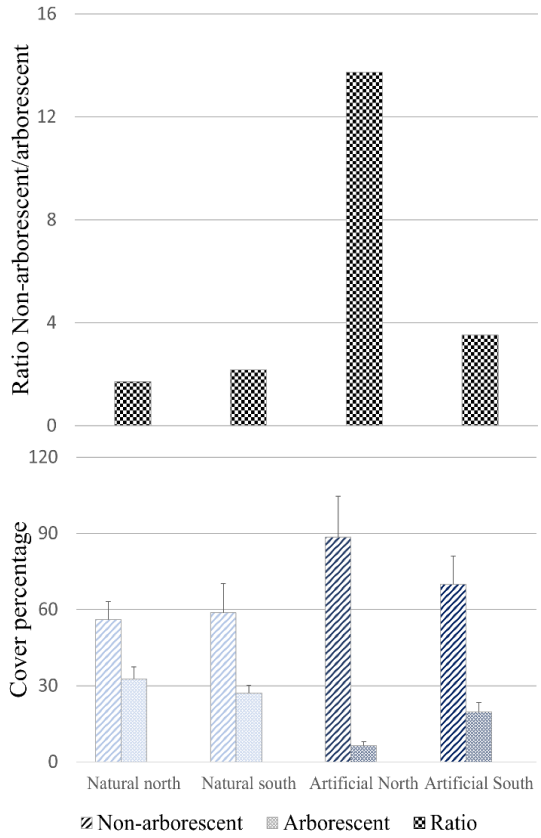

Fig. 5. Average cover (%) of arborescent and non-arborescent algae on artificial and natural substrates. The ratio non-arborescent/arborescent is also shown. Error bars represent standard deviation (SD).

Discussion

Shallow subtidal hard bottoms have been scarcely investigated in Crete, apart from some studies focusing on qualitative bionomic descriptions (Pérès and Picard, 1958), specific taxa (Poursanidis *et al*., 2016; Katsanevakis e*t al.*, 2017) or macrofaunal vagile assemblages (Chatzigeorgiou *et al*., 2012; Poursanidis *et al*., 2019). This work constitutes, therefore, the first quantitative comparative description of the shallow subtidal sessile benthos between artificial (rip-raps) and natural hard substrates in the area. The results supported our initial hypothesis and showed that rip-raps do not function as surrogates of natural hard substrates in the area since (1) the sessile assemblage was significantly different to that on natural rocky bottoms, (2) rip-raps supported fewer taxa and (3) had a significantly lower cover of habitat-forming arborescent macroalgae.

In shallow subtidal rocky bottoms, where light is not a limiting factor, macroalgae are expected to form a major component of sessile benthos, playing such important roles as nutrient cycling and ecosystem engineering, thus providing habitat for a broad range of organisms (e.g. Crooks, 2002; Ólafsson, 2017). Our study showed that macroalgae, and particularly rhodophytes, were the dominant taxa in natural substrates; on the contrary, macroalgae diversity was much lower on rip-raps. Indeed, rhodophytes have been previously reported as the dominant macroalgal taxon in shallow waters of Greece (Lazaridou *et al*., 1997). The

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species composition of the studied natural hard substrates was similar to that described from moderately exposed subtidal hard substrates in the Aegean Sea (Orfanidis *et al*., 2005) and light-demanding hard bottoms in the Mediterranean Sea (e.g. Boudouresque, 1971; Ballesteros, 1993).

Artificial substrates are often subjected to important levels of disturbance (Airoldi and Bulleri, 2011). These artificial habitats are usually characterized by low biodiversity (Odum, 1985), where usually a few opportunistic species thrive (Orfanidis *et al*., 2003; Dafforn *et al*., 2009). This is the case of *Cladophora* spp., which show tolerance to environmental disturbances (e.g. Peckol and Rivers, 1995; Orfanidis *et al*., 2001; Salomidi *et al*., 2016), and presented higher cover percentages on the studied rip-raps compared to natural substrates. In fact, opportunistic species could outcompete other species on hard substrates, thus resulting in fewer number of species than in natural habitats (Bacchiocchi and Airoldi, 2003).

It is noteworthy that 17 taxa were exclusively found on natural hard substrates while only three were found as exclusive on artificial ones (Table 1), including the cryptogenic species *Ganonema farinosum* (Verlaque *et al*., 2015; Zenetos *et al*., 2018) that was recently reported to be widely distributed in Crete Island (Gerovasileiou *et al*., 2017). Moreover, some species found exclusively on natural hard substrates in the study area (e.g. *Thylacodes arenarius* and *Cystoseira spinosa*) have been proposed as bioindicators of good environmental status within monitoring schemes under the Marine Strategy Framework Directive (MSFD) (WoRMS Editorial Board, 2018). They are also considered in some ecological indices, such as CARLIT (Ballesteros *et al*., 2007). In addition, *C. spinosa* is included in the list of endangered or threatened species (Annex II) of the Barcelona Convention (1996).

The sessile benthic assemblage on rip-raps had fewer taxa and lower values of diversity (H'), suggesting that those support a poorer and more homogeneous assemblage than natural rocky reefs. The construction of coastal defense infrastructures (e.g. rip-raps and seawalls) has been previously identified as a "driver of global biotic homogenization" (see review in Firth *et al*., 2016a) which is defined as the process under which communities become more uniform in terms of number of taxa, similarity of functions and genetic diversity (McKinney, 2006).

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Differences in assemblage structure between natural and artificial substrates were clearly portrayed by the MDS ordination. In fact, natural substrates were pooled together and separated from artificial ones indicating that the substrate type has a major role in structuring sessile benthos. Multivariate analyses (Supplementary Table 10) highlighted higher variability among localities than among sites within a given locality, indicating that local populations could have been established depending on the local variability of environmental conditions (e.g. Tofts and Silvertown, 2000). Although variability is usually larger at small spatial scales in shallow rocky coasts (Fraschetti *et al*., 2005), our results suggest higher variability at a broader scale (among different localities, tens of kilometers away); this contrasts with other studies for Mediterranean rocky beds with canopy-forming macroalgae (Dal Bello *et al*., 2016). Our results might be explained because depth, wave exposure, age and inclination of hard substrates was similar in all sites within localities in an effort to ensure comparability. Nevertheless, statistically significant differences were still found between artificial and natural substrates.

Differences of artificial versus natural hard substrate assemblages are mainly related to habitat complexity, wave exposure, age of the substratum, dispersal potential of propagules and larvae, substrate inclination and orientation (e.g. Glasby and Connell, 2001; Firth *et al*., 2016b; Ushiama *et al*., 2016), herbivory (Forrest *et al*., 2013; Ferrario *et al*., 2016), roughness and nature of building materials (e.g. Coombes *et al*., 2015; Cacabelos *et al*., 2016; Sempere-Valverde *et al*., 2018). The sampling design considered in our study eliminated potential confounding effects due to some factors (e.g. wave exposure, inclination and dispersal of propagules and larvae), thus allowing more rigorous conclusions with regard to the examined factors.

So far, it is uncertain how many years are needed for artificial structures to hold a “climax community” or to determine if that is even possible. Some authors have estimated that it takes between 5 and 20 years for artificial structures to reach climax communities (Hawkins *et al*., 1983; Pinn *et al*., 2005; Coombes, 2011) while others suggest that low crested structures (like the ones studied here) never become natural climax communities (Gacia *et al*., 2007) or that incomplete succession could be a persistent stable state (Ferrario *et al*., 2016 and references

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therein). The taxa which were exclusively found on natural substrates in the study area reproduce by releasing spores or larvae to the water column, being capable of colonising nearby hard substrates within the immersion time of the studied artificial substrates (>10 years). Thus, we believe that the immersion time of the artificial substrates was not a major factor structuring the communities in the present study.

Different substrate inclination (i.e. vertical versus horizontal surfaces) has been shown to affect small-scale variability on artificial substrates (Glasby, 2000; Ushiama *et al*., 2016). In this study, all examined surfaces were vertical in order to minimize heterogeneity linked to different surface inclination. Exposure to sunlight has been found to have more determinant effects on epibiotic assemblages compared to surface inclination (see Glasby and Connell, 2001). Nevertheless, in our study there were no significant differences between northern and southern

localities. In addition, the entire coastline of Crete belongs to the same biogeographical area (the South Aegean ecoregion) and there is high connectivity between the north and south sides due to the interconnection of cyclonic and anticyclonic gyres by currents and jets (Theocharis *et al*., 1999). All in all, and given that the sampled artificial structures in our study were adjacent to natural hard substrates, thus facilitating the potential nourishment of rip-raps (Gacia *et al*., 2007), it is improbable that poor larval or propagules dispersal limits the establishment of assemblages on rip-raps. On the other hand, their settlement could be affected by other factors such as nature of building materials and roughness (Coombes *et al*., 2015; Ido and Shimrit, 2015; Sempere-Valverde *et al*., 2018) or ecological processes, such as grazing, predation and competition (Foster *et al*., 2003; Bulleri, 2005; Marzinelli *et al*., 2011; Ferrario *et al*., 2017).

Besides the differences in assemblage composition and diversity, the cover of habitat-forming arborescent macroalgae was significantly lower in rip-raps, thus potentially generating differences in ecosystem functioning. These species can modify the community structure (Benedetti-Cecchi *et al*., 2001; Maggi *et al*., 2009) by providing new habitat and shelter (Boudouresque, 1971; Cheminée *et al*., 2017) and facilitating the establishment of propagules and larvae (Arenas *et al*., 2006; Bulleri, *et al*., 2009). In addition to the increase of habitat

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complexity, they constitute an important source of primary production, supporting rich vagile biota, such as fish (Thiriet *et al*., 2016; Cheminée *et al*., 2017).

In natural habitats, coexistence of arborescent and encrusting taxa on macroalgal communities is common since encrusting species are usually tolerant to overgrowth (Airoldi, 2000; Bulleri, 2006); this coexistence was observed in the studied natural substrates while rip-raps exhibited a shift towards non-arborescent algae. This might be explained by different grazing pressures between habitats. Indeed, grazing has been identified as relevant in shaping macroalgal assemblages (Underwood and Jernakoff, 1984; Coleman *et al*., 2006; Tsirintanis *et al*., 2018). For instance, Ferrario *et al*. (2016) reported higher grazing pressure in artificial structures in comparison to natural ones in the North Adriatic Sea. First, isolated artificial structures over soft bottoms would probably be subjected to higher grazing pressure compared to large rocky reefs due to the greater concentration of potential grazers in the only available, artificial rocky substrates (Ferrario *et al*., 2016). In our case, Gournes had rip-raps settled over soft bottoms approximately 1 km away from the nearest natural rocky shore. Second, the higher diversity and abundance of palatable algae in natural habitats results in a share-out of grazing pressure among targeted algae species. In accordance with this hypothesis, the most abundant arborescent species of the study area (*Jania adhaerens*, *Laurencia obtusa* and *Amphiroa rigida*) were absent from rip-raps. However, apart from Gournes, rip-raps in other localities were adjacent to natural hard substrates. Therefore, a different grazing pressure across localities from highly motile herbivores such as certain fishes is rather unlikely. Nevertheless, the invasive crab *Percnon gibbesi* (H. Milne Edwards, 1853) was abundant in all sampling localities in the boulder-like rip-raps (authors' personal observations, Fig. 6). *Percnon gibbesi* has been described as a herbivorous species, mostly feeding on articulated Corallinaceae and Sphacelariaceae (Deudero *et al*., 2005; Puccio *et al*., 2006), possibly exerting this way a differential grazing pressure. Katsanevakis *et al*. (2010) also measured higher densities of this crab in boulder-like habitats near marinas. Therefore, it is likely that the introduction of highly heterogeneous artificial structures for coastal defense purposes could facilitate the establishment of some non-indigenous species. The potential impact of such introductions

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should be considered in future management practices for deployment of coastal defense structures, especially in marine areas highly susceptible to biological invasions.

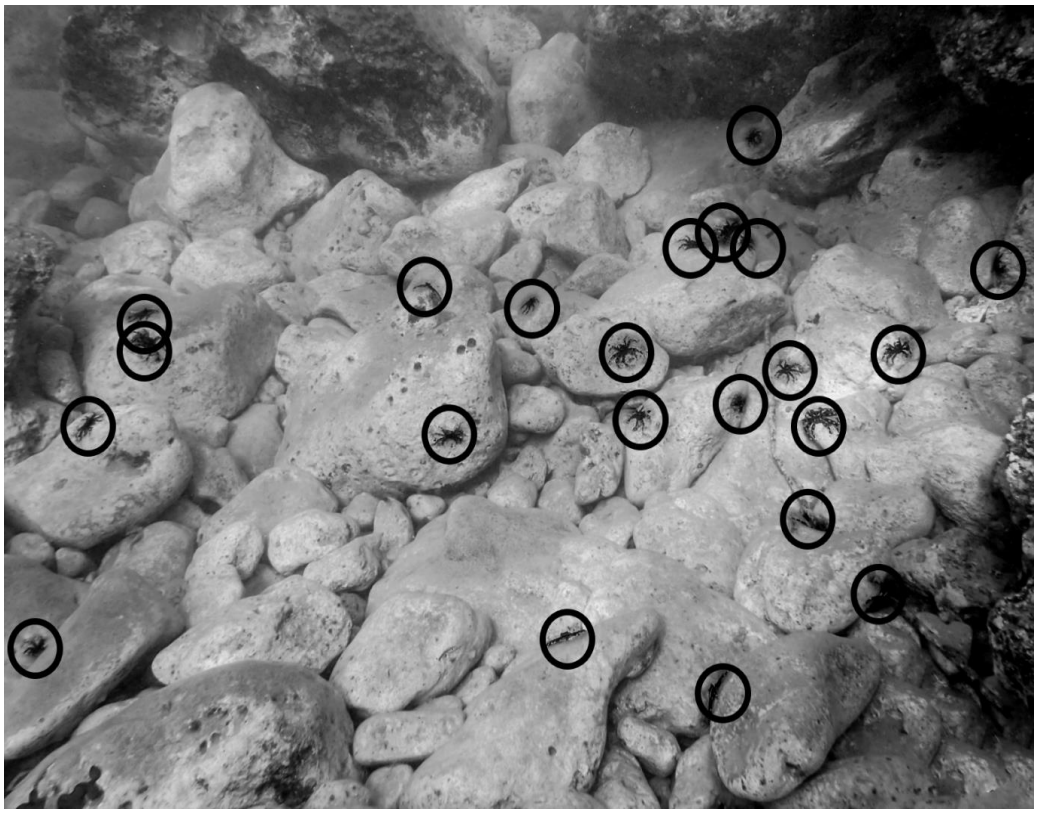

Fig. 6. Specimens of the invasive crab *Percnon gibbesi* (encircled) inhabiting a boulder-like rip-rap in one the sampling locations (July 2017, Kato Galatas, Crete).

Conclusions

In conclusion, the composition and diversity of shallow subtidal sessile assemblages on rip-raps suggest that these artificial structures do not function as surrogates of natural hard substrates in the study area, considering both a taxonomic and a functional approach. The deficient performance of this artificial habitat could be attributed to a combination of co-occurring abiotic and biotic factors such as the nature and roughness of the building material as well as differential grazing pressure. We suggest that future constructions should apply

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ecological criteria considering various materials (e.g. Sempere-Valverde *et al*., 2018) and novel designs (Ostalé-Valriberas *et al*., 2018) which could match the particular scenario of the Cretan coast. Further research for the ecological characterization of these structures is critical in order to improve our knowledge in support of better management practices, under the framework of green engineering, in coastal and marine infrastructure of the Eastern Mediterranean Sea.

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CHAPTER 3: Do coastal infrastructure produce trophic changes?

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3.1 Changes on trophic amphipod structure

General hypothesis: Amphipod community and trophic structure will differ between artificial and natural substrates, being the rip-raps more similar to their nearest natural substrates in comparison with concrete blocks (i.e cubes and tetrapods). Trophic structure of the community (percentage of carnivores, herbivores, detritivores and omnivores) will also be affected by the type of substrate (artificial vs natural). Differences are expected to be affected by the spatial scale of the study (Alboran Sea).

3.2 Effect on the diet at the individual level

General hypothesis: Artificial structures will affect the trophic niche of the limpet *Patella caerulea*. The isotopic ratios of $\delta^{13}C$ y $\delta^{15}N$ will also reflect the environmental conditions across the geographical gradient of the study (western to eastern Alboran Sea).

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CHAPTER 3.1

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3.1 Changes on trophic amphipod structure

Adapted from: Sedano, F., de Figueroa, J. T., Navarro-Barranco, C., Ortega, E., Guerra-García, J. M., Espinosa, F. (2020). Do artificial structures cause shifts in epifaunal communities and trophic guilds across different spatial scales?. Marine Environmental Research, 158, 104998. https://doi.org/10.1016/j.marenvres.2020.104998

Abstract

In the current frame of proliferation of artificial structures in the sea, the ecological effects of artificial substrates on marine environments and their associate biota become a topic of great scientific and conservationist interest. This study was focused on the amphipod communities from western Mediterranean Sea and tested, using the same secondary substrate, *Ellisolandia elongata*, if the community and trophic structure differ between artificial (two concrete-based: cubes and tetrapods, and one natural rock-based: rip-raps) and natural substrates. Results usually showed lower taxa number and diversity in artificial substrates, as well as differences in composition and trophic structure of the amphipod community. However, patterns were not consistent for all localities, evidencing the importance of local scale. Other potential factors, besides the substrate type, should be considered to understand particularities of each locality in management and conservation strategies.

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Introduction

The increase of human population in coastal areas is demanding the exploitation of natural resources, ocean's energy and leading to further industrialization that ultimately promotes the greenhouse gas emissions and the concomitant global change (van Vuuren and Riahi, 2011; IPCC, 2019). Consequently, extreme weather events, such as sea storms, are increasing worldwide (either intensity or frequency), which combined with the sea level rise, is further promoting the replacement of natural substrates by man-made structures. Therefore, the coastline is being 'hardened' as an adaptation option (*sensu* IPCC, 2014) for protecting human properties, infrastructures, industry, commerce and recreational areas (Zanuttigh et al., 2014). Globally, this phenomenon has been defined as 'ocean sprawl', i.e. the proliferation of artificial structures in the sea (Firth et al., 2016).

There is extensive literature dealing with the ecological effects of artificial substrates on the marine environment. In fact, many studies have reported that artificial structures such as breakwaters, rip-raps, jetties or seawalls do not support the same biota than natural rocky substrates and do not act as a surrogate for natural rocky shores (Moschella et al., 2005; Pister, 2009; Bulleri and Chapman, 2010; Sedano et al., 2019). Concrete-made artificial structures (such as cubes and tetrapods) usually have less heterogenous surfaces (ranging from meters to millimeters) than the natural rock, preventing the refuge from adverse abiotic and biotic conditions (Firth et al., 2013; Loke et al., 2015), especially in intertidal environments (Ostalé-Valriberas et al., 2018). Most of these studies have mainly focused on a comparison of sessile marine communities and on how novel habitats can be adapted to sustain biodiversity in artificial areas (Chapman and Underwood, 2011; Perkins et al., 2015). Studies on the influence of artificial substrates on vagile epifaunal communities are scarce due to the difficulties in sorting and identifying these small organisms (Carvalho et al., 2018). The artificial structures (artificial substrates) and the adjacent natural rocky shores (natural substrates) are usually referred as primary substrates, in which sessile flora and fauna settle (secondary substrates) (see Ros et al., 2016). The secondary substrates usually vary among sites, since different

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environmental factors, such as wave exposure, are likely to influence their community hcomposition in a particular habitat (Southward and Orton, 1954) and indirectly impact associated epibiont communities. In fact, densities of mobile epifaunal community can be strongly dependent on the species identity of the secondary substrate (Dumont et al., 2011; Thomsen et al., 2017). A comparison using the same sessile biota in all localities is needed to avoid the effect of the secondary substrate (sessile biota) when testing differences associated to primary substrates (artificial structures vs natural rocky shores). For all these reasons, comprehensive data focused on the same secondary substrate through extensive geographical ranges are mandatory to properly evaluate the impact of coastal defences structures.

Regarding trophic structure, the knowledge about the impact of ocean sprawl in coastal trophic webs is still poorly developed. Shoreline armouring compromises prey resources, but it remains unclear how this affects feeding ecology within urban shorelines (Munsch et al., 2015). Some studies have pointed out that microbial films differ between artificial and natural substrates (Tan et al., 2015), being such biofilms the basis of intertidal food webs. Previous studies have also indicated that the variety of diet for several marine species such as fish or mollusks is more restricted within artificial habitats (see Vose and Nelson, 1984; Burgos-Rubio et al., 2015). Nevertheless, there is a lack of knowledge about how artificial substrates affect the trophic relationships on rocky shores.

Amphipoda, with more than 10,000 species described (Ahyong et al., 2011; Horton et al., 2020), is a worldwide distributed group of crustaceans inhabiting marine and brackish waters, freshwater (both epigean and hypogean systems) and even terrestrial environments (Väinölä et al., 2008; Horton et al., 2020). Besides its great species richness, amphipods exhibit an impressive diversity of ecological and biological traits (e.g. De Broyer and Jazdzewski, 1996; Väinölä et al., 2008) that make them fundamental components of the biocoenosis in which they are part. So, they usually play important roles in the food webs (Väinölä et al., 2008), mainly in the aquatic ones, acting as primary and secondary consumers as well as being fundamental prey for many other animals (e.g. Legeżyńska et al., 2012; Vázquez-Luis et al., 2010). In fact, amphipods are also very diverse regarding their trophic roles, acting as carnivores, herbivores,

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detritivores or omnivores (Guerra-García et al., 2014). Amphipods constitute one of the dominant groups of marine rocky habitats and soft bottoms (Taylor, 1998; de-la-Ossa-Carretero et al., 2010), reaching high densities. In addition, they have been proposed as excellent bioindicators of the quality of marine habitats (Thomas, 1993; Conradi et al., 1997; Guerra-García and García-Gómez, 2001; de-la-Ossa-Carretero et al., 2012). Considering this, the study of the structure and functioning of amphipods communities can be particularly useful for evaluating the effects of anthropogenic modifications on coastal ecosystems. Indeed, amphipods have been used as model group to explore the environmental impact on coastal defence structures (Sedano et al., 2020a).

In the present study, we used a regional approach along the Alboran Sea (ca. 400 km coastline) to understand the potential effects of artificial structures on species composition, abundance and trophic structure of vagile communities, using amphipods as a model group. To avoid the potential effects of different secondary substrates on the species composition of amphipod communities, we selected the same substrate, the alga *Ellisolandia elongata*, throughout the whole study. Specifically, the following hypotheses were tested: (1) amphipod community structure differ between artificial and natural substrates and number of species, abundance and Shannon's diversity are higher in natural than in artificial habitats; (2) artificial substrates with natural boulders (i.e. rip-raps) are more similar to their nearest natural substrates in comparison with concrete blocks (i.e cubes and tetrapods), which would be more different to their corresponding natural habitats; (3) trophic structure of the community (percentage of carnivores, herbivores, detritivores and omnivores) are also affected by the type of substrate (artificial vs natural).

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Materials and methods

Experimental design and sampling collection

In May 2017, three types of artificial structures (two concrete-based: cubes and tetrapods, and one natural rock-based: rip-raps) and their nearest natural rocky substrates (Table 1), were sampled across the Alboran Sea (western Mediterranean Sea, Fig. 1). The experimental design for each kind of artificial structure was the following: Factor Substrate (Su), two levels (artificial, natural), fixed; Factor Locality (Lo), three levels, random and orthogonal with Su. The three localities with cubes were Ceuta (CEU), Fuengirola (FUE) and Motril (MOT); the three with rip-raps were Aguadulce (AGD), Algeciras (ALG) and Marina del Este (MES) and the three with tetrapods were Benalmádena (BEN), M'Diq (MDQ) and Marina Smir (SMR). The nearest natural rocky shore was the same for the tetrapods of M'Diq and Marina Smir. Therefore, the amphipod community structure from both artificial structures were compared with the same set of data from the same natural rocky shore. As secondary substrate, we selected the alga *Ellisolandia elongata* throughout the whole study, previously known as *Corallina elongata* (Hind and Saunders, 2013). This is one of the most common sessile species along the study area and host a diverse amphipod community (Guerra-García et al., 2006; Izquierdo and Guerra-García, 2011). *Ellisolandia elongata* has been useful as secondary substrate model in previous studies to explore biogeographical patterns and effects of invasive species for associated vagile communities (see e.g. Guerra-García et al., 2009, 2012). Indeed, dense fronds of articulated coralline algal turf provide an excellent habitat for diverse and abundant macrofaunal communities and it is a basis for investigating biological processes and physical factors responsible for structuring patterns of biodiversity of macrofaunal communities (Kelaher et al., 2001). At each locality three 10 x 10 cm scrapes of *E. elongata* were sampled at low intertidal level (5–20 cm over low spring tide). Each sample was preserved in 96% ethanol and brought to the laboratory where it was sieved through a 0.5 mm mesh to retain the associated macrofauna. The volume of each replicate of *E. elongata* was estimated

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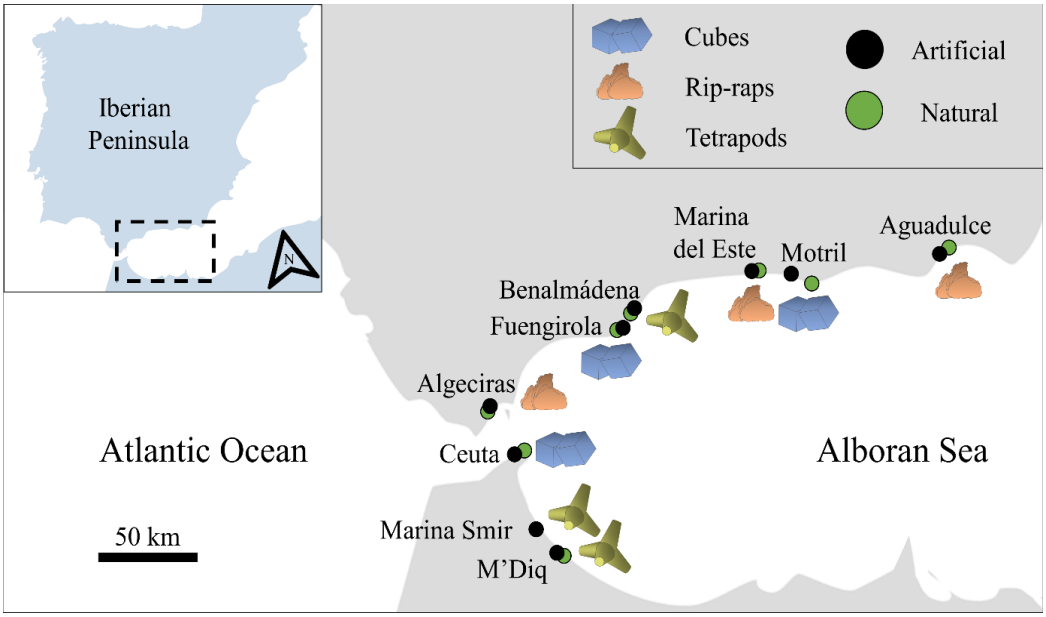

Fig. 1. Sampling map showing the distribution of the artificial coastal defence structures sampled across the Alboran Sea. The nearest natural rocky shore (green dots) was the same for the tetrapods of M'Diq and Marina Smir.

Table 1: List of sampling localities. Note that the nearest natural rocky shore was the same for the tetrapods of M'Diq and Marina Smir. n.a.: not applicable

Localities	Coordinates (Latitude/Longitude)	Date of deployment	Distance from nearest natural rock (km)	Material
Natural				
Ceuta	35º53'50.94''N/5º17'57.46''W	n.a.	n.a.	Natural rock
Algeciras	36º06'34.10''N/5º25'55.40''W	n.a.	n.a.	Natural rock
Fuengirola	36º30'23.34''N/4º38'21.76''W	n.a.	n.a.	Natural rock
Benalmádena	36º34'47.41''N/4º32'48.25''W	n.a.	n.a.	Natural rock
Marina del Este	36º43'23.31''N/3º43'35.22''W	n.a.	n.a.	Natural rock
Motril	36º42'10.27''N/3º24'40.06''W	n.a.	n.a.	Natural rock
Aguadulce	36º49'41.48''N/2º31'54.64''W	n.a.	n.a.	Natural rock
M'Diq	35º40'56.87''N/5º18'23.38''W	n.a.	n.a.	Natural rock
Marina Smir	35º40'56.87''N/5º18'23.38''W	n.a.	n.a.	Natural rock
Cubes				
Ceuta	35º54'01.03''N/5º19'27.26''W	2004	2.3	Concrete
Fuengirola	36º32'31.83''N/4º36'51.25''W	1986*	4.6	Concrete
Motril	36º43'07.38''N/3º31'29.14''W	1986*	10.4	Concrete
Rip-raps				
Algeciras	36º07'01.20''N/5º26'07.90''W	1997	0.9	Natural rock
Marina del Este	36º43'31.00''N/3º43'32.66''W	1986*	0.3	Natural rock
Aguadulce	36º48'58.70''N/2º33'20.98''W	1989*	5.8	Natural rock
Tetrapods				
Benalmádena	36º35'50.06''N/4º30'28.52''W	1986*	4.0	Concrete
Marina Smir	35º45'25.57''N/5º20'28.19''W	2003*	8.8	Concrete
M'Diq	35º41'03.12''N/5º18'40.51''W	2009*	0.5	Concrete

*Older data estimated according to historical aerial images from Google Earth and http://fototeca.cnig.es

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as the difference between the initial and final volume when placed into a graduated cylinder with a fixed amount of water. Amphipods were sorted and identified to the species level, whenever possible.

Dietary analyses and community trophic structure

To study the feeding contents, we selected the species which contributed with at least 2% to the total abundance. We studied 664 specimens of 6 amphipod species. For the diet study, individuals were analyzed following the transparency methodology proposed by Bello and Cabrera (1999) with slight variations. This method has been successfully used to analyze the gut contents of amphipods in previous studies (e.g. Guerra-García and Tierno de Figueroa, 2009; Alarcón-Ortega et al., 2012; Vázquez-Luis et al., 2013; Guerra-García et al., 2014, 2015). Specimens of each species were introduced in vials with Hertwig's liquid (consisting of 270 g of chloral hydrate, 19 ml of chloridric acid 1 N, 150 ml of distilled water and 60 ml of glycerin) and heated in an oven at 65 °C for 3–8 h depending on the cuticle thickness of the specimens. After this, they were mounted on slides for study under the microscope. The percentage of absolute gut content (at 40 x or 100 x), as the total area occupied by the content in the whole digestive tract, and relative gut content (at 100 x or 400 x), as the area occupied for each component within the total gut content, were estimated using a microscope equipped with an ocular micrometer. When using direct methods for quantifying gut contents, it is common that part of the collected individuals have empty or partially full guts so it has been proposed to collect, at least, around 15–20 individuals per species (Rosi-Marshall et al., 2016). Therefore, to have reliable diet data, we had to pool specimens from different localities of the same structures (cubes, rip-raps and tetrapods), preventing comparisons among localities in this case. Empty guts were not considered to calculate the total area occupied by the digestive content.

To characterize the amphipod trophic structure, data from the gut content analyses were subsequently used to assign each taxon to its feeding group (detritivores, carnivores, herbivores and omnivores). When the gut content included more than 50% of prey, we catalogued the

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species as a carnivorous one, considering that other food items can appear as the prey gut content or accidentally ingested when preying, as proposed by Navarro-Barranco et al. (2013). For the dominant species (> 2% of total abundance), we used the data obtained from the dietary analysis conducted in the present study. For the remaining species, the assignation to the trophic group was based on data of gut content analyses from the literature (see Supplementary Table 11). When data were not available for a particular taxon, the category was assigned based on other species of the genus or family. To elaborate the trophic matrix we calculated the percentage of specimens of each feeding group for each replicate (see experimental design above). Therefore, percentage was calculated based on the trophic assignment of each species and its contribution (in number of specimens) to the total abundance. When a species was not clearly associated with a single feeding category but two (Supplementary Table 11), half of the abundance was assigned to one category and the other half to the other category.

Besides the trophic characterization of the whole community (percentage of detritivores, carnivores, herbivores and omnivores), the six dominant species studied in detail were used to explore, within the same species, variations in the food items ingested in artificial and natural substrates of localities with cubes, rip-raps and tetrapods.

Satistical analyses

To verify that the amount of *E. elongata* (measured in volume) collected per replicate of 10 x 10 cm did not differ between artificial and natural substrates at each locality, a two-way analysis of variance (ANOVA) was conducted using the experimental design explained above. For each replicate, the number of amphipod taxa (S), abundance of individuals (individuals/1000 ml) and Shannon's Diversity index were calculated. To compare these community descriptive parameters, a two-way ANOVA was conducted. Homogeneity of variances was confirmed using Cochran's test. When ANOVA detected significant differences for a given factor or interaction of factors, the source of the difference was identified by applying the Student-Newman-Keuls (SNK) test (Underwood, 1997).

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A matrix of the community structure based on species composition and their abundances was employed to test the effect of Substrate and Locality using permutational multivariate analysis of variance (PERMANOVA). Using the experimental design explained above, PERMANOVAs were run on a triangular similarity matrix derived from the values of the Bray-Curtis similarity on square root transformed amphipod abundance data using 9999 permutations. In cases of small numbers of unique permutations (100 or less), p-values were obtained through a Monte Carlo test (Anderson et al., 2008). In order to evaluate if differences are due to species composition or species abundances, additional PERMANOVAs were conducted using data of presence/absence. To evaluate the potential effect of the geographical distance between the artificial substrate and the nearest natural rocky shore on the amphipod's community structure, we performed a Spearman correlation between the Bray Curtis similarity (artificial vs natural at each locality) and the distance (km between the artificial and natural substrate) for each locality.

To explore differences at trophic level, a matrix containing percentages of detritivores, carnivores, herbivores and omnivores was used with the same two factors experimental design. Two-way PERMANOVA (using Euclidean distances and untransformed data) and two-way ANOVA were also conducted using these trophic data. PERMANOVA analyses were carried out using PRIMER v.6+PERMANOVA package (Clarke and Gorley, 2006) and ANOVA was conducted on GMAV5 software (Underwood et al., 2002).

Results

Amphipod community structure

A total of 7779 individuals belonging to 27 taxa of Amphipoda (Table 2) were collected in the study. *Hyale stebbingi*, followed by *Protohyale (Protohyale) schmidtii* and *Stenothoe tergestina* were the most abundant taxa, while *Apolochus picadurus*, Lysianassidae and *Guernea (Guernea) coalita* were the scarcest (Table 2). According to the two-way ANOVA

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(data not shown), no significant differences were found in the volume per replicate of *E. elongata* between artificial and natural substrates, making comparable the data obtained for amphipods. Overall, the number of amphipod taxa was lower in artificial structures (except on Algeciras' and Aguadulce's rip-raps) and two-way ANOVA showed significantly lower number of taxa in the cubes of Ceuta, the cubes of Fuengirola and the tetrapods of M'Diq and Marina Smir (Fig. 2). Also, Shannon's diversity tended to be lower in artificial structures (except on the rip-raps of Algeciras and Marina del Este), being significantly lower in the tetrapods of M'Diq and Marina Smir. There were only significantly lower total amphipod abundance in the cubes of Ceuta (Supplementary Table 12, Fig. 2). However, some taxa, i.e. *Caprella hirsuta*, *Caprella liparotensis*, *Caprella penantis*, *Jassa marmorata*, *Lembos* aff. *websteri* and *Stenothoe monoculoides*, had a considerably higher abundance in natural versus artificial substrate, except on the rip-raps at Algeciras, in which an opposite trend was observed. In fact, all taxa present in Algeciras showed a higher abundance in artificial substrate than in natural one except *Apherusa mediterranea* and *Hyale stebbingi*. *Podocerus variegatus* was the only taxon with higher densities in artificial than natural substrate (Table 2).

PERMANOVA results (Table 3) showed significantly different amphipod community structure among localities (factor Lo) and between substrates (interaction Su x Lo). According to the pair-wise tests of the interaction, amphipod community on artificial structures was significantly different compared with the nearest natural substrate in Fuengirola (cubes), Aguadulce (rip-raps), Algeciras (rip-raps) and M'Diq (tetrapods). When presence/absence data was used (PERMANOVA table not shown), significant differences between artificial and natural substrates were found again in Fuengirola (cubes) ($t = 2.60$, $p < 0.05$), Algeciras (rip-raps) ($t = 2.22$, $p < 0.05$) and M'Diq (tetrapods) ($t = 3.52$, $p < 0.05$), but not for Aguadulce (rip-raps) ($t = 2.11$, $p = 0.07$). Additionally, a significant difference appeared in Marina Smir (tetrapods) ($t = 2.58$, $p < 0.05$). As shown by the correlation results ($R^2 = 0.0857$, $p > 0.05$), the distance between artificial and natural substrates did not have a direct relationship with the similarity between substrates at each locality.

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Table 2. Mean number of individuals per 1000 ml in each locality and substrate. C: Cubes; R: Rip-raps; T: Tetrapods; N: natural.

	Ceuta		Fuengirola		Motril		Aguadulce		Algeciras		Marina del Este		Benalmádena		M'Diq		Marina Smir	
	C	N	C	N	C	N	R	N	R	N	R	N	T	N	T	N	T	N
Ampithoe ferox (Chevreux, 1901)	0	0	0	173	0	0	0	0	193	0	30	50	0	0	0	0	0	0
Ampithoe ramondi Audouin, 1826	0	0	0	26	16	12	33	0	17	0	0	0	0	0	0	0	0	0
Apherusa mediterranea Chevreux, 1911	0	0	0	0	0	0	0	0	10	33	0	0	0	0	0	0	0	0
Apocorophium sp.	0	0	0	0	0	0	0	0	93	0	0	0	25	20	0	0	0	0
Apolochus picadurus (J.L. Barnard, 1962)	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0
Apohyale perieri (Lucas, 1849)	195	192	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caprella equilibra Say, 1818	0	0	0	0	0	0	0	0	0	0	0	167	0	0	0	0	0	0
Caprella grandimana Mayer, 1882	0	0	150	170	0	169	0	89	454	47	606	211	134	613	67	144	375	144
Caprella hirsuta Mayer, 1890	0	0	0	0	0	0	0	0	79	0	0	0	0	333	0	994	0	994
Caprella liparotensis Haller, 1879	0	0	0	38	0	0	0	0	0	0	0	0	14	202	0	450	17	450
Caprella penantis Leach, 1814	20	0	0	0	0	0	0	17	64	0	0	35	0	0	0	162	0	162
Coxischyrocerus inexpectatus (Ruffo, 1959)	0	0	20	70	76	0	161	11	17	0	0	0	0	0	0	0	0	0
Elasmopus rapax Costa, 1853	0	43	100	300	0	53	161	76	0	0	183	53	0	48	0	64	0	64
Elasmopus vachoni Mateus & Mateus, 1966	0	0	0	0	0	0	0	0	1177	22	0	0	0	0	57	862	0	862
Hyale pontica Rathke, 1847	108	417	0	0	0	0	0	133	0	0	0	0	0	0	0	0	0	0
Hyale stebbingi Chevreux, 1888	1023	3325	2479	3487	1183	460	100	1296	675	4116	548	1643	1507	2294	4001	1766	6383	1766
Jassa marmorata Holmes, 1905	0	1142	330	571	16	23	50	246	267	0	0	17	276	1749	0	1427	800	1427
Jassa ocia (Spence Bate, 1862)	7	232	0	0	0	0	17	0	10	0	0	0	0	0	0	33	75	33
Guernea (*Guernea*) *coalita* (Norman, 1868)	0	13	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lembos aff. *websteri* Spence Bate, 1857	0	0	0	167	0	0	0	0	194	0	0	0	0	0	0	37	0	37
Lysianassidae	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0
Podocerus variegatus Leach, 1814	0	0	51	0	0	0	0	0	26	0	0	0	7	0	28	13	17	13
Protohyale (*Protohyale*) *schmidtii* (Heller, 1866)	1358	2317	117	2092	2137	804	894	700	1824	122	1934	885	656	1457	0	394	0	394
Serejohyale spinidactylus (Chevreux, 1926)	0	408	0	0	0	140	0	0	0	0	1033	0	0	0	0	0	0	0
Stenothoe cattai Stebbing, 1906	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	42	0	42
Stenothoe monoculoides (Montagu, 1813)	36	205	71	139	115	144	0	0	1254	33	14	20	46	206	45	652	892	652
Stenothoe tergestina (Nebeski, 1881)	0	133	1539	0	365	889	50	816	692	0	284	1043	1523	131	0	3138	100	3138

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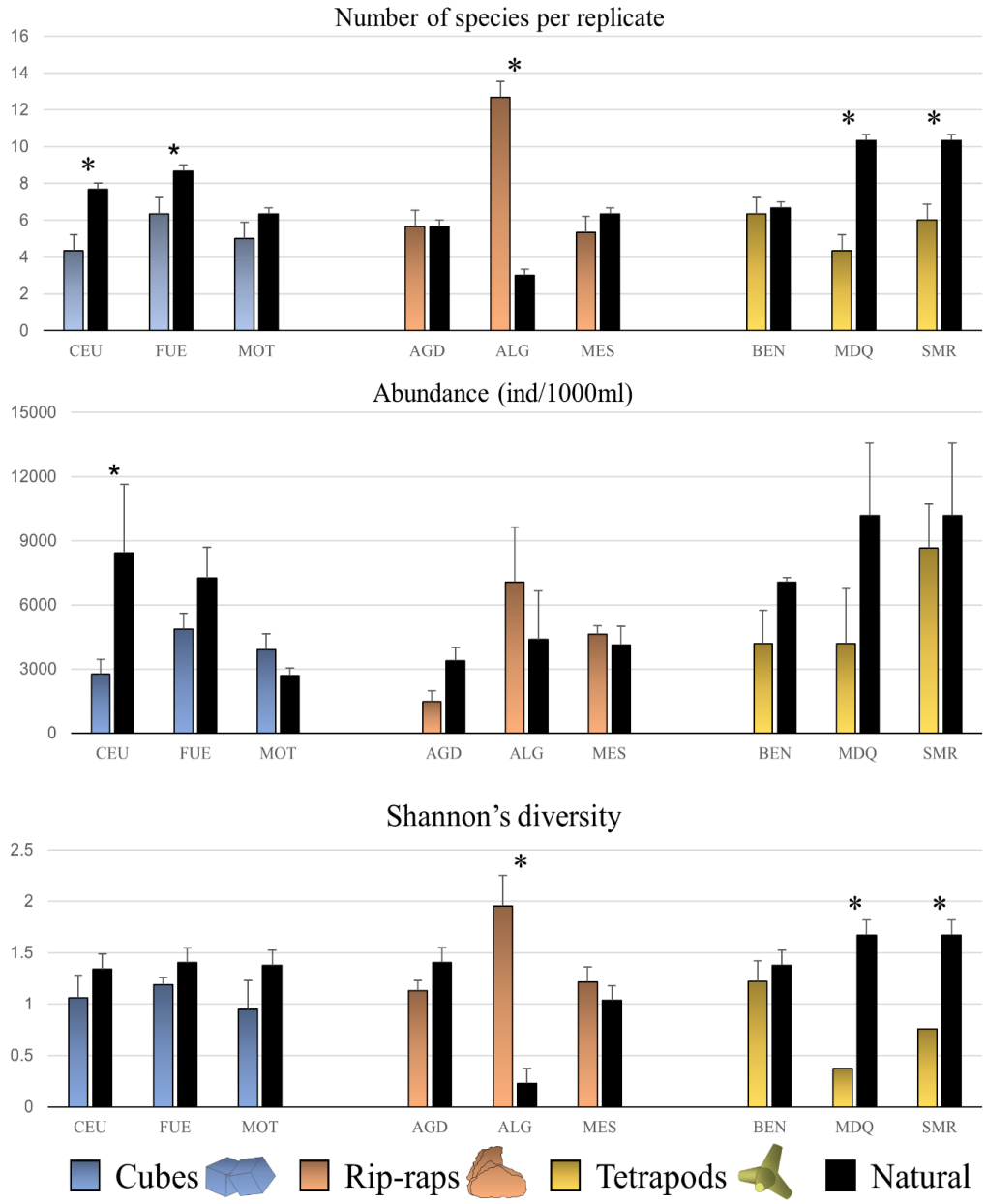

Fig. 2. Histograms comparing the average number of species (top), average total abundance (center) and Shannon's diversity (down) between artificial and natural substrates at each locality. Standard error bars are represented. Asterisks indicate significant differences ($p < 0.05$) according to the two-way ANOVAs (Supplementary Tables 12, 13 and 14). Localities with cubes: CEU (Ceuta), FUE (Fuengirola), MOT (Motril); localities with rip-raps: AGD (Aguadulce), ALG (Algeciras), MES (Marina del Este); localities with tetrapods: BEN (Benalmádena), MDQ (M'Diq), SMR (Marina Smir).

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Trophic structure

According to the amphipod trophic structure, PERMANOVA results (Table 4; Fig. 3) also showed significantly different trophic structure between substrates. According to the pair-wise tests of the interaction, amphipod trophic structure on artificial substrates was significantly different compared with the nearest natural substrate in Fuengirola (cubes), Aguadulce (rip-raps), Algeciras (rip-raps), Benalmádena (tetrapods), M'Diq (tetrapods) and Marina Smir (tetrapods). Therefore, differences between artificial and natural substrates were detected in all the localities except in Ceuta (cubes), Motril (cubes) and Marina del Este (rip-raps), and the tetrapods did not "mimic" the trophic structure of natural substrates at any locality. According to the two-way ANOVAs (Supplementary Table 15), there was significantly lower percentage of carnivores (compared with the natural substrate) on the tetrapods of M'Diq and Marina Smir. Additionally, there was significantly higher number of carnivores on the cubes of Fuengirola and on the rip-raps of Algeciras. The percentage of herbivores was significantly higher on the rip-raps of Algeciras and lower on the tetrapods of Marina Smir. Concerning detritivores, the percentage was significantly higher on the rip-raps of Algeciras but lower in the tetrapods of Benalmádena and M'Diq. There were not differences between substrates for the percentage of omnivores.

Within the species level, the study of the gut contents of the six most abundant species (*Caprella grandimana*, *Hyale stebbingi*, *Jassa marmorata*, *Protohyale schmidtii*, *Stenothoe monoculoides* and *Stenothoe tergestina*) in the different zones did not show appreciable differences between artificial and natural substrates for each particular taxon (Fig. 4). Regarding the occupation percentages of the whole digestive track, it is outstanding that exclusively detritivorous taxa had the higher values (e.g. *Caprella grandimana*), while those ingesting prey as important part of their feeding habits exhibited lower values (e.g. both species of *Stenothoe*). In general terms and taking into account that the small number of individuals in some cases prevented us to statistically analyze data separately by localities, it seems that each

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particular taxon did not change its feeding habits in relation with the zone and substrate occupied.

Table 3: PERMANOVA table of results for the amphipod community structure. Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; df: degrees of freedom; MS: mean square; p: level of significance; Ps.-F: Pseudo-F; Perm.: Permutations; n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Cubes					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	1330	0.653	n.s.	38
Lo	2	3804	5.243	***	9927
SuxLo	2	2037	2.808	**	9930
Residual	12	725			
Total	17				
Transformation	Square root				
Pair-wise	Level CEU: Cube = Natural				
	Level FUE: Cube≠Natural				
	Level MOT: Cube=Natural				
Rip-raps					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	7321	3.159	n.s.	38
Lo	2	3967	3.626	**	9943
SuxLo	2	2317	2.118	*	9918
Residual	12	1094			
Total	17				
Transformation	Square root				
Pair-wise	Level AGD: Rip-rap≠Natural				
	Level ALG: Rip-rap≠Natural				
	Level MES: Rip-rap=Natural				
Tetrapods					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	7817	3.151	n.s.	38
Lo	2	1853	2.002	n.s.	9940
SuxLo	2	2480	2.680	*	9929
Residual	12	925			
Total	17				
Transformation	Square root				
Pair-wise	Level BEN: Tetrapod=Natural				
	Level MDQ: Tetrapod≠Natural				
	Level SMR: Tetrapod=Natural				

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Table 4: PERMANOVA table of results for the amphipod trophic structure. Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; df: degrees of freedom; MS: mean square; p: level of significance; Ps.-F: Pseudo-F; Perm.: Permutations; n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Cubes					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	273	0.124	n.s.	38
Lo	2	1240	1.642	n.s.	9956
SuxLo	2	2209	2.926	n.s.	9954
Residual	12	755			
Total	17				
Transformation	None				
Pair-wise	Level CEU: Cube=Natural				
	Level FUE: Cube≠Natural				
	Level MOT: Cube=Natural				
Rip-raps					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	7021	3.699	n.s.	38
Lo	2	1261	4.299	*	9951
SuxLo	2	1898	3.966	*	9952
Residual	12	382			
Total	17				
Transformation	None				
Pair-wise	Level AGD: Rip-rap≠Natural				
	Level ALG: Rip-rap≠Natural				
	Level MES: Rip-rap=Natural				
Tetrapods					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	8610	2.690	n.s.	38
Lo	2	788	1.730	n.s.	9955
SuxLo	2	3200	7.026	**	9962
Residual	12	455			
Total	17				
Transformation	None				
Pair-wise	Level BEN: Tetrapod≠Natural				
	Level MDQ: Tetrapod≠Natural				
	Level SMR: Tetrapod≠Natural				

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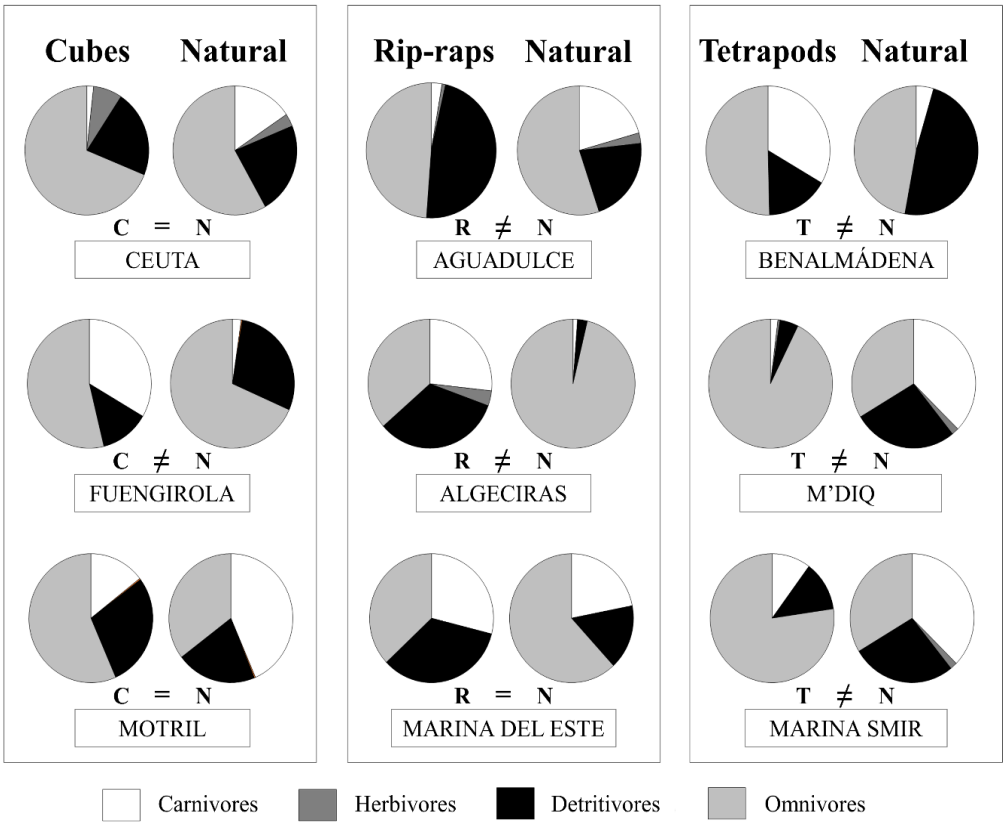

Fig. 3. Pie charts comparing amphipod trophic structure between artificial and natural substrates at each locality. Inequality signs represent significantly different trophic structure according to PERMANOVA. C: Cubes; R: Rip-raps; T: Tetrapods; N: Natural.

Discussion

Amphipod community structure

The present study reveals some differences in amphipod communities between artificial and natural substrates, although results were not consistent in all localities. When environmental conditions are similar between substrates, the physical characteristics of the artificial structures is well known to affect the biota (Coombes, 2011; Sempere-Valverde et al., 2018). In addition, the lack of microtextured surfaces is known to affect the settlement of invertebrate larvae (Koehl, 2007), leading to impoverished communities. This has been mainly addressed focusing on the sessile biota, although the effects of substrate complexity have been also studied in

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certain mobile organisms. For example, Moreira et al. (2007) found higher abundances of chitons in substrates with crevices and Sedano et al. (2020a) recently suggested that certain amphipods could get advantage of the microtextured features of the artificial structures. The materials of construction are also key factors for the development of sessile communities. For example, concrete-based artificial structures are known to increase pH levels (Sella and Perkol-Finkel, 2015) on the surface, affecting larvae settlement. Although it is unknown if material composition directly affects the associated epifaunal communities, they are indirectly influenced through the effects of material composition over the sessile biota (Sedano et al., 2020b). Therefore, considering material composition and complexity, bigger differences between artificial and natural substrates for the cubes and the tetrapods were expected.

According to the amphipod community structure (composition of taxa and their abundances), only one locality with cubes (Fuengirola) and with tetrapods (M'Diq) had significantly different structure (artificial vs natural), while two localities with rip-raps (Aguadulce and Algeciras) showed such differences. In contrast, when using presence/ absence data, no differences were found for Aguadulce and differences appeared in Marina Smir, suggesting that only in Aguadulce the differences were driven by differences in taxa abundances rather than community composition. Number of taxa and Shannon's diversity were generally lower in artificial substrates. The lower number of taxa on the cubes of Ceuta and Fuengirola, together with the lower number of taxa and Shannon's diversity on the tetrapods of M'Diq and Marina Smir, suggest that the negative impact of tetrapods and cubes was more pronounced than that of the rip-raps. In fact, the rip-raps of Algeciras had significantly higher number of taxa and Shannon's diversity in comparison with the nearest natural rocky shore, indicating that this natural rock-based artificial structures may be more suitable for maintaining amphipod biodiversity. Nevertheless, it is noteworthy that the amphipod community on the natural substrates of Algeciras was the most impoverished in our study. The pattern observed for the rip-rap of Algeciras may be the result of stochastic variability and/or patchiness in the distribution of amphipods (as discussed below). However, the benefits of including this type of artificial structures (rip-raps) have been previously highlighted mainly due to their higher

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structural complexity in comparison to concrete-based structures (Chapman, 2007; Liversage and Chapman, 2018). Material composition and complexity may be also a key factor driving the differences found for the cubes of Ceuta and the tetrapods of M'Diq and Marina Smir, although it could be also related to their young age (they were deployed in 2004, 2009 and 2003 respectively) and the environmental particularities of these localities. In fact, the tetrapods of M'Diq and Marina Smir were deployed over shallow soft bottom habitats (personal observation) that could affect the biota by sand abrasion (Blanco-Chao et al., 2007; Bulleri and Chapman, 2010 and references therein) or high sedimentation rates (Nicoletti et al., 2007).

Regarding the patterns for some of the identified taxa, most of the species found in the present study did not show a clear distribution pattern towards natural or artificial substrates, which seems likely due to the opportunistic behavior of these species. Despite being brooding species with a lack of planktonic larval stages, amphipods can potentially exhibit long-distance dispersal (Havermans et al., 2007; Wildish and Chang, 2017) and some of the recorded species has a proven capability to quickly colonize novel habitats (Vázquez-Luis et al., 2012; Navarro-Barranco et al., 2015). Moreover, many amphipod species are generalist inhabiting a wide variety of substrates under different environmental conditions (Saarinen et al., 2018; Navarro-Barranco et al., 2019). Indeed, dominant species found in the present study (such as *Stenothoe tergestina, Caprella grandimana, Elasmopus rapax, Jassa marmorata, Lembos* aff. *websteri* or *Hyale stebbingi*) are common along the Alboran Sea, being previously recorded at both natural and artificial substrates (Guerra-García et al., 2009, 2011; Navarro-Barranco et al., 2018; Gavira-O'Neill et al., 2018; Sedano et al., 2020a).

Nevertheless, a clear trend (natural vs artificial) is shown by some of the species found in the present study. For example, *Podocerus variegatus*, which is commonly found inside harbours and other polluted areas (Bellan-Santini, 1980; Gavira-O'Neill et al., 2015), showed higher abundance in artificial substrates. Conversely, *Caprella liparotensis*, a sensitive species to high levels of organic matter and suspended material (Bellan-Santini, 1980; Guerra-García et al., 2004) was mainly associated to natural substrates. *Lembos* aff. *websteri*, *Caprella hirsuta*, *Jassa marmorata* and *Stenothoe monoculoides* had lower abundances in artificial substrates in

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comparison with their nearest natural rocky shore except for one locality, Algeciras, where they show the opposite pattern. According to previous studies conducted inside Algeciras Bay, *Lembos websteri* and *Stenothoe monoculoides* are commonly associated to areas with greater hydrodynamism (Conradi et al., 1997, 2000), which is not necessarily in disagreement with our data since our sampling was conducted in the external sides (those facing to open sea) of the coastal defence structures considered. It is worth noting that this sampling strategy (the use of the same secondary substrate on exposed areas along the whole study area) may be responsible for the lack of constant differences observed between artificial and natural substrates. On the one hand, factors acting at small spatial scales would be the main drivers of spatial amphipod distribution. Taking into account that most amphipod species do not feed directly on their hosts (macroalgae and sessile invertebrates are mainly used as refuge) secondary substrates with similar morphology will provide a similar amount of available habitat of similar quality. In this sense, our findings agree with previous studies suggesting that the secondary substrate is the main driver of amphipod community structure inhabiting artificial substrates (Sedano et al., 2020a). Primary substrate characteristics would determine amphipod communities by means of shaping the sessile biota (Sedano et al., 2020a, 2020b). Moreover, the differences between substrates could be ameliorated by the high biodiversity supported by coralline turfs (Izquierdo and Guerra-García, 2011). In fact, Perkol-Finkel et al. (2012) proposed the transplantation of canopy-forming algae to increase the biodiversity in coastal structures of temperate areas because these species increase the complexity of such habitats. On the other hand, as a consequence of the exposed orientation of the artificial substrates considered, their surrounding abiotic environment (in terms of wave exposure, water temperature, oxygen concentration, pollutant levels) do not necessarily differ from their nearest rocky shores.

Coastal defence structures are often related with a decrease of ecological quality of the ecosystem, but such ecological impoverishment is mainly reported for internal areas. Thus, under such circumstances (same exposure and secondary substrate), existence of significant changes in amphipod communities between natural and artificial substrates will be hardly predictable, i.e. it is context dependent. This, together with the high degree of variability in

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their spatial distribution and temporal dynamics, may hinder the detection of constant patterns concerning substrate preferences of mobile species. Such high spatial heterogeneity of mobile communities inhabiting artificial structures has been recognized for many taxa (limpets, annelids, echinoderms, fishes) in a wide variety of environmental contexts (e.g. intertidal and subtidal, tropical and temperate ecosystems) and artificial structures (low crested breakwaters, floating pontoons, submerged artificial reefs, boat moorings, etc.) (Bayle-Sempere et al., 1994; Chapman, 2003; Strelcheck et al., 2005; Toh et al., 2017; Lanham et al., 2018). Due to this high spatial variability among different localities, many study designs and approaches may not provide a representative description of the impacts associated with the development of novel artificial structures (Lanham et al., 2018; Macolino et al., 2019). This could be a specially challenging problem when dealing with small mobile invertebrates such as crustacean peracarids (amphipods, tanaids and isopods) or polychaetes. Even subtle differences in environmental factors such as salinity, sedimentation rate, food availability, hydrodynamics, predation pressure and other habitat features, can determine significant changes in amphipod communities (Conradi et al., 2000; Carvalho et al., 2018). Their high natural spatial and temporal variability, detected at multiple scales, has been recognized as a major drawback in order to develop efficient monitoring methodologies and establish widespread ecological patterns (Fernández-González et al., 2013; Navarro-Barranco et al., 2013; Sturaro et al., 2015). Thus, in agreement with previous studies (Martin et al., 2005; Becchi et al., 2014), our results pointed out the context-dependency of the effects of artificial structures on small invertebrates.

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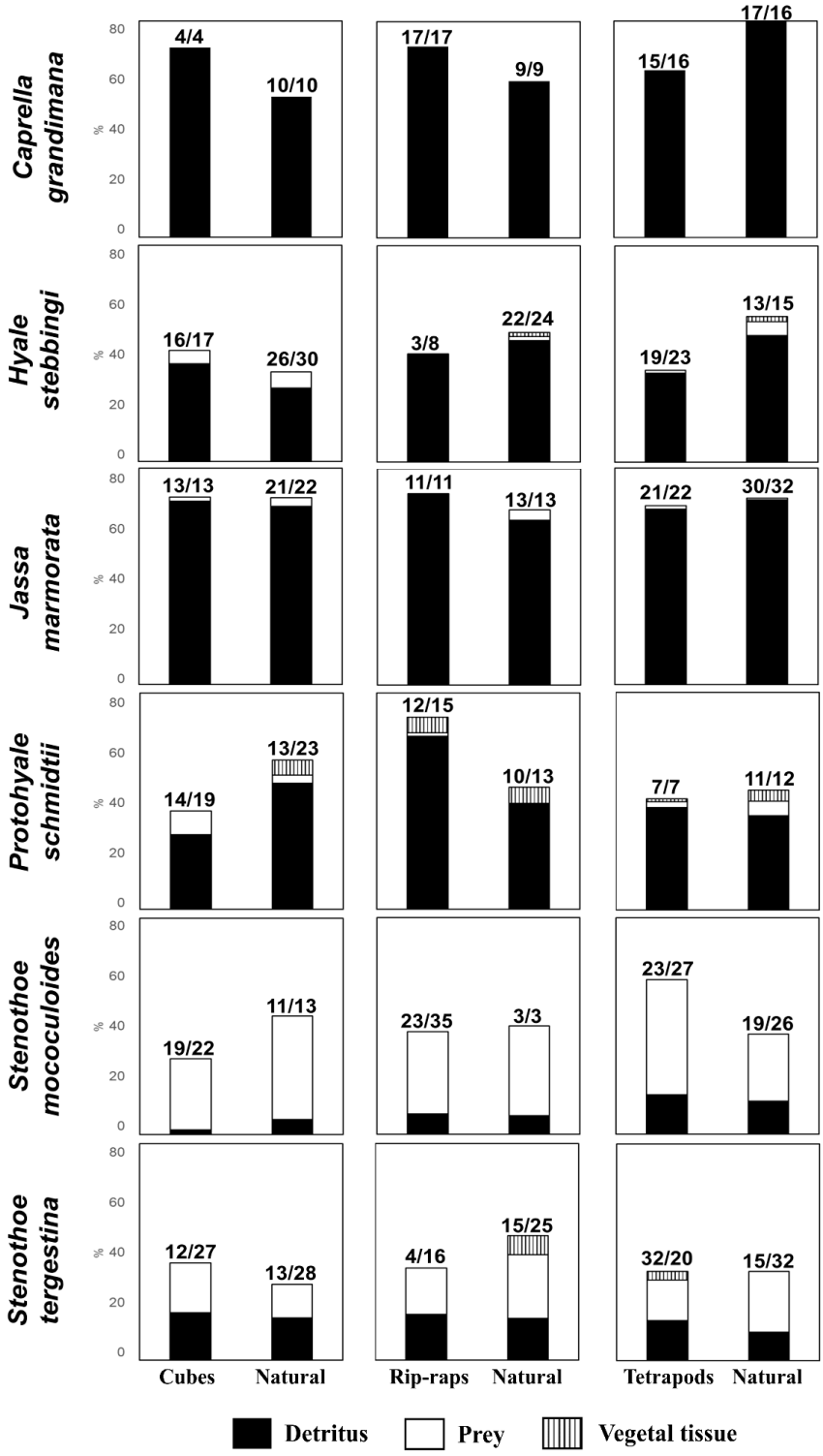

Fig. 4. Diet comparison in the most abundant amphipod species (> 2% total abundance) between artificial and natural substrates (cubes, rip-raps and tetrapods). Each bar represents the total area occupied by the content in the whole digestive tract, and the percentage of each food item (detritus, prey or vegetal issues) is included. Data are mean values of specimens analyzed. Numbers on the bar (n/N) indicate the number of specimens examined (N) and the number of those with some contents in the digestive tract (n).

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Trophic structure

Data about the influence of artificial substrates on the trophic structure of marine species are scarce, and available information about invertebrates is very limited (see e.g. Burgos-Rubio et al., 2015 for molluscs). Most studies have been focused mainly on fish assemblages (see Vose and Nelson, 1984; Fabi et al., 2006; Munsch et al., 2015; Pereira et al., 2017; Schwartzkopf et al., 2017). Some of these studies point out differences of diet between artificial and natural substrates; for example, Munsch et al. (2015) indicated that small specimens of chum salmon (*Oncorhynchus keta*) changed their diet composition between seawall and beach sites, feeding on planktonic or epibenthic copepods respectively.

Regarding epifaunal communities, the technical difficulties of studying the diet of very small invertebrates have probably prevented the development of integrate studies dealing with the trophic structure. Indeed, literature related to trophic categories often come from assumptions instead of direct analyses of digestive contents. During the last years, a novel methodology of transparency based on the Herwitg's liquid, initially developed by Bello and Cabrera (1999), has provided useful baseline data for small peracarids (Guerra-García and Tierno de Figueroa, 2009; Torrecilla-Roca and Guerra-García, 2012; Vázquez-Luis et al., 2013; Guerra-García et al., 2014). In the present study, trophic structure was significantly different between substrates in six of the nine localities. However, as for the community structure, the pattern clearly differed among artificial structures and localities (e.g. the percentages of carnivores and detritivores were higher in natural substrates in some localities and scarcely represented in other ones). These differences were due to changes in the species composition of the community and not to changes of the feeding strategy of a particular species. This is supported by the gut contents of the six dominant species in all the substrates; *Caprella grandimana*, *Hyale stebbingi*, *Jassa marmorata* and *Protohyale schmidtii* fed mainly on detritus in all the substrates, whereas *Stenothoe* species were mainly carnivorous along the whole study area. These patterns obtained here for intertidal rocky shores, have also been reported for soft bottoms in marine caves compared to open habitats (Navarro-Barranco et al., 2013). These

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authors found differences in trophic structure between caves and open habitats, but these differences were due to different species composition of the amphipod community rather than a shift in the food intake of each species (e.g. Fig. 5 in Navarro-Barranco et al., 2013). Similarly, other studies dealing with fish assemblages showed changes in trophic structure as a consequence of a shift in species composition. For example, Smokorowski and Pratt (2007) found that differences in architectural features and material composition among substrates were the main drivers to determine changes in fish species composition of each physical habitat, resulting in a change of the trophic structure. Pereira et al. (2017) highlighted that artificial structures such as concrete blocks and piers could provide different resource availability for many species, modifying the community species composition and, ultimately, the trophic composition.

Changes in the diet of some amphipod species according to the habitat have been reported in the literature (e.g. Alarcón-Ortega et al., 2012; Vázquez-Luis et al., 2013) but, in most cases, the diet shift was associated to a change in the secondary substrate where amphipod was directly clinging on (e.g. Fig. 1 in Vázquez-Luis et al., 2013 and Fig. 2 in Alarcán-Ortega et al., 2012). In the present work, changes in the primary substrates do not involve changes in the diet composition of a particular species provided that the secondary substrate *E. ellongata* is the same. However, we cannot consider this as a general assumption, since, for example, Ros et al. (2014) found significant differences in the food items' percentages for the amphipod *Paracaprella pusilla* between artificial substrates (floating pontoons of recreational marinas) and natural substrates (rocky shores) using the same secondary substrate, the hydroid *Eudendrium* sp., for both type of primary substrates (artificial vs natural). Probably, in this case, the environmental particularities of marinas, as extremely modified marine ecosystems, could determine the shift in the diet. Therefore, if additional samples in the present study would have been collected within harbour facilities, a diet's shift could have been observed.

In the present study, we have not found consistent differences in the percentage of carnivores among substrates, probably because the opportunistic trophic behaviour of amphipods facilitates a quick adaptation to the available resources depending on the

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environment (see Guerra-García et al., 2014). Lai et al. (2018) found that the lower coverage of turf algae on seawalls could limit the proliferation of grazers, especially those species that feed on this algal group. In fact, these authors pointed out that differences between seawalls and rocky shores could be explained by the scarcity of primary productivity on the former, limiting their capacity to support higher trophic levels and/or complex trophic interactions. This may lead to the proliferation of detritivores which are dependent on allochthonous detrital sources. This is not observed on natural rocky shores due to the abundance of algae that support many primary consumers. Indeed, in the present study the number of herbivores is very low in comparison with other studies (Vázquez-Luis et al., 2013; Guerra-García et al., 2014). Probably, the fact that only the coralline alga *E. elongata* was collected throughout the whole study also influenced the low grazing activity since the calcified thallus of *Ellisolandia* make it unpalatable to grazers (Ballesteros, 1988).

Implications for management and conservation

The present study reveals that inherent factors within different localities at regional scale prevent the establishment of general patterns to understand the effect of coastal defence structures on epifaunal communities. Relevant differences in species composition and trophic structure have been detected among localities, which makes difficult to separate the effects of the substrates on marine communities (see Fraschetti et al., 2002). It is known that artificial structures have local effects on marine ecosystems (see Dafforn et al., 2015) and their physical design has consequences at multiple trophic levels (Schwartzkopf et al., 2017) and across localities. In this sense, other factors (environmental quality, biological interactions, connectivity, etc) apart from the type of substrate (artificial or natural) could be responsible for the differences found during the present study.

From a conservational perspective, managers must deal with largely stochastic systems characterized by enormous uncertainties (see Agardy, 1994). Therefore, local factors must be taken into consideration when management purposes are suggested. For instance, locally

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managed marine area (LMMA) is an appropriate conservation approach, i.e. an area of nearshore waters with its associated marine resources that is managed at a local level (Jupiter et al., 2014; IUCN-WCPA, 2019).

Conclusions

In summary, this study indicates that artificial structures may affect the composition and trophic structure of the amphipod community even when the secondary substrate is the same, but the main differences are registered at local level. Regarding the three hypotheses raised in the present work we can summarise that (1) number of species and Shannon diversity is usually higher in natural than in artificial habitats; multivariate analyses also reveal differences between substrates, but only in some localities (2) natural rock-based artificial structures (i.e. rip-raps) seem to be better surrogates in terms of number of species, Shannon diversity and species composition (presence/absence data) of their nearest natural substrates in comparison with other concrete-based artificial substrates (i.e cubes and tetrapods) which were more different to their corresponding natural habitats; (3) trophic structure of the community (percentage of carnivores, herbivores, detritivores and omnivores) was also affected by the type of substrate, although the pattern clearly differed among localities; difference in the trophic structure was due to changes in the species composition of the community and not to a feeding change in the species, which had the same food items in the gut throughout the whole study area. The present study reveals that the lack of constant patterns prevents a generalization and stresses the importance of study the effects of artificial substrates locally. Besides the substrate effects, other potential factors (e.g. influence of river discharges, hydrodynamics, water currents, biological interactions among others) should be taken into consideration globally to understand particularities of each locality in the design of management and conservation strategies.

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Chapter 3.2

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3.2 Effects on the diet at the individual level.

Adapted from: Sedano, F., Guerra-García, J. M., Navarro-Barranco, C., Sempere-Valverde, J., Pavón, A., Espinosa, F. (2020). Do artificial structures affect the diet of the limpet *Patella caerulea* Linnaeus, 1758?. Regional Studies in Marine Science, 36, 101261. https://doi.org/10.1016/j.rsma.2020.101261

Abstract

The current scenario of global change and the increase of human population in coastal areas is leading to the introduction of numerous man-made structures into the coastal environment. Those artificial structures provide different services at the expenses of habitat loss and a range of widely documented ecological impacts. Limpets are keystone species that are worldwide established in these artificial habitats. However, little is known about the impact of artificial coastal defence structures on the diet of limpets. Therefore, the aim of this study was to evaluate if different kinds of artificial structures (cubes, rip-raps, seawalls and tetrapods) across a geographical gradient (western to eastern Alboran Sea), could affect the food consumption of the limpet *Patella caerulea* by using carbon and nitrogen isotopes analysis. Our results suggested that for certain localities, there was a shift in the trophic niche of *P. caerulea* inhabiting artificial substrates in comparison with the nearest natural rocky shore. However, patterns were not consistent for all localities and different types of artificial structures, which reinforces the importance of considering local scales for conservation and management purposes. Finally, $\delta^{15}N$ ratio in *P. caerulea* is a good indicator of eutrophication at regional scales, by showing a gradient of enrichment in the limpet tissues from oligotrophic to eutrophic waters within the Alboran Sea.

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Introduction

The current scenario of global change (e.g. sea level rise and increase of climatic extreme events) and the increase of human population in coastal areas (with the concomitant increase in coastal use) is leading to the introduction of numerous man-made structures into the coastal environment (Firth et al., 2016). Those artificial structures provide different services such as coastal protection, energy generation or aquaculture production, at the expenses of habitat loss and a range of widely documented ecological impacts (Dafforn et al., 2015). Particularly, artificial structures for coastal defence are known to harbour lower biodiversity values than the natural hard substrates they replace (Loke et al., 2015; Moschella et al., 2005), acting also as stepping stones for non-indigenous species (Adams et al., 2014) and in general they do not function as surrogates of the natural environment (Perkins et al., 2015). Their impacts are mainly driven by the nature of the building materials (usually concrete) (Ido and Shimrit, 2015), their low structural complexity (Loke and Todd, 2016) and their steep inclination (Moreira et al., 2006) among others.

Differently, some benefits associated with the use of artificial structures have been reported. Artificial reefs are used as tools against bottom trawling at the same time that they increase fisheries yield and production (Baine, 2001; Feary et al., 2011). Furthermore, artificial boulders can sustain populations of commercially important molluscs, such as the abalone (*Haliotis* spp.), or populations of threatened species (Liversage and Chapman, 2018). Indeed, it is not rare to find endangered species established in these artificial habitats, such as the limpets *Cymbula safiana* and *Patella ferruginea*. Some populations of *P. ferruginea* have a large number of individuals on coastal defence structures of southern Spain and northern Africa (Espinosa et al., 2018). This has led to the possibility of declaring some figure of environmental protection for these artificial areas (García-Gómez et al., 2011). Nevertheless, it is uncertain how artificial structures can affect the long-term viability of limpet populations. Moreira et al. (2006) stated that seawalls do not sustain viable populations of limpets in Sydney Harbour and Espinosa and Rivera-Ingraham (2016) detected evidences of physiological stress in populations of limpets inhabiting the rip-raps of Ceuta's harbour (Strait of Gibraltar). However, little is

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known about the impact of different artificial coastal defence structures on the diet of limpets. Della Santina et al. (1993) studied the gut content of limpets inhabiting boulder habitats, but a comparison with limpets inhabiting nearby natural substrates was not provided. Burgos-Rubio et al. (2015) did compare the diet of *Patella caerulea* inhabiting artificial and natural substrates in Algeciras Bay (Southern Spain), and suggested that artificial substrates hosted less diverse food items for consumption by limpets than natural ones. In fact, artificial structures have been reported to bear different microbial films in comparison with natural ones (Tan et al., 2015) and also lower cover of turf algae (Sedano et al., 2019), potentially shifting or affecting food availability (Pereira et al., 2017). The impact of artificial structures in available food items has also been reported in fish; man-made structures often provide a lower diversity of prey items (Schwartzkopf et al., 2017; Vose and Nelson, 1994). Nevertheless, knowledge is still very limited and studies assessing different kinds of artificial structures across different regions are lacking.

Therefore, the aim of this study was to evaluate if artificial structures could affect the food consumption of the limpet *Patella caerulea*. To this end, we analysed carbon and nitrogen isotopes across a geographical gradient (western to eastern Alboran Sea), comparing different artificial structures with their nearest natural rocky shore. These results will provide information about the trophic niche of limpets and will present new insights for the management of threatened limpets inhabiting artificial substrates.

Materials and methods

Experimental design and limpets collection

On May 2017, four types of artificial structures (three concrete-based: cubes, seawalls and tetrapods, and one natural rock-based: rip-raps) and their nearest natural rocky substrates (Table 1), were sampled across the Alboran Sea (western Mediterranean Sea). The experimental design for each kind of artificial structure was the following: Factor Substrate (Su), two levels

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(artificial, natural), fixed; Factor Locality (Lo), three levels, random and orthogonal with Su. The three localities with cubes were Ceuta (CEU), Fuengirola (FUE) and Motril (MOT); the three with rip-raps were Aguadulce (AGD), Algeciras (ALG) and Marina del Este (MES); the three with seawalls were Almería (ALM), Málaga (MAL) and Motril (MOT) and the three with tetrapods were Benalmadena (BEN), M'Diq (MDQ) and Marina Smir (SMR). Five specimens of *Patella caerulea* (size ranging from 20 mm to 35.6 mm) were collected on each artificial structure and five on the nearest natural rocky shore. The limpet *P. caerulea* is an endemic Mediterranean species commonly found in the lower part of the intertidal zone (Mauro et al., 2003). Because of its high abundance and widespread distribution along the Mediterranean basin, both in polluted and non-polluted areas, this species has been broadly used as a model species in a wide variety of ecological studies; phylogeography and population connectivity (Villamor et al., 2018), ethology (Keasar and Safriel, 1994; Sempere-Valverde et al., 2019) or environmental quality monitoring (Storelli and Marcotrigiano, 2005; Yuzereroğlu et al., 2010; Culha and Bat, 2010).

Limpets were immediately stored at −20 °C until stable isotope analyses. A section of the foot muscle was used for $\delta^{13}C$ and $\delta^{15}N$ determinations. The tissues were freeze-dried for 48 h into a IlShinBioBase Europe model FD8512 to constant weight and milled to fine powder using a ball mill Retsch MM400. Powdered material was weighted to the nearest 0.300 mg with an error of ± 0.002 mg and placed into tin capsules. All samples were combusted at 1020 °C using a continuous-flow isotope-ratio mass spectrometry system by means of Flash HT Plus elemental analyser coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface.

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Table 1.- List of sampling localities ordered from west to east. [+]: Dolomite, calcite and quartz.

Localities	Coordinates (Latitude/Longitude)	Date of deployment	Distance from nearest natural rock (km)	Dominant Mineral	Position in the Alboran Sea
Natural					
M'Diq	35º40'56.87''N/5º18'23.38''W	n.a.	n.a.	Natural rock	West
Marina Smir	35º40'56.87''N/5º18'23.38''W	n.a.	n.a.	Natural rock	West
Ceuta	35º53'50.94''N/5º17'57.46''W	n.a.	n.a.	Natural rock	West
Algeciras	36º06'34.10''N/5º25'55.40''W	n.a.	n.a.	Quartz	West
Fuengirola	36º30'23.34''N/4º38'21.76''W	n.a.	n.a.	Natural rock	West
Benalmádena	36º34'47.41''N/4º32'48.25''W	n.a.	n.a.	Natural rock	West
Málaga	36º42'41.73''N/4º19'39.19''W	n.a.	n.a.	Natural rock	West
Marina del Este	36º43'23.31''N/3º43'35.22''W	n.a.	n.a.	Dolomite	East
Motril	36º42'10.27''N/3º24'40.06''W	n.a.	n.a.	Natural rock	East
Aguadulce	36º49'11.89''N/2º31'54.64''W	n.a.	n.a.	Dolomite	East
Almería	36º49'41.48''N/2º29'34.89''W	n.a.	n.a.	Natural rock	East
Cubes					
Ceuta	35º54'01.03''N/5º19'27.26''W	2004	2.3	Concrete	West
Fuengirola	36º32'31.83''N/4º36'51.25''W	1986*	4.6	Dolomite	West
Motril	36º43'07.38''N/3º31'29.14''W	1986*	10.4	Dolomite[+]	East
Rip-raps					
Algeciras	36º07'01.20''N/5º26'07.90''W	1997	0.9	Calcite	West
Marina del Este	36º43'31.00''N/3º43'32.66''W	1986*	0.3	Calcite	East
Aguadulce	36º48'58.70''N/2º33'20.98''W	1989*	2.4	Dolomite	East
Seawalls					
Málaga	36º42'28.57''N/4º24'42.84''W	2003*	7.4	Concrete	West
Motril	36º42'59.64''N/3º31'15.12''W	2003*	10.4	Concrete	East
Almería	36º49'38.97''N/2º28'55.04''W	2015	0.9	Concrete	East
Tetrapods					
Marina Smir	35º45'25.57''N/5º20'28.19''W	2003*	8.8	Concrete	West
M'Diq	35º41'03.12''N/5º18'40.51''W	2009*	0.5	Concrete	West
Benalmádena	36º35'50.06''N/4º30'28.52''W	1986*	4.0	Concrete	West

*Older data estimated according to historical aerial images from Google Earth and http://fototeca.cnig.es; n.a.: not pplicable

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Statistical analyses

Four permutational multivariate analysis of variance (PERMANOVA) (one for each kind of artificial structure) was used in order to test the effect of Substrate (artificial vs. natural), Locality and the interaction Substrate x Locality on the isotopic signal ($\delta^{13}C$ and $\delta^{15}N$). Using the experimental design explained above, PERMANOVAs were run on a triangular matrix derived from the values of Euclidean distances of untransformed data using 9999 permutations. When PERMANOVA detected significant differences, the source of the difference was identified using pair-wise comparisons. The differences in $\delta^{13}C$ and $\delta^{15}N$ ratios were also graphically portrayed using a biplot.

Since our sampling was conducted across a clear geographical gradient (from west to east in the Alboran Sea), we tested this geographical effect performing univariate PERMANOVAs for $\delta^{13}C$ and $\delta^{15}N$. Atlantic waters entering in the Alboran Sea describe and anticyclonic gyre that generates upwelling of nutrients (Cebrian and Ballesteros, 2004) resulting in a major phytoplankton productivity in the western part of the Alboran Sea (being the eastern limit close to 4°W, see Fig. 2 in Hauschildt et al., 1999). Accordingly, we 'split' all our replicates (including all the limpets inhabiting both, artificial and natural substrates) according to Position factor (two levels 'West' and 'East'). All the replicates positioned to the left of meridian 4°W were considered as western replicates, while the ones positioned to the right were considered as eastern replicates (Table 1). Since number of replicates between 'West' and 'East' was unbalanced, we opted for the above-mentioned permutational approach and reduced the significance level to $p < 0.01$ in order to avoid Type I error.

In order to evaluate the potential effect of limpet size on the isotopic values, Pearson correlation between $\delta^{13}C$, $\delta^{15}N$ and shell size was calculated. The effect of shell size was also controlled as a covariate in the PERMANOVAs, but since it was not significant, we performed the tests without covariates. PERMANOVA analyses were carried out using PRIMER v.6+PERMANOVA package (Clarke and Gorley, 2006).

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Results

As shown by the PERMANOVA results (Table 2), the significant effect of substrate (artificial vs. natural) was not constant across localities for each kind of artificial substrate. Only five (M'Diq, Ceuta, Motril, Aguadulce and Almería) out of twelve localities had significant differences for the isotopic signal between artificial and natural substrates. Two localities with cubes (Ceuta and Motril), one with rip-raps (Aguadulce), one with seawalls (Almería) and one with tetrapods (M'Diq) had significantly different isotopic signals between the artificial and the natural substrate (see pair-wise tests in Table 2).

Table 2: PERMANOVA table of results for the isotopic signal ($\delta^{13}C$ and $\delta^{15}N$). Zn: Zone [four levels: C (cube), R (rip-rap), S (Seawall) and T (tetrapod)]; Lo(Zn): Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este), localities with seawalls (ALM: Almería, MAL: Málaga, MOT: Motril) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; Su(Zn): Substrate [two levels: A (Artificial) and N (Natural)]; df: degrees of freedom; MS: mean square; p: level of significance; n.s.: not significant; *: $p < 0.05$; ***: $p < 0.001$.

Isotopic signal					
Source of variation	df	MS	Pseudo-F	p	Perm.
Zn	3	22.337	0.91062	n.s.	7373
Lo(Zn)	8	24.529	6.1353	***	9935
Su(Zn)	4	47.329	3.9725	*	9950
Lo(Zn)xSu(Zn)	8	11.93	2.984	***	9912
Residual	96	3.998			
Total	119				
Transform	None				
Pair-wise tests for Lo(Zn)xSu(Zn)	Levels Cube-CEU: Artificial≠Natural Levels Cube-FUE: Artificial=Natural Levels Cube-MOT: Artificial≠Natural Levels Rip-rap-AGD: Artificial≠Natural Levels Rip-rap-ALG: Artificial=Natural Levels Rip-rap-MES: Artificial=Natural Levels Seawall-ALM: Artificial≠Natural Levels Seawall-MAL: Artificial=Natural Levels Seawall-MOT: Artificial=Natural Levels Tetrapod-BEN: Artificial=Natural Levels Tetrapod-MDQ: Artificial≠Natural Levels Tetrapod-SMR: Artificial=Natural				

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These differences were also graphically visible in the biplot (Fig. 1), where the limpets feeding on the artificial structures of the five above-mentioned localities appeared to exploit a different trophic niche than the ones on natural substrates (indicated by the separation on the biplot). However, there was a better separation between samples according to their geographical position (west/east). In fact, univariate PERMANOVA results (Table 3) showed that $\delta^{15}N$ values were significantly higher in western localities than eastern ones (Fig. 2), while there were not significant differences for $\delta^{13}C$. The size of the shell appeared to be uncorrelated with the values of $\delta^{13}C$, $\delta^{15}N$ (Fig. 3).

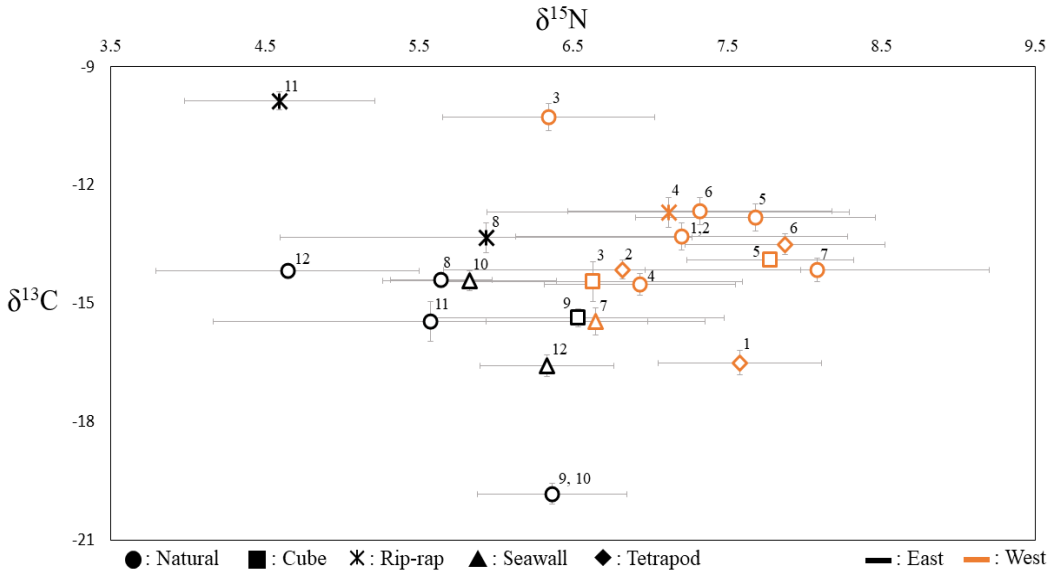

Fig. 1. Biplot representing average (± standard error) isotopic values ($\delta^{13}C$ and $\delta^{15}N$) measured in the muscle tissue of *P. caerulea* inhabiting the different substrates sampled across the Alboran Sea. Numbers next to the symbols indicate the localities from west to east (1: M'Diq, 2: Marina Smir, 3: Ceuta, 4 Algeciras, 5: Fuengirola, 6: Benalmadena, 7: Málaga, 8: Marina del Este, 9 and 10: Motril, 11: Aguadulce, 12: Almería.

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Table 3: Univariate PERMANOVA table for $\delta^{13}C$ and $\delta^{15}N$ isotopic values between the two geographical positions [factor Position (Po) with two levels: West (western Alboran Sea) and East (eastern Alboran Sea)]. df: degrees of freedom; MS: mean square; p: level of significance; n.s.: not significant; ***: $p < 0.001$.

$\delta^{13}C$					
Source of variation	df	MS	Pseudo-F	p	Perm.
Po (West vs East)	1	41.223	6.2196	n.s.	9841
Residual	108	6.628			
Total	109				
$\delta^{15}N$					
Source of variation	df	MS	Pseudo-F	p	Perm.
Po (West vs East)	1	41.501	45.075	***	9833
Residual	108	0.9207			
Total	109				

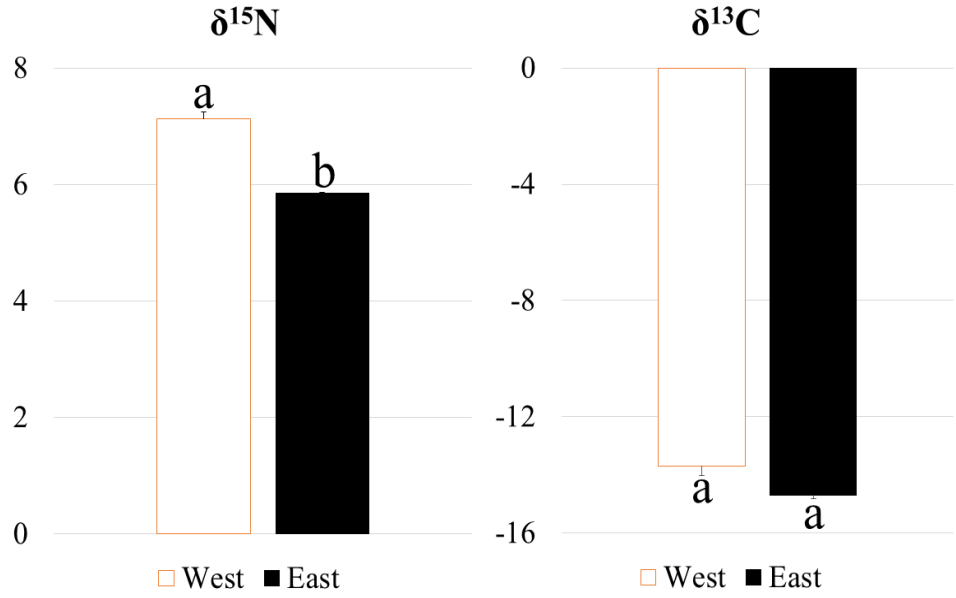

Fig. 2. Histograms for the average (± standard error) $\delta^{13}C$ and $\delta^{15}N$ values between western and eastern localities. a and b represent significant differences according to univariate PERMANOVA.

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Discussion

The impacts of the introduction of man-made structures into the marine envirionment have been recently reviewed (Bishop et al., 2017; Firth et al., 2016; Heery et al., 2017) highlighting their effects on marine biodiversity, distribution of species and ecological connectivity, among others. However, their impact on the trophic niche and trophic behaviour of species inhabiting man-made structures is largely unknown. Few studies have addressed this question so far. For example, Kurz (1995) suggested that artificial reef configuration (dis persed vs. aggregated refugia) affected the foraging activity of grey triggerfish. The diet of fish inhabiting artificial reefs was less varied than that of fish from natural habitats (Vose and Nelson, 1994). Also, coastal armouring with seawalls can affect the diet composition of the small chum salmon (*Oncorhynchus keta*) (Munsch et al., 2015). On the contrary, Fabi et al. (2006) stated that three species of fish feeding on artificial reefs had access to a larger variety of food items and that they had broaden their feeding spectrum. In the particular case of limpets, Burgos-Rubio et al. (2015) found out that *Patella caerulea* on rip-raps consumed a lower number of taxa (including microalgae and some animal taxa) than those on natural rocky shores. However, in addition to the difficulties in identifying

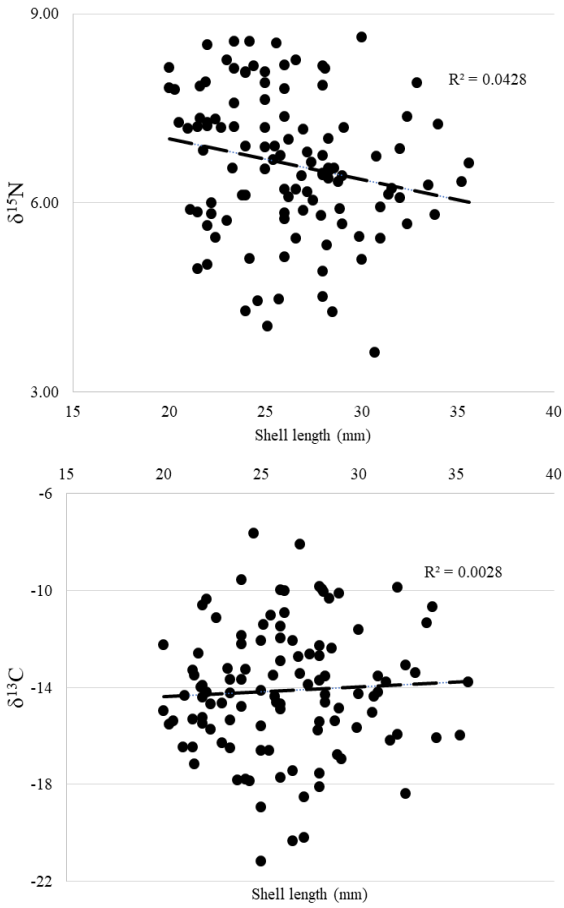

Fig. 3. Dispersion diagrams for the values of $\delta^{13}C$ and $\delta^{15}N$ corresponding to each shell size. Coefficient of determination based on Pearson's correlation is included.

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the gut content (e.g. it can be rapidly digested), those results based on gut content constitute a 'snapshot' of the feeding ecology of this species at a specific moment (Layman et al., 2012).

The approach presented in our study (using $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios) provides a picture of the long-term feeding niche (weeks to months) (Greenwell et al., 2019; Layman et al., 2012; Young et al., 2018). The use of carbon and nitrogen isotopic ratios allowed to find out that differences in primary productivity between seawalls and natural rocky shores was a limiting factor to support higher trophic levels (e.g. carnivorous whelks; Lai et al., 2018). In comparison to Cresson et al. (2014), who indicated that diet was similar between fish inhabiting artificial reefs and natural habitats, our results indicated that for some localities the diet of limpets was different between the artificial and the natural habitats. For the cubes of Ceuta and Motril, the rip-raps of Aguadulce, the seawall of Almería and the tetrapods of M'Diq, the significant differences between the artificial structure and the natural rock are mainly due to big differences in the $\delta^{13}C$ signal, indicating that the limpets are feeding on different primary producers (e.g. different macroalgae, diatoms and cyanobacteria). This agrees with previous studies that have demonstrated that artificial habitats can have different biofilms (Tan et al., 2015) and different macroalgae community (Sedano et al., 2019), providing therefore different trophic sources for limpets. For example, Choy et al. (2011) found a dietary shift in the limpet *Nacella concinna* due to differences in food availability between habitats, being macroalgae a major contributor to the diet of limpets in tide pools. The creation of tide pools in artificial structures has been proposed as a useful method of ecological enhancement (Evans et al., 2016; Ostalé-Valriberas et al., 2018). In this sense, the addition of tide pools, pits and crevices on the surface of artificial structures could facilitate additional food resources for the maintenance of intertidal populations. It is known that the intertidal area of artificial structures can support important populations of endangered limpets such as *Patella ferruginea* and *Cymbula safiana* (Espinosa et al., 2018; Rivera-Ingraham et al., 2011), which is one of the main arguments that calls for the protection of some of these artificial habitats (García-Gómez et al., 2011). If this is the case, a proper evaluation of limpet populations is needed, including physiological indicators and temporal and genetic population dynamics that would help to predict the fate of the population

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(see Espinosa et al., 2018 for population dynamics of *Patella ferruginea*). According to this, Espinosa and Rivera-Ingraham (2016) detected evidences of physiological stress in limpets inhabiting the rip-raps of Ceuta's harbour. In addition, we detected possible trophic shifts between limpets inhabiting artificial and natural substrates, although their physiological/energetic implications remain uncertain.

It is important to note that the differences found were not consistent across types of artificial structures nor across localities. This indicates that other factors rather than the kind of structure, such as nutrient enrichment or biological interactions, should be taken into account to fully assess trophic dynamics of species inhabiting artificial structures. However, the fact that in our study seven localities (out of twelve) did not present a significant trophic shift between artificial and natural substrates is promising for conservation purposes but also highlights the importance of local conditions for a successful management. Therefore, the conservation of limpets in man-made habitats constitutes an important challenge for coastal managers and eco-engineers. A locally managed marine area (LMMA) could be a feasible approach in this scenario (IUCN-WCPA, 2019; Jupiter et al., 2014).

The limpet *P. caerulea* feeds on a variety of items including cyanobacteria, diatoms, macroalgae and even animals (Burgos-Rubio et al., 2015; Della Santina et al., 1993). This was also reflected in our results, indicated by the high levels and wide range of the N signal, suggesting, in turn, that *P. caerulea* can feed on different prey over time, and hence, occupies a higher trophic level than pure primary consumers (Espinosa et al. unpublished results), whose N values are very low (Greenwell et al., 2019; Guest et al., 2008). Other studies have reported differences in the isotopic ratios of limpets due to differences in size (Choy et al., 2011; Žvab Rožič et al., 2014) but this is unlikely to be our case since shell length and isotopic signal (for both $\delta^{13}C$ and $\delta^{15}N$) were not significantly correlated. This also suggests that the specimens of *P. caerulea* considered in our study (20 mm to 35.6 mm in length) did not substantially change their feed with age. We chose this narrow size range for adequate comparisons between habitats and among localities in accordance with our hypothesis, but this prevents comprehensive

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comparisons of different size classes; therefore, further studies are necessary to fully understand the potential effect of age in isotopic profiles.

A clear west–east pattern was found for the $\delta^{15}N$ signal, indicating a change in nitrogen sources along the Alboran Sea. This was probably linked to upwelling zones that affect the western Alboran Sea (Cebrian and Ballesteros, 2004; Sarhan et al., 2000), and is also in accordance with the known depletion of N ratios towards the eastern basin of the Mediterranean Sea (Huertas et al., 2012; Pantoja et al., 2002). Furthermore, the coasts of the west Alboran Sea are significantly more urbanized (see e.g. values of the index of anthropogenic stress for some localities of Cádiz and Málaga in Figure 1 of Guerra-García et al., 2009). Therefore, measures of $\delta^{15}N$ ratios in the muscle tissue of *P. caerulea* constitute a good bioindicator of eutrophication at regional scales. Indeed, stable isotopes have been suggested as indicators of nutrient source for other molluscs (see e.g. Graniero et al., 2016); therefore, this seems promising for future research and environmental management of urbanized coastlines.

Conclusion

Our results suggested that there was a shift in the trophic niche of *P. caerulea* inhabiting artificial substrates in comparison with the nearest natural rocky shore, at least in some localities. However, there was no constant pattern across the four types of artificial structures sampled. In fact, seven out of twelve localities did not present significant differences, suggesting that the threats for maintaining limpet populations inhabiting coastal defence structures may rely on different factors rather than only on trophic resources. This issue should be considered carefully in the management of limpet populations inhabiting artificial substrates, since the contrasting results among localities demonstrated that different conclusions can be raised depending on the local conditions.

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DISCUSIÓN GENERAL

En zonas costeras muy urbanizadas, la construcción de estructuras artificiales de defensa suele ser la única opción viable para proteger la valiosa infraestructura urbana (Chee et al., 2017). Sin embargo, antes de instalar estas estructuras masivas se deben sopesar otras opciones. Hoggart et al. (2014) aboga por el enfoque "no hagas nada" (del inglés '*do nothing*'), apoyando la conservación de hábitats biogénicos y defensas naturales siempre que sea posible y dejando la construcción como último recurso. En caso de ser necesaria la instalación de estructuras artificiales por razones de protección o seguridad pública, la ingeniería civil de costas debería dar prioridad a enfoques ecológicos (Dafforn et al., 2015a; Morris et al., 2018). Por ejemplo, la utilización de vegetación o bancos de arena que disipen el oleaje (Hanley et al., 2014; Morris et al., 2018) o la construcción de túneles hidrodinámicos que mejoren la calidad del agua en entornos portuarios (Guerra-García y García-Gómez 2004). Cuando un enfoque puramente ecológicos no es posible, es necesario buscar un buen compromiso entre las técnicas tradicionales y las ecológicas (buscar un equilibrio entre las denominadas '*hard*' y '*soft engineering*'). Un buen ejemplo es la utilización de escolleras de roca natural para proteger de la erosión una porción de hábitat natural o incluso propiciar su creación mediante la sedimentación controlada (Polk y Eulie 2018). Este hábitat creado o protegido por la estructura artificial actúa como reservorio de organismos bentónicos, larvas pelágicas y organismos estuarinos o intermareales. No obstante, ante la situación de rápido crecimiento actual que se da en entornos costeros, la búsqueda y aplicación de enfoques ecológicos e integradores se presentan como un escenario bastante utópico. En la actualidad solo unos pocos proyectos piloto a nivel local han abordado las nuevas construcciones desde este tipo de enfoques. Es por ello, que en esta tesis hemos aumentado el conocimiento sobre el impacto de estas estructuras de defensa costera con el objetivo de favorecer que las nuevas construcciones maximicen los beneficios ecológicos a través de la ingeniería ecológica de dichas estructuras.

En el primer capítulo de esta tesis hemos relacionado una serie de variables abióticas (ej. composición y complejidad del sustrato) con el impacto que producen sobre la biodiversidad y estructuración de las comunidades de distintos niveles ecológicos (biota sésil, macro- y meiofauna asociada). La inclusión de estos grupos de fauna asociada proporciona datos importantes para estimar

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el impacto de las estructuras artificiales, ya que la pequeña fauna asociada (< 5 mm) a la fauna sésil y al dosel algal suelen pasar desapercibidos en este tipo de estudios (Schaal et al., 2016). De acuerdo con los resultados presentados por otros investigadores, en general hemos identificado la importancia de la composición (Coombes et al., 2015; Sempere et al., 2018) y la complejidad (Ostalé-Valriberas et al., 2018) del sustrato en la estructuración de las comunidades que se asientan en estructuras artificiales. Además, hemos presentado indicios de que dichos factores afectan a la fauna asociada tanto a nivel de grandes grupos como a nivel de especie. Por ejemplo, bajo las mismas condiciones ambientales, hemos detectado cierta preferencia de balanos y bivalvos (taxones que toleran la alcalinidad, Guilbeau et al., 2003) por las estructuras hormigonadas, así como indicios de preferencia de algunas especies de anfípodos en función de la rugosidad del sustrato (Lavender et al. 2017). Sin embargo, lo más llamativo y novedoso de nuestros resultados, radica en el alto grado de relación que hemos encontrado entre la biota sésil y la fauna asociada. Hemos visto como grupos completos (ej. isópodos con balanos y copépodos con algas) presentaban abundancias drásticamente distintas en función del sustrato sésil (Yakovis et al., 2007), y como distintas especies del mismo género presentaban una afinidad estrecha por taxones sésiles completamente diferentes (ej. *Stenothoe monoculoides* con *Ellisolandia elongata* y *S. eduardi* con *Mytilus galloprovincialis*). Es cierto que la facilitación entre especies es algo de sobra conocido (Bulleri et al., 2016; Saarinen et al., 2018). Por ejemplo, el alga *E. elongata* tiene una complejidad estructural totalmente diferente a la de otras algas como *Asparagopsis* spp. o *Palmaria palmata*, y por tanto proporciona unos microhábitats totalmente distintos (protección ante la desecación o depredadores diferente) que determinan la abundancia y composición de especies asociadas (Guerra-García et al., 2012; Navarro-Barranco et al., 2018; Schaal et al., 2016). No obstante, el hecho de que los factores abióticos de las estructuras artificiales determinen en gran medida la biota sésil, implica que esos mismos factores abióticos acabarán determinando la fauna asociada de forma indirecta, sugiriendo que puede haber importantes efectos cascada en la estructuración de las comunidades asentadas en estructuras artificiales. Esto, aparte de ser un gran desafío a la hora de prever las consecuencias que tendrá cualquier medida de mitigación (uso de nuevos materiales, creación de microrugosidades, etc.), puede tener implicaciones ecológicas muy importantes. Por un lado, los sustratos artificiales suelen presentar una biota sésil menos diversa que los sustratos naturales (Firth et al., 2016; Sedano et al.,

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2019) y por tanto, la disponibilidad de nichos y recursos para la fauna asociada es menor. Esto, inevitablemente se traducirá en un menor número de taxones asociados a la biota sésil (Le Hir y Hily, 2005; Schaal et al., 2016), afectando por ejemplo a la disponibilidad de presas para niveles tróficos superiores, hecho que ya ha sido reportado por Munsch et al. (2015), o disminuyendo la producción y flujo de energía en el bentos y hacia otros niveles (Mancinelli y Rossi, 2002). Por otro lado, una comunidad sésil y vágil empobrecida ofrece menos competencia por el espacio y los recursos, lo que puede significar una ventaja para especies oportunistas y el asentamiento de especies exóticas. De hecho, las especies exóticas suelen ser más abundantes en estructuras artificiales, las cuales además pueden actuar como '*stepping stones*' ayudando a ampliar su distribución (Mineur et al., 2012; Salomidi et al., 2013).

En el segundo capítulo hemos enfocado el estudio de las estructuras artificiales a nivel regional, por un lado, para determinar si la pérdida de biodiversidad observada a nivel local (capítulo 1) se produce también a una escala geográfica mayor, y por otro lado para estimar si el comportamiento de distintas estructuras se conserva a lo largo de una región amplia (cientos de kilómetros). Aunque, con ciertas limitaciones, algunas estructuras artificiales se hayan considerado similares a los sustratos naturales (Bulleri y Chapman, 2004), existe un consenso generalizado en que las estructuras artificiales albergan una biota distinta a la de los sustratos naturales adyacentes y que albergan una menor biodiversidad (Firth et al., 2016). Este patrón ha sido observado de forma constante a lo largo de los estudios de esta tesis, tanto a nivel local como regional, y tanto a nivel intermareal como submareal. Sin embargo, no hemos encontrado un patrón evidente para algún tipo concreto de estructura que haga pensar que es posible predecir su 'comportamiento' a nivel regional, ya que hay multitud de factores bióticos y abióticos que interaccionan entre sí y determinan los patrones de distribución de especies (Le Hir y Hily, 2005 y referencias en el interior). Nuestros datos apoyan que los diques verticales de hormigón son la estructuras con menor valor ecológico de entre las 5 estudiadas (acrópodos, cubos, diques verticales, escolleras de roca natural, y tetrápodos). Esto es ampliamente apoyado en la literatura (Lai et al., 2018; Loke et al., 2017; Moreira et al., 2006), principalmente debido a las extremas diferencias que presentan en comparación con los sustratos naturales: intermareal muy reducido por la inclinación, compuestos de hormigón, mínima rugosidad, etc. A pesar de ello, en la localidad de Motril no se encontraron

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diferencias significativas en comparación con la comunidad del natural y también se encontraron especies de interés como el coral naranja (*Astroides calycularis*, datos no publicados) entre otras, sugiriendo, que a pesar de presentar una pérdida de biodiversidad neta, su valor ecológico no es despreciable. Del mismo modo, las escolleras de roca natural, la estructura artificial que ha ofrecido de manera general un valor ecológico superior al resto, también presentaron un 'comportamiento' poco predecible, diferente en función de la localidad y del grupo biológico estudiado. Incluso cuando hemos reducido la variabilidad al máximo (muestreando el mismo sustrato secundario bajo similares condiciones ambientales, capítulo 3.1), seguimos encontrando una alta variabilidad espacial. Este 'comportamiento' estocástico de las estructuras artificiales implica un gran desafío en la gestión de las mismas y en el diseño de soluciones de ecoingeniería, ya que idealmente éstas deberán aplicarse y diseñarse en función de los factores locales, limitándose así la creación de diseños o recomendaciones generalistas. A pesar de ello, no creemos que esto sea necesariamente un contratiempo del desarrollo en el campo de la ingeniería ecológica. De hecho, puede suponer una oportunidad para promover acciones municipales dirigidas a la mejora de la fauna local, integrando el conocimiento de instituciones de investigación locales e incluso la ciencia ciudadana. Esto puede ayudar a acercar el medio ambiente a los ciudadanos, dando lugar a una mayor aceptación de los proyectos de ingeniería civil que, en última instancia, mejoren el valor ecológico de las comunidades marinas que se desarrollan sobre estructuras artificiales. Este enfoque local puede ser necesario para el desarrollo de estructuras artificiales multifuncionales que ofrezcan servicios recreativos, educativos, producción de alimentos, etc., además de su función básica (Dafforn et al., 2015b). En este contexto podemos fijarnos en el ejemplo de la construcción de arrecifes artificiales diseñados para proteger ecosistemas importantes (ej. praderas de *Posidonia* en el Mediterráneo), a la par que aumentan la producción pesquera (Jensen, 2002), en ocasiones de especies concretas (Baine, 2001) y ofrecen una alternativa para el buceo recreativo (Dounas, 2018) disminuyendo el impacto turístico sobre los arrecifes locales. En este sentido, ha sido durante la última década cuando los diseños han empezado a incorporar funciones medioambientales, sociales y económicas (Chapman y Underwood, 2011). Durante este tiempo, numerosos diseños han surgido con el objetivo de promover una mayor biodiversidad (Strain et al., 2018), sin embargo, es importante definir qué tipo de biodiversidad y por qué. Un aumento de la diversidad puede resultar en

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un incremento de especies exóticas en vez de autóctonas (Glasby et al., 2007). Por otro lado, si las condiciones naturales presentan fondos blandos, promover el diseño de estructuras que favorecen la biodiversidad de ambientes rocosos en vez de favorecer un ambiente sedimentario puede que no sea la aproximación más adecuada. Por ello, tal vez los esfuerzos deban centrarse en minimizar el cambio y replicar todo lo posible el ambiente natural para favorecer el asentamiento de la biota autóctona (Dafforn et al., 2015b).

En el capítulo 2.2 también hemos podido observar la falta de cobertura algal sobre las estructuras de defensa costera a lo largo de la Isla de Creta. Ya hemos comentado anteriormente la importancia de una biota rica sésil en el mantenimiento de la biodiversidad de macroinvertebrados asociados. No solo la gran cantidad de hábitat que proporcionan algas ramificadas (ej. *Ellisolandia elongata*) juega un papel importante, también tiene gran influencia las condiciones microclimáticas que crean (ej. reducción de la temperatura en un 25 %, Coombes et al., 2013) o la capacidad de bioprotección contra la erosión . En este sentido, una de las medidas locales que pueden darse son los cultivos y trasplantes de algas autóctonas (Firth et al., 2014; Perkol-Finkel et al., 2012), las cuales, además de las ya mencionadas ventajas, tienen la capacidad de actuar como sumideros de C por acumulación de biomasa (Chung et al., 2012). Ésta representa una fuente directa de alimento o indirecta mediante el aporte de detritus para las comunidades bentónicas asociadas, el cual forma gran parte de la dieta de algunos invertebrados asociados (Fredriksen, 2003; Schaal et al., 2009). Esto enlaza directamente con nuestro último capítulo.

Por último, en el capítulo 3 hemos abordado los cambios a nivel trófico que pueden darse en la fauna asociada a estructuras artificiales, tanto a nivel de la comunidad (analizando el contenido estomacal de los anfípodos) como a nivel de individuo (analizando el ratio de $\delta^{13}C$ y $\delta^{15}N$ en la lapa *Patella caerulea*). En el caso de la comunidad de anfípodos, detectamos cambios en la estructura trófica en función del tipo de sustrato y de la localidad, pero debido a un cambio en la composición de especies y no de sus hábitos alimenticios. Esto último también fue observado por Cresson et al. (2014), quienes no encontraron diferencias en la dieta de peces habitando arrecifes artificiales o naturales. Esto puede ser debido a que ambos grupos (peces y anfípodos) son capaces de explotar, de manera más o menos selectiva, un recurso determinado. De hecho, el alga *Ellisolandia elongata* (el sustrato secundario en el

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que habitaban los anfípodos muestreados) tiene bajo contenido orgánico y poco valor nutricional, por lo que no constituye una fuente de alimento para los anfípodos (Maneveldt et al., 2006), sin embargo, su movilidad les permite nadar hacia otras fuentes de alimentación (Kovalenko et al., 2012; Nicotri, 1980; Schaal et al., 2016). De este modo, el hecho de que las estructuras artificiales ofrezcan una biota sésil empobrecida (Capítulo 2), podría limitar el acceso a distintos recursos tróficos y en última instancia limitar la abundancia y riqueza de especies. No obstante, en el caso de los anfípodos aquí estudiados, no tenemos indicios de que una limitación trófica pueda ser responsable de una menor riqueza, de hecho, en casi todas las localidades se observaron los mismo grupos tróficos tanto en el sustrato natural como el artificial. Además, los anfípodos pueden presentar un comportamiento trófico oportunista y adaptarse a los recursos disponibles (Guerra-García et al., 2014), aunque en nuestro caso, los anfípodos del género *Stenothoe* presentaron una alimentación bastante especialista (estómagos no muy saturados y ocupados de gran cantidad de presa). Esta especialización también ha sido observada por Fredriksen (2003), quien encontró una comunidad de anfípodos asociados al kelp (*Laminaria hyperborea*) principalmente herbívora, lo que contrasta con nuestro resultado (solo aparecieron herbívoros de forma anecdótica), posiblemente por la ya mencionada poca palatabilidad del alga coralinacea *E. elongata*. Aunque el alga *E. elongata* en sí no constituya un recurso trófico para los anfípodos, es sabido que gracias a su alta ramificación, el césped de algas coralinas actúa como una trampa de sedimento y detritus (Kelaher y Castilla, 2005). De hecho, la proporción de detritus encontrada en las especies más abundantes era muy alta, indicando que se trata de una fuente de alimento importante. Por lo tanto, el aporte de detritus (existencia de una fuente) y la capacidad de retenerlo posiblemente jueguen un papel importante en el mantenimiento de esta comunidad de anfípodos, lo cual ya ha sido reportado por Schaal et al. (2016) para la comunidad de anfípodos asociados a *E. ellongata* en un bosque de kelp. La descomposición de algas constituye una fuente de detritus, y existen evidencias de que las redes tróficas de ecosistemas basados en macroalgas se basan principalmente en el consumo de detritus más que en el ramoneo directo de las algas (Schaal et al., 2009 y referencias en el interior). Además, una fuente alóctona de detritus algal puede contribuir a la mayor parte de la dieta de consumidores que viven en sustratos artificiales (Schaal et al., 2008). Todo ello, pone de manifiesto de nuevo la importancia que puede tener un dosel algal rico y abundante, tanto sobre el mismo sustrato como en hábitats adyacentes. Esto puede tener aún

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más relevancia en zonas más oligotróficas donde el aporte de nutrientes de otras fuentes (ej. *upwelling*) sea escaso, como podría ser el caso estudiado de Creta, en la cuenca Este del Mediterráneo.

Por otro lado, aunque la utilización exclusiva de isótopos estables en un momento determinado no es suficiente para el establecimiento de relaciones tróficas (O'Reilly et al. 2002), los datos obtenidos en el capítulo 3.2 para la lapa *P. caerulea* en algunas localidades, apuntan a la explotación de un nicho trófico diferente en función del sustrato (artificial vs natural). A diferencia de lo comentado para peces o anfípodos, las lapas tienen una movilidad muy reducida que les limita en su capacidad de adaptación o de búsqueda de alimento, siendo por lo tanto más vulnerables a un estrés trófico. No obstante, la gran amplitud detectada en la señal del $\delta^{13}C$ indica que esta lapa se está alimentando de distintos productores primarios, sugiriendo cierta capacidad adaptativa a los recursos presentes, aunque las consecuencias a nivel fisiológico que ello pueda tener son desconocidas. Si bien, estas diferencias se encontraron solo en algunas localidades y es necesario un estudio más exhaustivo, tomando más ejemplares, en varias épocas del año, de distintas clases de talla, así como de las posibles fuentes de alimento, para determinar con más precisión si las estructuras artificiales pueden provocar algún tipo de cambio en el comportamiento trófico de estas lapas.

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CONCLUSIONS

1. Artificial coastal defence structures harbour different community structure and taxa composition of intertidal sessile biota, vagile macrofauna and meiofauna in comparison with near natural substrates. Substrate composition, roughness and age seems to be the main drivers of those differences at local level.

2. Although the abiotic features of the primary substrate can have some direct effects on the associated fauna, they primarily affected the sessile community, initiating strong cascading effects that were detectable at high taxonomic level in the associated fauna.

3. Artificial structures can shape the amphipod community directly through the provision of new habitats and conditions but most importantly indirectly through facilitation effects exerted by the different sessile taxa.

4. Among the artificial structures studied (acropods, cubes, rip-raps, seawalls and tetrapods), rip-raps were in general the best surrogate of natural hard substartes, however we did not find them as suitable surrogates of natural shallow subtidal sessile communities in Crete (Greece).

5. Three-dimensional branched algae canopy was reduced on rip-raps in comparison with natural substrates in the shallow subtidal communities of Crete (Greece).

6. There is both, an intertidal and subtidal biodiversity loss associated with coastal defence structures at local and regional level.

7. The impact of coastal defence infrastructure seems hardly predictable at regional level, which constitutes a great challenge in the development of mitigating measures and ecological designs that could be applied at regional or global scales.

8. Even when the secondary substrate was the same, artificial structures affected the trophic structure of amphipod communities. These differences were due to a change in taxa composition rather than a change in the feeding habit.

9. A trophic shift was observed in some limpets (*Patella caerulea*) living on artificial structures, however the pattern was not constant, suggesting that the maintenance of limpet

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populations inhabiting coastal defence structures may rely on different factors rather than only on trophic resources.

10. Measures of $\delta^{15}N$ ratios in the muscle tissue of *P. caerulea* constitute a good bioindicator of eutrophication at regional scales.

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SUPPLEMENTARY MATERIAL

Table S1: Elemental composition of each substrate measured by X-ray fluorescence. Data shown are average percentages ± standard deviation. CP: Calcination Percentage.

	Natural	Rip-rap	Seawall	Cube	Acropod
SiO_2	95.63 ± 1.25	3.88 ± 2.71	11.34 ± 1.25	31.96 ± 11.28	6.51 ± 1.76
Al_2O_3	1.21 ± 0.32	0.43 ± 0.33	1.33 ± 0.18	0.77 ± 0.29	2.22 ± 0.53
Fe_2O_3	0.29 ± 0.10	0.32 ± 0.18	0.87 ± 0.10	0.66 ± 0.22	1.02 ± 0.30
MnO	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.02	0.03 ± 0.01	0.00 ± 0.00
MgO	0.24 ± 0.10	0.50 ± 0.19	1.84 ± 0.72	2.48 ± 0.76	14.27 ± 3.06
CaO	0.02 ± 0.03	52.66 ± 2.23	45.83 ± 1.85	33.74 ± 7.91	33.14 ± 1.89
Na_2O	0.19 ± 0.06	0.07 ± 0.03	0.36 ± 0.08	0.58 ± 0.29	0.42 ± 0.14
K_2O	0.16 ± 0.03	0.12 ± 0.06	0.19 ± 0.02	0.11 ± 0.04	0.22 ± 0.07
TiO_2	0.08 ± 0.07	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.06
P_2O_5	0.00 ± 0.00	0.03 ± 0.04	0.06 ± 0.01	0.03 ± 0.01	0.06 ± 0.03
SO_3	0.00 ± 0.00	0.00 ± 0.00	1.28 ± 0.20	1.06 ± 0.76	1.33 ± 0.28
CP	1.17 ± 0.41	41.56 ± 1.10	36.62 ± 1.60	29.10 ± 5.20	40.48 ± 1.40

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Table S2: Mineralogical composition (average percentage ± standard deviation) of each substrate quantified by interpretation of X-ray fluorescence (XRF) and X-ray diffraction (XRD) data using DRIFAC.EVA.4.1. The pattern used and the degree of quality assigned by the ICDD (International Centre for Diffraction Data) is indicated. Star (*): High quality pattern; Calculated: pattern computed from single-crystal structural parameters; PDF: Powder Diffraction File; Mg.: magnesium.

Mineral	Natural	Rip-rap	Seawall	Cube	Acropod	Pattern PDF	Quality
Quartz	0.96 ± 0.01	0.08 ± 0.04	0.18 ± 0.03	0.57 ± 0.16	0.01 ± 0.00	33-1161	Star (*)
Albite	0.01 ± 0.00	0.00	0.00	0.00	0.00	89-6427	Calculated
Muscovite	0.02 ± 0.00	0.00	0.00	0.00	0.00	85-2147	Calculated
Calcite	0.00	0.92 ± 0.04	0.00	0.34 ± 0.07	0.17 ± 0.13	05-0586	Star (*)
Mg. calcite	0.00	0.00	0.78 ± 0.04	0.07 ± 0.12	0.00	89-1304	Calculated
Sillimanite	0.00	0.00	0.01 ± 0.02	0.00	0.00	84-0983	Calculated
Aragonite	0.00	0.00	0.01 ± 0.02	0.00	0.01	41-1475	Star (*)
Ettringite	0.00	0.00	0.01 ± 0.01	0.00	0.00	41-1451	Star (*)
Gypsum	0.00	0.00	0.00	0.02 ± 0.03	0.02 ± 0.01	21-0816	Star (*)
Dolomite	0.00	0.00	0.00	0.00	0.80 ± 0.12	36-0426	Star (*)

	Exact formula of the pattern
Quartz, synthethic	SiO_2
Albite (Heat treated)	$Na(AlSi_3O_8)$
Muscovite 2M#1	$(Na_{0.37}K_{0.60})(Al_{1.84}Ti_{0.02}Fe_{0.10}Mg_{0.06})(Si_{3.03}Al_{0.97})O_{10}(OH)_2$
Calcite, synthethic	$CaCO_3$
Mg. calcite synthethic	$(Mg_{0.03}Ca_{0.97})(CO_3)$
Sillimanite	$(Al_{1.98}Fe_{0.02})SiO_5$
Aragonite	$CaCO_3$
Ettringite, synthethic	$(Mg_6Fe_2(OH)_{16}CO_3(H2O)_{4.5})_{0.25}$
Gypsum	$Ca_6Al_2(SO_4)_3(OH)_{12}{\cdot}_{26}H_2O$
Dolomite	$CaMg(CO_3)_2$

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Table S3: Average abundances for the three community levels studied on each substrate.

Sessile community (ml ± SD)					
	Natural	Seawall	Cube	Acropod	Riprap
Ellisolandia elongata	172.8 ± 48.8	0.0 ± 0.0	5.8 ± 4.6	28.3 ± 33.4	25.8 ± 15.3
Mytilus galloprovincialis	0.0 ± 0.0	365.0 ± 305.1	12.2 ± 18.7	0.0 ± 0.0	0.0 ± 0.0
Perforatus perforatus	1.0 ± 1.7	234.9 ± 88.8	41.2 ± 16.5	41.0 ± 29.6	0.8 ± 1.0
Spirobranchus sp./*Denropoma* sp. *reef*	20.9 ± 14.3	0.0 ± 0.0	1.1 ± 1.7	16.1 ± 19.6	2.4 ± 2.8
Jania rubens	6.6 ± 2.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Gelidium/Caulacanthus turf	1.0 ± 0.3	0.7 ± 0.6	0.9 ± 0.2	0.1 ± 0.2	0.4 ± 0.6
Ceramium sp.	0.8 ± 0.2	0.2 ± 0.4	0.1 ± 0.2	0.1 ± 0.2	0.4 ± 0.6
Laurencia sp.	0.2 ± 0.4	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Pyura dura	2.6 ± 4.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Rugulopteryx okamurae	0.0 ± 0.0	0.6 ± 0.4	0.0 ± 0.0	0.2 ± 0.4	0.2 ± 0.4
Ulva sp.	0.0 ± 0.0	0.7 ± 0.4	0.1 ± 0.2	0.1 ± 0.2	0.1 ± 0.2
Bryozoa indet.	0.7 ± 0.4	0.3 ± 0.4	0.1 ± 0.2	0.3 ± 0.4	0.0 ± 0.0
Lithophyllum incrustans	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.1 ± 0.2
Vagile macrofauna (individuals per 400 cm^2 ± SD)					
	Natural	Seawall	Cube	Acropod	Rip-rap
Non-Caprellidae Amphipoda	1208.2 ± 422.2	775.2 ± 405.5	53.1 ± 44.4	98.3 ± 63.4	112.7 ± 109.7
Isopoda	57.3 ± 37.4	175.4 ± 53.5	26.6 ± 12.8	67.3 ± 33.5	48.9 ± 28.0
Bivalvia	96.0 ± 78.1	0.6 ± 0.6	39.7 ± 42.4	39.6 ± 34.7	58.8 ± 41.7
Annelida	82.4 ± 35.4	90.8 ± 51.6	42.9 ± 16.6	48.7 ± 34.5	29.8 ± 19.7
Tanaidacea	32.8 ± 16.2	90.8 ± 65.5	20.8 ± 13.9	13.3 ± 4.9	13.8 ± 14.1
Gastropoda	64.9 ± 38.2	2.0 ± 2.1	8.3 ± 7.9	27.7 ± 24.4	13.0 ± 4.3
Caprellidae	57.9 ± 36.0	0.0 ± 0.0	32.4 ± 42.7	17.1 ± 14.6	11.2 ± 14.0
Pycnogonida	42.7 ± 17.4	5.4 ± 3.5	1.2 ± 2.1	4.0 ± 3.4	5.7 ± 5.6
Decapoda	6.1 ± 3.2	16.6 ± 14.5	0.6 ± 0.7	1.9 ± 2.2	0.1 ± 0.2
Sipuncula	1.8 ± 1.7	2.1 ± 1.4	0.2 ± 0.4	0.4 ± 0.8	0.6 ± 0.8
Nemertea	1.1 ± 1.5	7.4 ± 5.7	1.0 ± 1.2	5.7 ± 2.9	0.0 ± 0.0
Platyhelminthes	0.1 ± 0.2	5.4 ± 3.6	0.7 ± 0.8	2.1 ± 1.1	0.2 ± 0.4
Polyplacophora	2.9 ± 1.3	0.1 ± 0.2	0.9 ± 1.1	11.1 ± 9.9	4.7 ± 3.3
Insecta	18.1 ± 18.8	0.0 ± 0.0	0.9 ± 1.2	4.4 ± 6.3	17.8 ± 23.4
Echinoidea	0.7 ± 1.2	1.4 ± 0.9	0.3 ± 0.6	0.6 ± 0.6	0.6 ± 0.7
Cnidaria	1.3 ± 1.9	11.0 ± 9.3	1.6 ± 2.7	0.4 ± 0.5	0.3 ± 0.3
Vagile meiofauna (individuals per 400 cm^2 ± SD)					
	Natural	Seawall	Cube	Acropod	Riprap
Nematoda	10008 ± 3732	13372 ± 3123	3761 ± 1791	1423 ± 753	1288 ± 708
Copepoda	9564 ± 4569	5938 ± 1930	2831 ± 822	1946 ± 781	1051 ± 522
Ostracoda	5772 ± 2638	2834 ± 1030	1904 ± 495	845 ± 505	672 ± 289

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Foraminifera	4269 ± 2843	5509 ± 1634	979 ± 541	757 ± 495	803 ± 402
Nauplii	234 ± 185	4630 ± 2846	2065 ± 2810	932 ± 953	128 ± 106
Polychaeta	3759 ± 1338	1788 ± 595	308 ± 121	317 ± 266	247 ± 195
Non-Caprellidae Amphipoda	1142 ± 576	1214 ± 666	96 ± 83	155 ± 113	75 ± 43
Mollusca	979 ± 597	299 ± 128	432 ± 353	410 ± 275	223 ± 125
Acari	872 ± 389	491 ± 284	232 ± 107	420 ± 243	268 ± 230
Turbellaria	58 ± 38	556 ± 349	57 ± 68	17 ± 24	45 ± 33
Kinorhyncha	383 ± 410	0 ± 0	0 ± 0	4 ± 7	1 ± 2
Insecta	235 ± 208	0 ± 0	0 ± 0	79 ± 63	44 ± 24
Oligochaeta	48 ± 54	172 ± 104	61 ± 70	4 ± 6	4 ± 7
Caprellidae	105 ± 101	0 ± 0	47 ± 58	32 ± 48	3 ± 6
Nemertea	7 ± 12	411 ± 448	0 ± 0	0 ± 0	0 ± 0
Isopoda	43 ± 18	142 ± 82	18 ± 18	31 ± 41	21 ± 29
Tardigrada	16 ± 17	277 ± 172	24 ± 33	0 ± 0	6 ± 7
Tanaidacea	80 ± 52	115 ± 103	48 ± 41	43 ± 33	15 ± 22
Pycnogonida	17 ± 20	19 ± 34	0 ± 0	0 ± 0	0 ± 0
Cnidaria	0 ± 0	0 ± 0	8 ± 14	4 ± 7	0 ± 0
Sipuncula	6 ± 11	11 ± 14	0 ± 0	0 ± 0	6 ± 11

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Table S4: Results for the comparison between substrates of number of taxa and Shannon's diversity measured at sessile, associated macro and meiofaunal community levels. Ha: Habitat [five levels: N(natural), R(rip-rap), A(acropod), C(cube) and S(seawall)]; Si(Ha): Site; df: degrees of freedom; MS: mean square; p: level of significance; Intercept: reference value = Natural; .: p < 0.1; *: p < 0.05; ** p < 0.01; *** p < 0.001; n.s.: not significant.

Number of taxa						**Shannon**					
Sessile community											
Method:	2-way ANOVA					Method:	2-way ANOVA				
Source	df	MS	F		p	Source	df	MS	F		p
Ha	4	12.94	9.10		**	Ha	4	0.15	5.30		*
Si(Ha)	10	1.42	0.65		n.s.	Si(Ha)	10	0.03	0.50		n.s.
Residual	30	2.20				Residual	30	0.05			
Total	44					Total	44				
Cochran's test					n.s.	Cochran's test					n.s.
Transformation: None						Transformation: None					
SNK test	Levels of factor (Ha)					SNK test	Levels of factor (Ha)				
	N>(R=A=C=S)						N=(R,A,C,S), R<A=S				
Associated macrofauna											
Method:	GLMM					Method:	GLMM				
Source	Estimate	S.E.	z	Pr(>|z|)		Source	Estimate	S.E.	z	Pr(>|z|)	
Intercept	2.51	0.11	22.92	<0.001	***	Inercept	1.24	0.07	16.97	<0.001	***
Cube	-0.25	0.15	-1.66	0.097	.	Cube	0.43	0.09	4.06	<0.001	***
Rip-rap	-0.19	0.15	-1.26	0.209	n.s.	Rip-rap	0.44	0.09	4.67	<0.001	***
Seawall	-0.10	0.18	-0.57	0.571	n.s.	Seawall	0.14	0.11	1.19	0.2326	n.s.
Acropod	-0.05	0.14	-0.37	0.714	n.s.	Acropod	0.62	0.09	6.76	<0.001	***
Volume	0.00	0.00	0.41	0.684	n.s.	Volume	0.00	0.00	-1.97	0.049	n.s.
Model:	Taxa ~ Substrate + Vol + (1 | Substrate:Site)					Model:	Shannon~Substrate + Vol				
Family:	Poisson					Family:	Gaussian				
Associated meiofauna											
Method:	GLMM					Method:	GLMM				
Source	Estimate	S.E.	z	Pr(>|z|)		Source	Estimate	S.E.	z	Pr(>|z|)	
Intercept	2.71	0.10	27.11	<0.001	***	Intercept	1.88	0.05	39.70	<0.001	***
Cube	-0.23	0.13	-1.65	0.099	.	Cube	-0.15	0.06	-2.52	0.012	n.s.
Rip-rap	-0.22	0.14	-1.66	0.093	.	Rip-rap	0.01	0.06	0.03	0.975	n.s.
Seawall	-0.07	0.16	-0.41	0.686	n.s.	Seawall	-0.05	0.07	-0.72	0.474	n.s.
Acropod	-0.27	0.14	-2.00	<0.05	*	Acropod	0.05	0.06	0.80	0.423	n.s.
Volume	0.00	0.00	0.04	0.967	n.s.	Volume	0.00	0.00	0.62	0.533	n.s.
Model:	Taxa ~ Substrate + Vol + (1 | Substrate:Site)					Model:	Shannon~Substrate + Vol				
Family:	Poisson					Family:	Gaussian				

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Table S5: Elemental composition of each substrate measured by X-ray fluorescence. Data are average percentages. : Rip-rap, : Cube, : Tetrapod, : Seawall, C

	AGD	ALG	MES	AGD-N	ALG-N	MES-N	FUE	MOT	CEU	FUE-N	MOT-N	CEU-N	BEN	MDQ	SMR	BEN-N	MDQ-N	SMR-N	ALM
SiO_2	0.3	3.9	2.0	1.6	95.6	0.1	13.9	4.1	23.4	73.5	56.8	72.9	5.4	29.1	41.6	59.4	67.3	67.3	3.8
Al_2O_3	0.0	0.4	0.6	0.5	1.2	0.0	1.5	1.2	4.1	12.9	6.1	13.5	1.2	6.5	11.7	19.6	15.2	15.2	1.0
Fe_2O_3	1.1	0.3	0.7	0.7	0.3	0.0	1.0	0.7	1.4	3.2	2.3	2.5	0.8	2.7	4.9	8.0	5.3	5.3	1.3
MnO	0.1	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	0.1
MgO	20.5	0.5	6.0	16.8	0.2	21.5	16.4	11.5	13.8	1.0	4.7	1.0	14.8	9.6	2.1	2.5	1.7	1.7	16.4
CaO	31.2	52.7	46.7	33.5	0.0	31.8	27.4	38.3	22.2	0.6	12.7	0.6	34.6	22.3	18.8	1.7	2.1	2.1	32.8
Na_2O	0.0	0.1	0.0	0.1	0.2	0.0	0.3	0.4	0.9	4.3	1.2	3.0	0.5	0.4	0.8	1.1	1.5	1.5	0.3
K_2O	0.0	0.1	0.2	0.1	0.2	0.0	0.3	0.2	0.6	1.2	0.8	3.1	0.1	1.2	2.1	3.4	2.5	2.5	0.2
TiO_2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.5	0.3	0.2	0.0	0.3	0.6	0.9	0.7	0.7	0.0
P_2O_5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.3	0.0	0.1	0.2	0.2	0.1	0.1	0.0
SO_3	0.0	0.0	0.0	0.0	0.0	0.1	0.7	1.8	0.0	0.0	0.8	0.0	1.8	0.6	0.6	0.0	0.0	0.0	0.7
PC	46.6	41.6	43.4	45.3	1.2	45.6	39.4	41.8	46.3	2.6	14.9	2.4	41.1	27.9	16.7	3.1	8.7	8.7	42.4

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Table S6: Two-way ANOVA table of results for the taxa richness. Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este), localities with seawalls (ALM: Almería, MAL: Málaga, MOT: Motril) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; df: degrees of freedom; MS: mean square; p: level of significance; n.s.: not significant; **: $p < 0.01$; ***: $p < 0.001$.

Cubes

Source of variation		df	MS	F	p
Su		1	107.56	15.74	**
Lo		2	176.89	25.89	***
SuxLo		2	6.22	0.91	n.s.
Residual		12	6.83		
Total		17			
Trasnformation	None				
Cochran's test	n.s.				
SNK	Level CEU: Cube<Natural				
	Level FUE: Cube=Natural				
	Level MOT: Cube<Natural				

Rip-raps

Source of variation		df	MS	F	p
Su		1	6.722	2.37	n.s.
Lo		2	5.167	1.82	n.s.
SuxLo		2	32.72	11.55	**
Residual		12	2.83		
Total		17			
Trasnformation	None				
Cochran's test	n.s.				
SNK	Level AGD: Rip-rap>Natural				
	Level ALG: Rip-rap<Natural				
	Level MES: Rip-rap=Natural				

Seawalls

Source of variation		df	MS	F	p
Su		1	329.39	20.30	***
Lo		2	20.06	1.24	n.s.
SuxLo		2	8.39	0.52	n.s.
Residual		12	16.22		
Total		17			
Trasnformation	Log(x+1)				
Cochran's test	n.s.				
SNK	Level ALM: Seawall<Natural				
	Level MAL: Seawall<Natural				
	Level MOT: Seawall=Natural				

Tetrapods

Source of variation		df	MS	F	p
Su		1	133.39	41.40	***
Lo		2	56.17	17.43	***
SuxLo		2	1.06	0.33	n.s.
Residual		12	3.22		
Total		17			
Trasnformation	None				
Cochran's test	n.s.				
SNK	Level BEN: Tetrapod<Natural				
	Level MDQ: Tetrapod<Natural				
	Level SMR: Tetrapod<Natural				

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Table S7: PERMANOVA table of results for the taxonomic structure. Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este), localities with seawalls (ALM: Almería, MAL: Málaga, MOT: Motril) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; df: degrees of freedom; MS: mean square; Ps.F: Pseudo-F; p: level of significance; Perm.: Permutations; n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Cubes					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	3053.4	3.20	n.s.	38
Lo	2	3371.2	8.44	***	9936
SuxLo	2	954.26	2.39	*	9938
Residual	12	399.59			
Total	17				
SNK	Level CEU: Cube≠Natural				
	Level FUE: Cube≠Natural				
	Level MOT: Cube=Natural				
Rip-raps					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	2153.2	2.00	n.s.	38
Lo	2	2240.5	5.59	**	9937
SuxLo	2	1076.6	2.69	**	9935
Residual	12	400.6			
Total	17				
SNK	Level AGD: Rip-rap≠Natural				
	Level ALG: Rip-rap≠Natural				
	Level MES: Rip-rap=Natural				
Seawalls					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	6883.8	3.41	n.s.	38
Lo	2	4031.6	7.70	***	9914
SuxLo	2	2020.6	3.86	***	9937
Residual	12	523.9			
Total	17				
SNK	Level ALM: Seawall≠Natural				
	Level MAL: Seawall≠Natural				
	Level MOT: Seawall=Natural				
Tetrapods					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	2954.4	4.13	*	38
Lo	2	2825.2	13.27	***	9950
SuxLo	2	715.16	3.36	**	9936
Residual	12	212.92			
Total	17				
SNK	Level BEN: Tetrapod≠Natural				
	Level MDQ: Tetrapod≠Natural				
	Level SMR: Tetrapod≠Natural				

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Table S8: PERMANOVA table of results for the taxa cover percentages on vertical exposed surfaces. Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este), localities with seawalls (ALM: Almería, MAL: Málaga, MOT: Motril) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; df: degrees of freedom; MS: mean square; Ps.F: Pseudo-F; p: level of significance; Perm.: Permutations; n.s.: not significant; **: $p < 0.01$; ***: $p < 0.001$.

Cubes					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	20394	2.1331	n.s.	38
Lo	2	23879	14.823	***	9948
SuxLo	2	9560.4	5.9349	***	9936
Si(LoxSu)	12	1610.9	1.7303	***	9841
Residual	72	931			
Total	89				
SNK (SuxLo)	Level CEU: Cube≠Natural				
	Level FUE: Cube≠Natural				
	Level MOT: Cube≠Natural				
Rip-raps					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	9038.1	1.085	n.s.	38
Lo	2	10119	4.0377	***	9934
SuxLo	2	8330.3	3.324	**	9934
Si(LoxSu)	12	2506.1	1.8603	***	9864
Residual	72	1347			
Total	89				
SNK	Level AGD: Rip-rap=Natural				
	Level ALG: Rip-rap≠Natural				
	Level MES: Rip-rap=Natural				
Seawalls					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	54770	3.7925	n.s.	38
Lo	2	26801	11.055	***	9951
SuxLo	2	14442	5.9573	***	9935
Si(LoxSu)	12	2424.2	3.7294	***	9841
Residual	72	650.03			
Total	17				
SNK	Level ALM: Seawall≠Natural				
	Level MAL: Seawall≠Natural				
	Level MOT: Seawall≠Natural				
Tetrapods					
Source of variation	df	MS	Ps.-F	p	Perm.
Su	1	42025	4.6643	n.s.	38
Lo	2	9972.9	5.8043	***	9947
SuxLo	2	9009.9	5.2439	***	9942
Si(LoxSu)	12	1718.2	2.1414	***	9878
Residual	72	802.37			
Total	17				
SNK	Level BEN: Tetrapod≠Natural				
	Level MDQ: Tetrapod≠Natural				
	Level SMR: Tetrapod≠Natural				

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Table S9: PERMANOVA table of results for the full taxonomic structure of each region: West region (Algeciras, Ceuta, M'Diq and Marina Smir), Middle West region (Benalmádena, Fuengirola and Málaga), Middle East region (Marina del Este and Motril) and East region (Aguadulce and Almería). Factors: Factor Region (Re), a fixed factor with the abovementioned regions as levels; and Factor Locality (Lo), a random factor nested in Region with eleven levels (each of the studied localities). df: degrees of freedom; MS: mean square; Ps.F: Pseudo-F; p: level of significance; Perm.: Permutations; ***: $p < 0.001$.

Regions					
Source of variation	df	MS	Ps.-F	p	Perm.
Re	3	7293.6	3.2453	***	9925
Lo(Re)	7	2176.3	3.0481	***	9849
Res	61	713.97			
Total	71				
SNK (Re)	West≠Middle West≠(Middle East=East)				

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Table S10: Pair-wise comparisons of significant sources ovariation detected under PERMANOVA test for taxa cover percentages. Su: substrate; Or: orientation; Lo: locality; St: site; Nat: natural; Art: artificial; Nor: North; Sou: South; Ka: Kato Galatas; Ba: Bali; Go: Gournes; Ho: Hora Sfakion; Ag: Agia Galini; Tsou: Tsousouros; p: level of significance; n.s.: not-significant; * p<0.05; ** p<0.01

Source of variation	Pairs of factor	Level(s)	Groups	p
Su	Substrate		Nat VS Art	**
Lo(Or)	Locality	North	Ka VS Ba	**
			Ka VS Go	**
			Ba VS Go	**
		South	Ho VS Ag	**
			Ho VS Ts	*
			Ag VS Ts	**
Su x Or	Orientation	Natural	Nor VS Sou	n.s.
		Artificial	Nor VS Sou	n.s.
	Substrate	North	Nat VS Art	*
		South	Nat VS Art	**
Su x Lo(Or)	Substrate	Nor-Ka	Nat VS Art	**
		Nor-Ba	Nat VS Art	**
		Nor-Go	Nat VS Art	**
		Sou-Ho	Nat VS Art	**
		Sou-Ag	Nat VS Art	**
		Sou-Ts	Nat VS Art	n.s.
	Locality	Nat-Nor	Ka VS Ba	**
			Ka VS Go	*
			Ba VS Go	**
		Nat-Sou	Ho VS Ag	**
			Ho VS Ts	n.s.
			Ag VS Ts	**
		Art-Nor	Ka VS Ba	**
			Ka VS Go	**
			Ba VS Go	**
		Art-Sou	Ho VS Ag	*
			Ho VS Ts	*
			Ag VS Ts	**

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Table S11: Trophic categories of the collected taxa based on data from the present study when available, or data from literature. *: When data are not available for a particular taxon, the category has been assigned based on other species of the genus or family.

Taxa	Trophic category	References
Ampithoe ferox (Chevreux, 1901)	Omnivorous	Guerra-García *et al*., 2014
Ampithoe ramondi Audouin, 1826	Omnivorous/Herbivorous	Guerra-García *et al*., 2014; Vázquez-Luis *et al*., 2013
Apherusa mediterranea Chevreux, 1911	Omnivorous/Detritivorous*	Guerra-García *et al*., 2014
Apocorophium sp.	Detritivorous*	Guerra-García *et al*., 2014; Vázquez-Luis *et al*., 2013
Apolochus picadurus (J.L. Barnard, 1962)	Omnivorous	Guerra-García *et al*., 2014
Apohyale perieri (Lucas, 1849)	Herbivorous/Omnivorous	Torrecilla and Guerra-García, 2012; Guerra-García *et al*., 2014
Caprella equilibra Say, 1818	Omnivorous	Guerra-García and Tierno de Figueroa, 2009; Guerra-García *et al*., 2014; Guerra-García *et al*., 2015
Caprella grandimana Mayer, 1882	Detritivorous	Present study
Caprella hirsuta Mayer, 1890	Detritivorous	Guerra-García and Tierno de Figueroa, 2009; Guerra-García *et al*., 2014
Caprella liparotensis Haller, 1879	Omnivorous	Guerra-García and Tierno de Figueroa, 2009; Guerra-García *et al*., 2014
Caprella penantis Leach, 1814	Omnivorous	Guerra-García and Tierno de Figueroa, 2009; Guerra-García *et al*., 2014; Martínez-Laiz and Guerra-García, 2015
Coxischyrocerus inexpectatus (Ruffo, 1959)	Detritivorous	Guerra-García *et al*., 2014
Elasmopus rapax Costa, 1853	Omnivorous	Guerra-García *et al*., 2014
Elasmopus vachoni Mateus & Mateus, 1966	Omnivorous/Herbivorous	Guerra-García *et al*., 2014
Hyale pontica Rathke, 1847	Omnivorous/Herbivorous	Guerra-García *et al*., 2014
Hyale stebbingi Chevreux, 1888	Omnivorous	Present study
Jassa marmorata Holmes, 1905	Detritivorous	Present study
Jassa ocia (Spence Bate, 1862)	Detritivorous*	Guerra-García *et al*., 2014
Guernea (*Guernea*) *coalita* (Norman, 1868)	Carnivorous	Guerra-García *et al*., 2014
Lembos aff. *websteri* Spence Bate, 1857	Detritivorous/Omnivorous	Guerra-García *et al*., 2014
Lysianassidae	Omnivorous*	Guerra-García *et al*., 2014
Podocerus variegatus Leach, 1814	Detritivorous	Guerra-García *et al*., 2014
Protohyale (*Protohyale*) *schmidtii* (Heller, 1866)	Detritivorous/Omnivorous	Present study
Serejohyale spinidactylus (Chevreux, 1926)	Carnivorous	Guerra-García *et al*., 2014
Stenothoe cattai Stebbing, 1906	Carnivorous*	Guerra-García *et al*., 2014; Vázquez-Luis *et al*., 2013
Stenothoe monoculoides (Montagu, 1813)	Carnivorous	Present study
Stenothoe tergestina (Nebeski, 1881)	Carnivorous	Present study

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Table S12: Two-way ANOVA table of results for amphipod total abundance. Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; df: degrees of freedom; MS: mean square; p: level of significance; n.s.: not significant; *: $p < 0.05$.

Cubes				
Source of variation	df	MS	F	p
Su	1	0.55	0.79	n.s.
Lo	2	0.54	3.04	n.s.
SuxLo	2	0.70	3.92	*
Residual	12	0.18		
Total	17			
Transformation	Ln(x)			
Cochran's test	n.s.			
Pair-wise SuxLo	CEU: Cube<Natural			
	FUE: Cube=Natural			
	MOT: Cube=Natural			

Rip-raps				
Source of variation	df	MS	F	p
Su	1	801808	0.10	n.s.
Lo	2	16428881	2.46	n.s.
SuxLo	2	7936311	1.19	n.s.
Residual	12	6672266		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	AGD: Rip-rap=Natural			
	ALG: Rip-rap=Natural			
	MES: Rip-rap=Natural			

Tetrapods				
Source of variation	df	MS	F	p
Su	1	26950034	1.26	n.s.
Lo	2	21779295	1.20	n.s.
SuxLo	2	21308285	1.18	n.s.
Residual	12	18075745		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	BEN: Tetrapod=Natural			
	MDQ: Tetrapod=Natural			
	SMR: Tetrapod=Natural			

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Table S13: Two-way ANOVA table of results for species richness. Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; df: degrees of freedom; MS: mean square; p: level of significance; n.s.: not significant; **: $p < 0.01$.

Cubes				
Source of variation	df	MS	F	p
Su	1	24.50	16.33	n.s.
Lo	2	5.72	3.55	n.s.
SuxLo	2	1.50	0.93	n.s.
Residual	12	1.61		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	CEU: Cube<Natural			
	FUE: Cube<Natural			
	MOT: Cube=Natural			
Rip-raps				
Source of variation	df	MS	F	p
Su	1	37.56	0.72	n.s.
Lo	2	8.72	2.04	n.s.
SuxLo	2	52.06	12.17	**
Residual	12	4.28		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	AGD: Rip-rap=Natural			
	ALG: Rip-rap>Natural			
	MES: Rip-rap=Natural			
Tetrapods				
Source of variation	df	MS	F	p
Su	1	2.00	0.05	n.s.
Lo	2	4.17	1.01	n.s.
SuxLo	2	40.17	9.77	**
Residual	12	4.11		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	BEN: Tetrapod=Natural			
	MDQ: Tetrapod<Natural			
	SMR: Tetrapod<Natural			

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Table S14: Two-way ANOVA table of results for Shannon's diversity. Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; df: degrees of freedom; MS: mean square; p: level of significance; n.s.: not significant; *: $p < 0.05$; ***: $p < 0.001$.

Cubes				
Source of variation	df	MS	F	p
Su	1	0.42	22.85	*
Lo	2	0.03	0.25	n.s.
SuxLo	2	0.02	0.16	n.s.
Residual	12	0.11		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	CEU: Cube=Natural			
	FUE: Cube=Natural			
	MOT: Cube=Natural			
Rip-raps				
Source of variation	df	MS	F	p
Su	1	1.32	0.81	n.s.
Lo	2	0.05	0.56	n.s.
SuxLo	2	1.64	17.59	***
Residual	12	0.09		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	AGD: Rip-rap=Natural			
	ALG: Rip-rap>Natural			
	MES: Rip-rap=Natural			
Tetrapods				
Source of variation	df	MS	F	p
Su	1	0.15	0.08	n.s.
Lo	2	0.12	1.18	n.s.
SuxLo	2	1.83	17.94	***
Residual	12			
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise SuxLo	BEN: Tetrapod=Natural			
	MDQ: Tetrapod<Natural			
	SMR: Tetrapod<Natural			

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Table S15: Two-way ANOVA for the percentage of the four trophic categories (carnivorous, herbivorous, detritivorous and omnivorous). Lo: Locality [three levels: Localities with cubes (CEU: Ceuta, FUE: Fuengirola, MOT: Motril), localities with rip-raps (AGD: Aguadulce, ALG: Algeciras, MES: Marina del Este) and localities with tetrapods (BEN: Benalmádena, MDQ: M'Diq, SMR: Marina Smir)]; Su: Substrate [two levels: Artificial (the artificial structure) and Natural (the closest natural rocky shore)]; df: degrees of freedom; MS: mean square; p: level of significance; n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

CARNIVORES

Cubes

Source	df	MS	F	p
Su	1	841	0.00	n.s.
Lo	2	419085	1.56	n.s.
SuxLo	2	2347206	8.73	**
Residual	12	268733		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise	CEU: Cube=Natural			
SuxLo	FUE: Cube>Natural			
	MOT: Cube=Natural			

Rip-raps

Source	df	MS	F	p
Su	1	989825	0.36	n.s.
Lo	2	944152	0.91	n.s.
SuxLo	2	2739192	2.63	n.s.
Residual	12	1041274		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise	AGD: Rip-rap=Natural			
SuxLo	ALG: Rip-rap>Natural			
	MES: Rip-rap=Natural			

Tetrapods

Source	df	MS	F	p
Su	1	14558408	1.37	n.s.
Lo	2	3325079	1.40	n.s.
SuxLo	2	10664579	4.49	*
Residual	12	2376816		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise	BEN: Tetrapod=Natural			
SuxLo	MDQ: Tetrapod<Natural			
	SMR: Tetrapod<Natural			

HERBIVORES

Cubes

Source	df	MS	F	p
Su	1	29.27	1.92	n.s.
Lo	2	247.39	9.49	**
SuxLo	2	15.26	0.58	n.s.
Residual	12	26.06		
Total	17			
Transformation	Square root (x+1)			
Cochran's test	n.s.			
Pair-wise	CEU: Cube=Natural			
SuxLo	FUE: Cube=Natural			
	MOT: Cube=Natural			

Rip-raps

Source	df	MS	F	p
Su	1	74.11	0.68	n.s.
Lo	2	96.34	4.06	*
SuxLo	2	108.55	4.57	*
Residual	12	23.75		
Total	17			
Transformation	Square root (x+1)			
Cochran's test	n.s.			
Pair-wise	AGD: Rip-rap=Natural			
SuxLo	ALG: Rip-rap>Natural			
	MES: Rip-rap=Natural			

Tetrapods

Source	df	MS	F	p
Su	1	866666	3.99	n.s.
Lo	2	24830	1.81	n.s.
SuxLo	2	21743	1.58	n.s.
Residual	12	13721		
Total	17			
Transformation	None			
Cochran's test	n.s.			
Pair-wise	BEN: Tetrapod=Natural			
SuxLo	MDQ: Tetrapod=Natural			
	SMR: Tetrapod<Natural			

DETRITIVORES

Cubes

Source	df	MS	F	p
Su	1	1.14	0.35	n.s.
Lo	2	0.28	0.66	n.s.

OMNIVORES

Cubes

Source	df	MS	F	p
Su	1	8498190	1.02	n.s.
Lo	2	8675836	2.69	n.s.

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SuxLo	2	1.72	2.10	n.s.	SuxLo	2	8363704	2.59	n.s.
Residual	12	0.82			Residual	12	3224444		
Total	17				Total	17			
Transformation	Ln(X)				Transformation	None			
Cochran's test	n.s.				Cochran's test	n.s.			
Pair-wise	CEU: Cube=Natural				Pair-wise	CEU: Cube=Natural			
SuxLo	FUE: Cube=Natural				SuxLo	FUE: Cube=Natural			
	MOT: Cube=Natural					MOT: Cube=Natural			

	Rip-raps					**Rip-raps**			
Source	df	MS	F	p	Source	df	MS	F	p
Su	1	1124.69	2.48	n.s.	Su	1	678.95	21.61	*
Lo	2	68.50	0.88	n.s.	Lo	2	607.36	2.57	n.s.
SuxLo	2	453.24	5.83	*	SuxLo	2	31.44	0.13	n.s.
Residual	12	77.74			Residual	12	236.49		
Total	17				Total	17			
Transformation	Square root (x+1)				Transformation	Square root (x+1)			
Cochran's test	n.s.				Cochran's test	n.s.			
Pair-wise	AGD: Rip-rap=Natural				Pair-wise	AGD: Rip-rap=Natural			
SuxLo	ALG: Rip-rap>Natural				SuxLo	ALG: Rip-rap=Natural			
	MES: Rip-rap=Natural					MES: Rip-rap=Natural			

	Tetrapods					**Tetrapods**			
Source	df	MS	F	p	Source	df	MS	F	p
Su	1	24262578	37.17	*	Su	1	3959298	0.47	n.s.
Lo	2	762610	0.47	n.s.	Lo	2	7120356	1.28	n.s.
SuxLo	2	652816	0.40	n.s.	SuxLo	2	8469267	1.52	n.s.
Residual	12	1639467			Residual	12	5576725		
Total	17				Total	17			
Transformation	Square root (x+1)				Transformation	None			
Cochran's test	n.s.				Cochran's test	n.s.			
Pair-wise	BEN: Tetrapod<Natural				Pair-wise	BEN: Tetrapod=Natural			
SuxLo	MDQ: Tetrapod<Natural				SuxLo	MDQ: Tetrapod=Natural			
	SMR: Tetrapod=Natural					SMR: Tetrapod=Natural			

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Gordo siendo un pringadillo, me dijo que me veía con madera de Doctor y aquí estoy escribiendo estas líneas 7 años después. Es un orgullo que un premiado a la *Mejor tesis eskisa* sea tu codirector y espero sinceramente que nuestra relación se alargue por encima de la profesional, ya que estar a su lado siempre es sinónimo de frikismo marino.

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