Do artificial *vs* natural substrates cause a difference in assemblages of peracarids? A case study in the Western Mediterranean basin

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Abstract

The aim of this investigation was to assess the differences in terms of α-diversity, species composition and trophic structure between peracarid assemblages inhabiting artificial hard substrates and those present on natural ones at two sites in the Western Mediterranean Sea. In each one, samples were collected from natural and artificial substrates, and the extracted peracarids were identified to the species level. Each sample was characterised by its Total Abundance, Species Richness, and 1-D Simpson, Shannon, Margalef and Equitability indices. A cluster plot based on the Bray-Curtis coefficient was conducted to detect the presence of distinct assemblages. In addition, the proportion of individuals belonging to each feeding guild was studied. The ecological indices revealed that assemblages from the artificial substrates at the Villaricos site showed lower values of diversity, while they were more diverse at the Calpe site. These results indicated that artificial hard substrates were not always inadequate ground for these animals. The species composition differed between artificial and natural hard substrates in the two studied sites and the trophic structure was also modified, although, in this case, the changes were similar in both sites. However, the difference in both respects seems to be higher between sites than between substrates, evidencing the importance of local scale processes.

Keywords: Hard substrates; Crustacea; Macrobenthos; Trophic structure; Spatial scale.

Introduction

The response of the natural marine communities to anthropogenic disturbances has become a priority research subject in recent years. These perturbations, identified as any human activity that may cause stress to natural populations and assemblages (Benedetti-Cecchi *et al.*, 2001), are rapidly and dramatically increasing (Gittman *et al.*, 2016). One of the best examples can be found in the modification of coastlines (Bulleri & Chapman, 2010). This alteration of the environment is due to shoreline urbanisation combined with the increase in tourism, recreational and commercial activities among others (Bulleri & Chapman, 2010; Melero *et al.*, 2017; Mosbahi *et al.*, 2019). This results in the introduction and proliferation of artificial structures and in the replacement of natural substrates in marine coastal habitats worldwide (Sedano *et al.*, 2019), the so-called shoreline hardening (Gittman *et al.*, 2016). For instance, in various areas of Italy, France and Spain, shoreline hardening exceeds 45% of terrestrial cover (Bulleri & Chapman, 2010). These new hard substrates are usually engineered structures of different categories, such as seawalls, jetties, groynes, breakwaters, or other rock armoured structures (Airoldi *et al.*, 2005). Due to this replacement of natural substrates, dramatic environmental changes occur (Momota & Hosokawa, 2021), resulting in the alteration of the ecosystem functioning (Bustamante *et al.*, 2014) through process of habitat loss, fragmentation and homogenization (Latham *et al.*, 2006; Aguilera, 2018).

These new artificial rocky substrates support distinct assemblages, which are generally considered less biodiverse with low ecological value compared to natural rocky marine habitats (Grasselli & Airoldi, 2021; Sedano *et al.*, 2021; Doods *et al.*, 2022). Most studies have focused on comparing community structures between natural and artificial habitats based on differences in material type (Hartanto *et al.*, 2022), substrate complexity (Evans *et al.*, 2021), substrate inclination (Grasselli & Airoldi, 2021) and orientation among others (Hanlon *et al.*, 2018). Generally, these studies have concluded that artificial structures do not function as real surrogates of natural rocky habitats (Bulleri & Chapman, 2004, 2010; Burt *et al.*, 2009; Sedano *et al.*, 2019). Furthermore, they may be enhancing a lower reproductive success (Moreira *et al.*, 2006). Nevertheless, the consequences of these impacts

in natural habitats have not been widely explored (Airoldi *et al.*, 2005; Moreira *et al.*, 2006; Momota & Hosokawa, 2021). Overall, there is no information on the long-term environmental impacts of these structures (Komyakova *et al.*, 2022). Besides, the effects of artificial structures are not only noteworthy at their placement but may also produce larger-scale impacts through their alteration of ecological connectivity (Airoldi *et al.*, 2005; Bishop *et al.*, 2017).

Many biological indicators haven been used to assess the disturbance by anthropogenic pressures on coastal marine ecosystems (Casazza *et al.*, 2002). The most widely used organisms to describe changes in the marine environment belong to the benthic macrofauna (Pinedo *et al.*, 2007; Mosbahi *et al.*, 2019), as they are sedentary or at least bottom-dependent, have relatively long lifespans, exhibit different tolerance to stress and are mediators of material and energy (Borja *et al.*, 2000; Dauvin *et al.*, 2010). Among the macrofaunal taxa, crustaceans show a ubiquitous distribution in aquatic environments (Fuller *et al.*, 2015) and display a wide range of morphological diversity (Izquierdo & Guerra-García, 2011). Within the crustaceans, the superorder Peracarida includes 53% of the total species (Reaka-Kudla, 2001); among them, the orders Amphipoda, Tanaidacea and Isopoda often represent the most dominant and diverse mobile but also bottom-dependent taxa in many rocky benthic assemblages (Lourido *et al.*, 2008; Sedano *et al.*, 2020; Araújo-Silva *et al.*, 2022).

Peracarids play an important role in marine ecosystems as they are the dominant taxon of hyperbenthic macrofauna, while they are geographically widely distributed (Koulouri *et al.*, 2013; Welborn *et al.*, 2015). They can influence the structure and composition of benthic communities (Duffy & Hay, 2000), and are an important source of food for other benthic and pelagic fauna (Lourido *et al.*, 2008; Padovani *et al.*, 2012). This is attributable to their diverse lifestyles, reproductive and feeding biology and ontogenetic variations (Thiel & Hinojosa, 2009). Most peracarids are bottom-dwelling animals (Izquierdo & Guerra-García, 2011) with versatile feeding strategies (carnivory, surface deposit feeding, filter feeding, omnivory and even foraminiferivory) (Poor & Bruce, 2012; Torrecilla-Roca & Guerra-García, 2012; Guerra-García *et al.,* 2014). Due to this fact, they play a key role in energy flow (Karlson *et al.*, 2007; Dunn *et al.*, 2009). Most of them show narrow ecological ranges and relatively poor dispersion abilities in response to changes in their environment (De la Ossa *et al.*, 2012), so they are widely used as bioindicators in different scenarios, such as pollution or increase of CO_2 and temperature (Chintiroglou *et al.*, 2004; Araújo-Silva *et al.*, 2022).

The main aim of this study was to examine the effect of the introduction of hard substrates of anthropogenic origin on the peracarid assemblages at two sites from the Western Mediterranean Sea, from the point of view of their biodiversity patterns and feeding traits. We hypothesised that α–diversity of the peracarid assemblages will be lower on artificial hard substrates in comparison with natural ones, and that this trend will be repeated with-

in each site. Our second hypothesis was that the species composition and the trophic structure of the assemblages (herbivores, carnivores and detritivores) will also be affected by the type of substrate (artificial and natural) in a similar way within the two selected sites.

Material and Methods

Study area

The present study was conducted along the south-eastern coast of the Iberian Peninsula, belonging to the Western Mediterranean area. Two sites, separated by nearly 250 km and covered by two types of hard substrate (artificial and natural), were selected. At both sites, both types of substrate were located within approximately 500 m.

The first study site was located in Calpe (38.6447000° N, 0.0445000° E), a medium-sized municipality of about 23,000 inhabitants (Fig. 1). Calpe is subjected to high anthropogenic pressure, being a destination for a multitude of aquaculture and tourism companies (Perles-Ribes *et al.*, 2022). To the south, this stretch of coast is restricted by a breakwater formed by loose artificial concrete rocks located in Cala El Raco (Cal-1, artificial type); the second sampling station is located northward, at Cantal Roig Beach and consists of natural conglomerates of rocks (Cal-2, natural type).

The second site was located in Villaricos (34.248242° N, -1.769814° W), a small village of 670 inhabitants (Fig. 1). The coast in this region suffers relatively light human disturbance (López, 2022) and consists of a series of gently stepping rocky areas alternating with little sandy beaches. The studied cove (López, 2019) is limited on its southern side by a wharf built of conglomerate rock extracted from nearby quarries (Vill-1, artificial type) and on its northern side by a group of flat outcrops of schist rock (Vill-2, natural type).

At both sites, dense turfs mainly composed of corallinaceous (*Ellisolandia elongata* (J. Ellis and Solander) K. R. Hind and G. W. Saunders, 2013) and fleshy (*Jania rubens* (L.) J. V. Lamouroux, 1816 and *Padina pavonica* (L.) Thivy) algae covered both artificial and natural substrates.

Sampling methods

Sampling was conducted in late summer (September of 2014 in Calpe and August of 2015 in Villaricos), coinciding with the highest phytal development and faunal population densities (Thrush *et al.*, 2011) and aiming to minimise the influence of seasonal trends (Bueno *et al.*, 2016). At each site, four haphazardly selected samples from the artificial substrate and four from the natural one, were collected. They were labelled based on the type of substrate (artificial = 1 and natural = 2) and the number of samples (numerical codes 1, 2, 3 and 4). Samples were collected by scraping off a 100 cm² area of rocky bottom from the littoral depth, such a sample size has proved to be representative for studies on peracarid populations
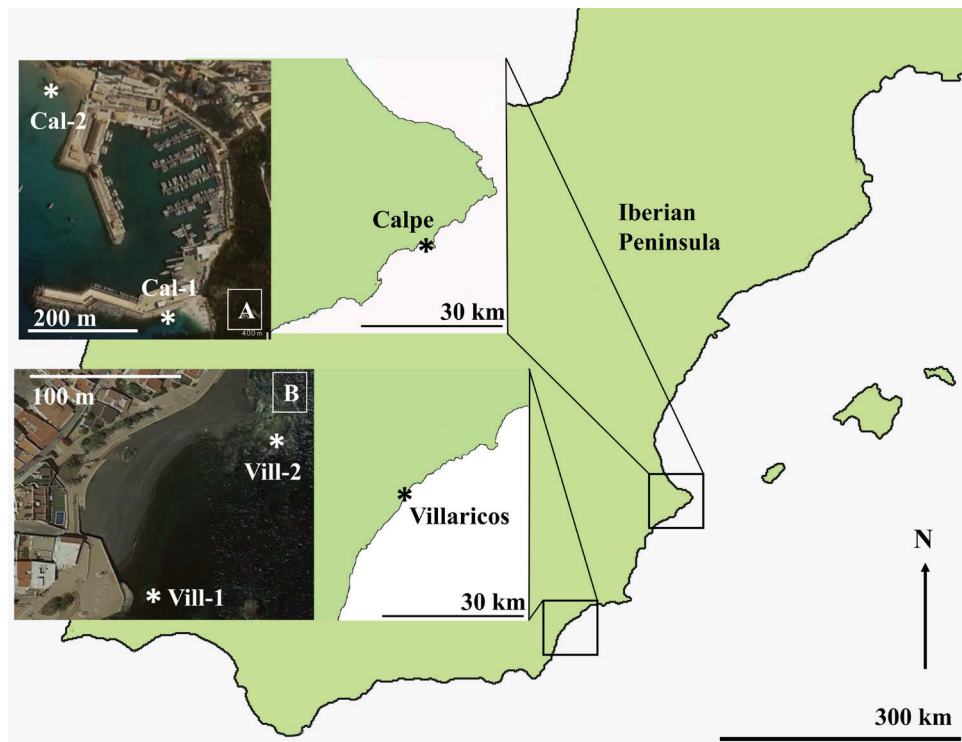
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Fig. 1: Map of south-eastern Spain showing the collection sites of this study. A) Detail of Calpe, B) Detail of Villaricos. Aerial photograph by PNOA ceded © Instituto Geográfico Nacional, Spain.

from other locations (Bueno *et al.*, 2016). The scraped material was preserved in 70% ethanol and stored in hermetic plastic bags. This material was examined under a dissecting microscope in the laboratory, and the organisms were classified into higher taxonomic groups.

Crustacean specimens were classified, and those belonging to Peracarida were preserved while the rest were discarded. In order to create a species/abundance matrix reflecting the number of individuals in each sample, all the specimens were identified to the species level whenever possible. It was achieved mainly by following the Mediterranean amphipod inventories by Ruffo (1982; 1989; 1993; 1998), as well as the species reports provided by Bellan-Santini & Costello (2001a, b, c) and other references, such as Guerra-García *et al.,* (2001a, b, c). For analyses of the feeding traits, the species abundance matrix was coded into three feeding guilds (carnivores, herbivores, and detritivores). Species were assigned to guilds according to Poore & Bruce (2012), Torrecilla-Roca & Guerra-García (2012) and Guerra-García *et al.* (2014).

Data analyses

Differences between the peracarid assemblages inhabiting the hard substrates of different types (Natural and Artificial) of the two sites (Calpe and Villaricos) were tested by means of univariate and multivariate statistical analyses. Apart from the species/abundance matrix, each sample was characterised by its α–diversity, computing the following ecological descriptors: Total Abundance, Species Richness, and 1-D Simpson, Shannon, Margalef and Equitability indices. Relative abundance (species abundance/total species peracarid abundance) was calculated for all the species in every sample, and the mean value was then calculated for the entire matrix. Samples were also characterised by the proportion of peracarid individuals belonging to each feeding guild.

Significant differences between descriptors of the samples were investigated by applying a two-way fixed-factor ANOVA test (Underwood, 1997), followed by a *post-hoc* Tukey's test. "Site" was considered to be factor 1 (two levels: Villaricos and Calpe), and "Type" was factor 2 (two levels: Artificial and Natural Substrate); both factors were orthogonal and fixed. The significance level was set at $p < 0.05$ (Southwood & Henderson 2000). Significant differences for a given factor or interaction between factors were obtained. Prior to this analysis, the normal distribution of all the descriptors was checked by means of a Shapiro-Wilk W test, rejecting the normal distribution at a significance level of $p < 0.05$ (Underwood, 1997; Cacabelos *et al.*, 2016).

Aiming to detect the presence of different assemblages between sites and types of substrate, another analysis was conducted. A second matrix was made reflecting the similarity between the species composition of the samples using the Bray-Curtis index as a measure of distance. Prior to this analysis, all abundance values were log (x + 1) transformed to avoid overestimating the influence of the most abundant species (Clarke & Warwick, 2001) and species present only in a single sample were dismissed. For graphical representation of the results, a cluster plot, applying the UPGMA agglomerative algorithm, was created. In case more than one assemblage was detected, differences in their species composition were tested using a two-way PERMANOVA test run in the Bray-Curtis similarity matrix, obtaining p-values from 9999 permutations of residuals under a reduced model and considering p <

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0.05 as a level of significance (Anderson, 2001). For this analysis, "Site" was factor 1 (with two levels: Villaricos and Calpe) and "Type of substrate" was factor 2 (with two levels: Artificial and Natural); both factors were orthogonal and fixed. All the statistical analyses were conducted using the software package PAST 4.08 (Hammer *et al.*, 2001).

Results

A total of 3233 specimens of peracarids, belonging to 27 species and 13 families, were collected (Supplementary Material, Table S1). Six species achieved mean relative abundances over 10%, namely the tanaidacean *Hexapleomera bultidactyla* (mean relative abundance 44.25 ± 21.89%); the amphipods *Elasmopus pocillimanus* (42.69 ± 21.12%), *Jassa marmorata* (32.8 ± 16.23%), *Ampithoe ramondi* (12.50 ± 6.18%) and *Hyale stebbingi* (12.31 ± 6.09%); and the isopod *Ischyromene lacazei* (14.87 ± 7.36%). Of these ones, only *E. pocillimanus* occurred in all the samples. Of the total number of species, nine were found only in the Calpe site (*Anthura gracilis, Carpias stebbingi, Caprella hirsuta, Hyale pontica, Protohyale (Boreohyale) camptonyx, Protohyale (Protohyale) schmidtii, Quadrimaera inaequipes, Stenothoe monoculoides* and *Zeuxo holdichi*), while seven were exclusive to the Villaricos site (*Dynamene magnitorata, Elasmopus brasiliensis, Gnathia vorax, I. lacazei, Janira* sp., *J. marmorata, Jassa* sp. and *Monocorophium sextonae*). In addition to those mentioned, six species (*D. magnitorata, Janira* sp., *Jassa* sp., *M. sextonae, P. camptonyx* and *Q. inaequipes*) appeared in only one sample, so they were considered accidental and dismissed from the statistical analysis.

The raw values of the ecological descriptors calculated from the species/abundance matrix are presented in Table S2 of the supplementary material. Their values are presented as mean ± standard deviation, are presented in Figure 2. The largest difference regarding the ecological descriptors can be observed in the Total Abundance and to a lesser extent, in the Species Richness and other values of α-diversity. The number of individuals ranged from 436 at Vill-2.3 to 48 at Cal-1.1, mean value ± standard deviation for abundance was 202.19 ±119.93. Regarding the substrate types, the natural ones showed a higher abundance with respect to the artificial ones at both sites. Sample Vill-2.2 harboured the highest Species Richness (14 species), and Cal-2.2 the lowest (4 species); the mean value was 9.43 ± 2.68. In reference to the number of species, in Villaricos the highest value occurred in the natural substrate, while in Calpe, it was observed in the artificial one. The Simpson index ranged from 0.85 at Cal-1.2 to 0.48 at Cal-2.2 (mean value of 0.70 ± 0.10), Shannon index ranged from 2.07 at Cal-1.2 to 0.76 at Cal-2.2 (mean value of 1.56 ± 0.34), Margalef index ranged from 2.33 at Cal-1.2 to 0.62 at Cal-2.2 (mean value of 1.64 ± 0.46), and Equitability ranged from 0.88 at Cal-1.4 to 0.54 at Vill-2.1 (mean value of 0.71 ± 0.10). The Simpson, Shannon and Margalef indices, as well as
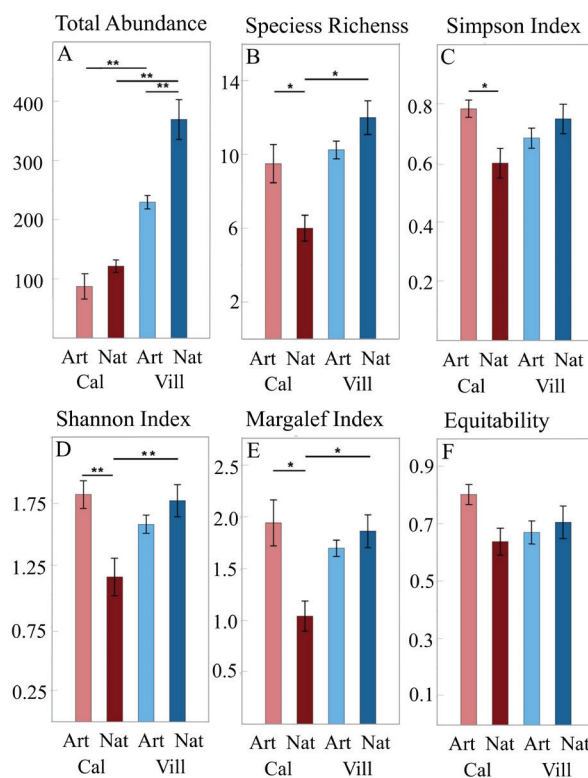

Fig. 2: Ecological descriptors of each group of samples. Results are expressed in mean ± standard deviation of mean (two-way ANOVA followed by Tukey *post hoc* test, *: p < 0.05, **: p < 0.01). A) Total Abundance, B) Species Richness, C) Simpson index, D) Shannon Index, E) Margalef Index, F) Equitability. Abbreviations: Art, artificial substrate (type). Cal, Calpe (site). Nat, natural substrate (type). Vill, Villaricos (site).

Equitability, followed a similar pattern regarding the type of substrate. They reached higher mean values in the artificial substrate in Calpe than in Villaricos, where higher values of the same indices were presented in the natural substrate of both sites.

The results of the two-way ANOVA analyses (Table 1) showed that differences between types of substrate and sites were significant only for Total Abundance. Species Richness was significantly different between sites, while the Shannon and Margalef indices were significantly different between types of substrate. In turn, the Simpson and Equitability indices did not differ significantly either between sites or types of substrate. However, the results of the Tukey's post-hoc test showed a more complex situation (Fig. 2). Total Abundance was significantly different between the two types of substrate in Villaricos, the natural subtrates and the artificial ones from both sites. In turn, Species Richness and the Shannon and Margalef indices differed significantly only between the natural substrate from the two sites and the two types of substrate from Calpe. Finally, the Simpson Index was only significantly different between the two types of substrate from Calpe.

Based on their species composition, the samples collected from each site formed separated groups in the Bray-Curtis similarity cluster plot (Fig. 3). Moreover, all samples from the same type of substrate were grouped to-

Table 1. Results of the two-way ANOVA test for ecological indices. *: p < 0.05. **: p < 0.01. n.s.: not significant. Abbreviations: MS, mean square; df, degrees of freedom.

Source	df	Total Abundance		Species Richness		Simpson Index	
		MS	F	MS	F	MS	F
Site	1	152295.000	83.43 **	45.563	17.220 **.	0.003	0.374 n.s.
Type	1	30363.100	16.63 **	3.063	1.157 n.s.	0.014	2.028 n.s.
Site x Type	1	11183.100	6.126 *	22.563	10.420 **	0.062	8.867 *
Residual	12	1825.440		2.646		0.007	
Total	15						
Shapiro-Wilks test		0.928 n.s.		0.971 n.s.		0.949 n.s.	
Transformation		None		None		None	

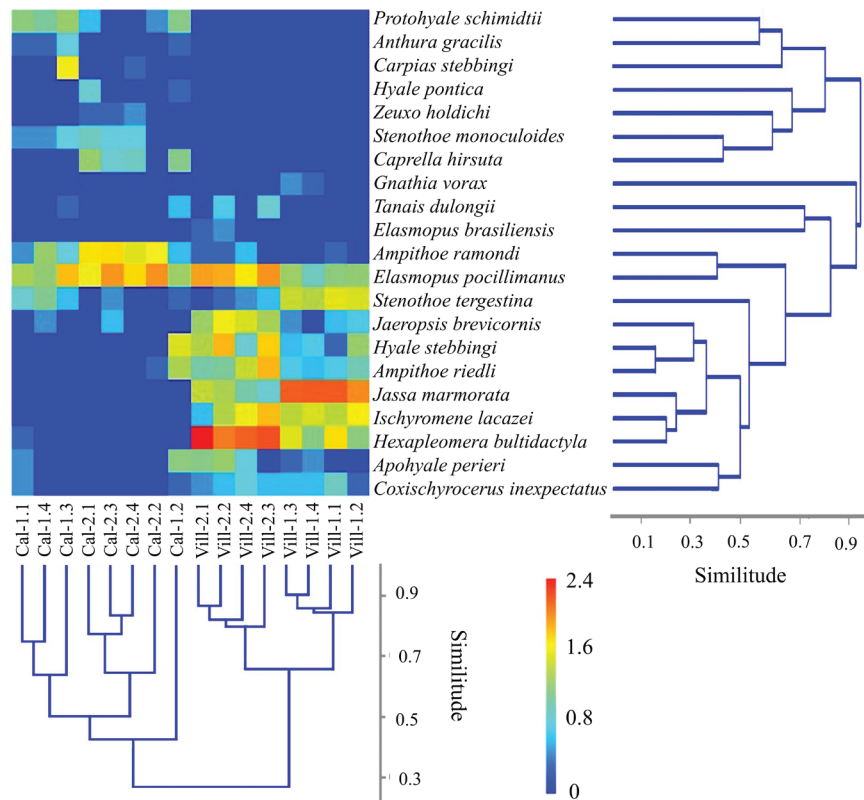| Source	df	Shannon Index		Margalef Index		Equitability	
		MS	F	MS	F	MS	F
Site	1	0.135	2.439 n.s.	0.333	3.270 n.s.	0.004	0.509 n.s.
Type	1	0.216	3.897 *	0.542	5.319 *.	0.017	1.998 n.s.
Site x Type	1	0.703	12.710 **	1.138	11.160 **	0.040	4.791 *
Residual	12	0.055		0.102		0.008	
Total	15						
Shapiro-Wilks test		0.962 n.s.		0.967 n.s.		0.955 n.s.	
Transformation		None		None		None	

Fig. 3: Bray–Curtis similarity cluster analysis based on species composition of peracarid assemblages across samples. Abbreviations: Vill-1, Villaricos (site) artificial substrate (type). Vill-2, Villaricos (site) natural substrate (type). Cal-1, Calpe (site) artificial substrate (type). Cal-2, Calpe (site) natural substrate (type).

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Table 2. Results of the two-way PERMANOVA test run in Bray-Curtis similarity matrix for species composition. *: p < 0.05. **: p < 0.01. [n.s.]: not significant. Abbreviations: MS, mean square; df, degrees of freedom.

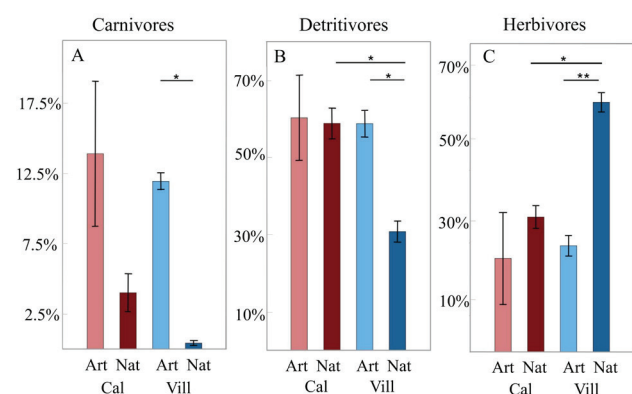| Source	df	MS	Pseudo-F
Site	1	1.550	18.091 **
Type	1	0.358	4.175 *
Interaction	1	0.261	3.047 *
Residual	12	0.086	

Fig. 4: Composition of trophic groups of each group of samples. Results are expressed in mean ± standard deviation of mean (two-way ANOVA followed by Tukey *post hoc* test, *: p < 0.05, **: p < 0.01). A) Carnivores, B) Detritivores, C) Herbivores. Abbreviations: Art, artificial substrate. Cal, Calpe (site). Nat, natural substrate. Vill, Villaricos (site).

gether within each site cluster, except for sample Cal-1.2, indicating that natural and artificial substrates harbour distinct assemblages irrespective of the geographical location. The same analysis showed a clear association between specific species and substrates. Thus, *J. marmorata* seem to be strongly associated with the artificial substrate in Villaricos as well as *Stenothoe tergestina*. However, the latter species appeared less associated with Villaricos and slightly associated with the artificial substrate in Calpe. The species *H. bultidactyla* and *E. pocillimanus* were strongly associated with the natural substrate in Villaricos, but the latter was also associated with both substrates in the Calpe site. In turn, *A. ramondi* was asso-

ciated with the natural substrate from Calpe. The results of the two-way PERMANOVA analysis revealed that the difference of the peracarid assemblages was significant both between sites and types of substrate (Table 2).

The raw values of the trophic groups are presented in Table S3 of the supplementary material. The composition of trophic groups showed a wide variation (Fig. 4). The proportion of carnivores ranged from 25.45% at Cal-1.4 to 0.00% at Cal-2.2 and Vill-2.1. Regarding the different substrates, the artificial ones from both sites showed higher numbers of carnivores with respect to the natural ones. The mean value for carnivores was 7.57 ± 7.49. Sample Cal-1.3 harboured the highest proportion of detritivores (85.93%) and Vill-2.3 the lowest one (25.00%). In reference to the type of substrate, high number of detritivores occurred in the artificial substrates in Villaricos, while there were not remarkable differences in Calpe. The mean value for detritivores was 52.21 ± 17.00. The highest proportion of herbivores was found at Vill-2.1 (70.49%) and the lowest at Cal-1.3 (4.44%). For this guild, the highest values were achieved in the natural substrates from both sites. The mean value for herbivores was 40.22 ± 21.35. The results of the two-way ANOVA analyses showed that differences in the percentage of detritivores and herbivores were significant for both factors, Site and Type, while the percentage of carnivores was significantly different only between the types of substrate (Table 3). According to Tukey's test (Fig. 4), the percentage of detritivores and herbivores was significantly different between both substrates in Villaricos and between the natural substrates from both sites. The percentage of carnivores was only significantly different between the two substrates at the Villaricos site.

Table 3. Results of the two-way ANOVA test for trophic guilds. *: p < 0.05. **: p < 0.01. [n.s.]: not significant. Abbreviations: MS, mean square; df, degrees of freedom.

Source	df	Carnivores		Detritivores		Herbivores	
		MS	*F*	MS	*F*	MS	*F*
Site	1	30.791	1.062 [n.s.]	873.217	5.540 *	1231.90	6.639 *
Type	1	459.674	15.850 **	866.817	5.500 *.	2588.88	13.950 **
Site x Type	1	2.610	0.900 [n.s.]	703.297	4.462 [n.s.]	791.606	4.266 [n.s.]
Residual	12	29.004		157.614		185.549	
Total	15						
Shapiro-Wilks test		0.891 [n.s.]		0.966 [n.s.]		0.935 [n.s.]	
Transformation		None		None		None	

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Discussion

In terms of α–diversity, values for all indices seem to be higher in the natural substrate than in the artificial one in Villaricos, which was expected from previous analysis testifying that artificial substrates degrade biodiversity in the marine environment (Aguilera *et al.*, 2014; Sedano *et al.*, 2019; Momota & Hosokawa, 2021). However, it cannot be affirmed that the peracarid assemblage on artificial substrate is always poor in terms of diversity, as diversity indices were significantly higher in the artificial substrate than in the natural one in Calpe. The observed low α–diversity values in the natural substrate in Calpe could be attributable to another anthropogenic impact (Perles-Ribes *et al.*, 2022). According to Bonnici *et al.* (2018), the rocky shores located close to overcrowded human settlements seem to be under strong human-mediated pressure and it may have significant effects on the nearby benthic assemblages (Crowe *et al.*, 2000). For instance, Gacia *et al.* (2007) described the water quality as the major driver for structuring the epibiotic assemblages on the Catalan coast, for both natural and artificial substrates. Thus, local environmental variables such as anthropogenic pressure could be shaping peracarid populations specifically within sites (Gacia *et al.*, 2007; Sedano *et al.*, 2019), by impoverishing the natural hard substrates of Calpe.

Most of the previous studies have pointed out that artificial substrates do not act as natural surrogates (Bulleri & Chapman, 2004; 2010; Burt *et al.*, 2009) due to differences in material type, substrate complexity, inclination, orientation and wave exposure among others (Hanlon *et al.*, 2018; Evans *et al.*, 2021; Grasselli & Airoldi, 2021; Hartanto *et al.*, 2022). However, few exceptions have evidenced that artificial substrates are not generally ecologically poor (Gacia *et al.*, 2007; López, 2022; Baxter *et al.*, 2023). For instance, artificial rocky substrates from locally quarried stones, as in the Villaricos site, are generally considered beneficial for colonization by marine organisms (Sempere-Valverde *et al.*, 2018; MacArthur *et al.*, 2019). This was consistent with the fact that the artificial rocky concrete blocks of the Calpe site showed a lower Total Abundance in comparison to the artificial rocky stones from nearby quarries at the Villaricos site. Thus, it seems that peracarid assemblages were affected by different rock compositions from the studied sites. In addition, similarly dense turfs of algae that covered both the natural and artificial substrates of the present study have been proven to structure peracarid communities (Carvalho *et al.*, 2018; Sedano *et al.*, 2020).

Several studies in the Mediterranean Sea have already reported no significant differences in diversity indices between artificial and natural hard substrates and between different sites (Bonnici *et al.*, 2018; Sedano *et al.*, 2019; 2020). These studies support the results obtained here for the Calpe site, where the artificial substrate reached relatively high diversity indices. The presence of assemblages on artificial hard substrates being more diverse than their counterparts on natural ones has been attributed to different drivers. For instance, the presence of opportunistic species that could colonise readily rocky artificial substrates has been proposed (Bacchiocchi & Airoldi, 2003; Sedano *et al.*, 2019). Sedano *et al.* (2020) attributed the presence of a significantly higher number of taxa on artificial hard substrates in comparison with the nearest natural rocky shores in some areas of southern Spain to stochastic variability in the distribution of the epifauna assemblages on the artificial structures. However, results varied depending on the site, indicating that local environmental and anthropogenic factors could be more deterministic than substrate type in structuring benthic assemblages (Bulleri, 2005; Cacabelos *et al.*, 2016; Baxter *et al.*, 2023).

The results of our analyses showed significant differences in the species composition between natural and artificial rocky substrates within the two selected sites, suggesting that the type of substrate somehow influenced the settlement of peracarids. The only exception was the sample Cal-1.2, where a high abundance of four species (*Ampithoe riedli*, *C. hirsuta*, *H. stebbingi* and *Tanais dulongii*) was found. These species have been previously recorded as very abundant in the region (Guerra-García & Izquierdo, 2010; Izquierdo & Guerra-García, 2011; Guerra-García *et al.*, 2012). It is noteworthy that no exclusive taxa for each substrate was found in any of the sites. In fact, the proximity between natural and artificial substrates may somehow operate in terms of species sharing and influence species composition (Momota & Hosokawa, 2021). In both sites, the two types of substrate were located within approximately 500 m; so, the natural rocky assemblages might be providing the artificial ones with new individuals, in a process known as "nourishment" (Gacia *et al.*, 2007).

In the present study, dissimilarities were also found regarding the trophic structure and the pattern significantly differed among sites and types of substrate. In these respects, assemblages from both sites behaved in a similar way indicating a connection between species distribution and their feeding traits (Aslan-Cihangir & Pancucci-Papadopoulou, 2011; Momota & Hosokawa, 2021). So, it seems that changes in the species composition of the community can be mirrored by a shift in the proportions of the trophic groups. Sedano *et al.* (2020) observed differences in the trophic structure when comparing artificial and natural substrates in other areas of the Mediterranean Sea. As in our study, these differences were due to changes in the species composition of the amphipod community and not to changes of the feeding strategy of any given species. However, modifications of the trophic preferences of some of the herein reported species have been reported when comparing different habitats. Vázquez-Luis *et al.* (2012) pointed out that some herbivorous species such as *A. ramondi* and *Dexamine spiniventris* can modify their feeding habits due to changes in the food availability related to the spread of invasive algae and used detritus as an alternative source. In another study, Torrecilla-Roca & Guerra-García (2012) studied the feeding habits of *Hyale perieri*, which is associated with *Fucus spiralis* and reported a decreasing tendency in the amount of alga consumed in summer and a slight increase in crustacean prey.

It should be noted that our results highlighted high-

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er variability between sites than between types of substrate and implied that there was greater variability on larger spatial scales. This observation indicates that biotic or abiotic drivers acting at the local scale somehow influenced the settlement of the peracarid populations and contradicts previous findings implying that variability is usually larger on small spatial scales (Fraschetti *et al.*, 2005). These previous findings have been assumed that similar ecological processes, acting on small spatial scales, produce similar patterns of variability on large spatial scales (Dal Bello *et al.*, 2016). However, Sedano *et al.* (2019) found higher variability among different areas in the Mediterranean Sea than among natural and artificial rocky substrates within the same area, hence local populations could have been established depending on local environmental conditions. Besides, other factors (environmental quality, biological interactions, connectivity, etc.) have been proposed as possible drivers of the variability found on large spatial scales (Sedano *et al.*, 2020). Underwood & Chapman (1996) identified both small-scale differences (from centimetres to metres) and large-scale differences (hundreds of metres alongshore) in intertidal invertebrates in Sydney, while large spatial scale variability (over 1000 kilometres) has been demonstrated for the macrofauna of the Mediterranean basin diversity (Baldrihui *et al.*, 2014). Even higher variability was found comparing sessile benthos and invertebrates on rocky shores when measured at scales of 100 metres to tens of kilometres away (Benedetti-Cecchi, 2001; Sedano *et al.*, 2019). What arises from this is the need to identify relevant scales of natural variability prior to any monitoring. Thus, considering this natural variability the locations should not be separated by more than a few kilometres in order to correctly and avoid biased results. Despite this, in our study, significant differences were still found between both types of substrate within sites, so processes acting on a broader spatial scale, such as the specific environmental conditions of each area, wave exposure, orientation, coastal slope, or even coastal geomorphology, appeared to be influencing more strongly than biotic processes acting on a small spatial scale, such as grazing, competition or facilitation.

In conclusion, the introduction of hard substrates of anthropogenic origin into the studied sites influenced the peracarid assemblages, but the results obtained varied depending on the site. Regarding the hypotheses raised, the study of α–diversity indices of the peracarid assemblages associated with natural *vs* artificial rocky substrates revealed an inconsistent pattern; artificial substrates at the Villaricos site seemed not to function as surrogates, while the diversity indices at the Calpe site reflected rather the contrary. This observation may be the result of the intense anthropogenic pressure on the natural hard substrates at the Calpe site. Thus, the first hypothesis was not supported. However, our results support the second hypothesis. The species composition differed between artificial and natural rocky substrates, but no exclusive species were found either from natural or artificial substrates. The trophic structure was also modified between sites and types of substrate, while the changes were similar in the two

sites. These differences may be due to changes in species composition that triggered a shift in the proportions of the trophic groups. However, the variability of the results turned out to be greater between sites than between substrates, indicating that variability is higher on larger scales than on smaller scales in our case. Thus, generalising consistent biodiversity patterns in the study of the effects of introducing artificial rocky substrates over biogeographic scales may not be suitable and may need to be studied locally (on scales lesser than a few kilometers away).

Acknowledgements

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. List of peracarid species collected in all the samples.

Table S2. Raw values of the ecological descriptors. Abbreviations: Vill-1, Villaricos (site) artificial substrate (type). Vill-2, Villaricos (site) natural substrate (type). Cal-1, Calpe (site) artificial substrate (type). Cal-2, Calpe (site) natural substrate (type). SD, standard deviation.

Table S3. Values of trophic guilds in all the samples. Abbreviations: Vill-1, Villaricos (site) artificial substrate (type). Vill-2, Villaricos (site) natural substrate (type). Cal-1, Calpe (site) artificial substrate (type). Cal-2, Calpe (site) natural substrate (type). SD, standard deviation.