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Unexpected Biotic Homogenization Masks the Effect of a Pollution Gradient on Local Variability of Community Structure in a Marine Urban Environment.

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Abstract. Urbanization of coastal habitats, often exemplified by harbors and marinas, has led to various ecological paradigms, questioning the functioning of these new ecosystems. In the present study we investigated, in a large Mediterranean harbor, whether spatial variation of pollution is present and if this variability drives the structure of the sessile community. We hypothesized locations to have significantly different communities, based on the assumption on the occurrence of environmental gradients of pollution that would constitute selective filters. Three distinct community types were identified in June, coinciding with spatially variable contaminants in sediments. We observed then an unexpected shift of the community between June and August associated to a sharp decrease in biodiversity and a decline of most species, masking the effects of local variation and thus leading to the homogenization of the biodiversity within the harbor. This shift coincided with successive heatwaves (the longest lasting 13 days over 25°C, with a thermal peak at 28°C) which might potentially be associated with a die-off in the harbor communities, regardless of location.

Keywords: fouling communities, harbor, Marina, local variation, pollution, heat-wave, introduced species

Introduction

Urbanization of coastal habitats has led to various ecological paradigms, questioning the functioning of these new ecosystems (Bulleri, 2006; Bulleri and Chapman, 2010). At the forefront, harbors and marinas have been used as models, representative of marine urbanization. A particular focus has been accorded to the role of introduced species, established and abundant in these environments (Mineur et al., 2012). The number of species introductions rose exponentially since the beginning of marine trade traffic, a trend which will continue in the coming decades (Carrasco et al., 2017; Levine and D'Antonio, 2003; Sardain et al., 2019; Seebens et al., 2016). Non Indigenous Species (NIS), if they become invasive, can have high ecological impacts, completely restructuring the ecosystems which can lead to the loss of biodiversity and ecosystem services (Johnston et al., 2015; Pejchar and Mooney, 2009; Walsh et al., 2016). This loss of services and the investment to combat these species can also cause severe economic impacts, ranging from hundreds of millions to tens of billions dollars for individual countries (Diagne et al., 2021; Jardine and Sanchirico, 2018).

Artificial structures constitute a new substratum to be colonized by sessile fauna, but diverging from natural habitats with distinct communities and altered diversity (Chan and Briski, 2017; Glasby et al., 2007; Mineur et al., 2012; Oricchio et al., 2016). Diversity at all scales is generally regarded as a contributor to biotic resistance against introduced species (Arenas et al., 2006; Elton, 1958; Gestoso et al., 2018; Megina et al., 2016). Associated with the proximity to the primary vector of species introductions (ships' hull and ballast waters) it makes these substrates highly susceptible to marine introduced species (Ferrario et al., 2017; Glasby et al., 2007; Megina et al., 2016; Oricchio et al., 2016). NIS, especially in urban habitats, are regarded as a major actor of global homogenization of biodiversity (Alberti, 2015; Mckinney and Lockwood, 1999; Mineur et al., 2012; Tsirintanis et al., 2022) and are among the major causes of species extinctions (Blackburn et al., 2019; Clavero and García-Berthou, 2005; Mckinney and Lockwood, 1999).

High ambient pollution in Persistent Organic Pollutants (POPs), Polycyclic Aromatic Hydrocarbons (PAHs) and Elemental Trace Metals (ETMs) constitutes strong selective filters which profoundly affect local communities, potentially favoring introduced species and leading to strong environmental patchiness (Gauff et al., 2022a; Je et al., 2004; Kenworthy et al., 2018b; Oricchio et al., 2016). Copper, which is used as active component in many antifouling coatings of ships, has been shown to be a major selective agent in harbor environments and seems to favor introduced species, due to their higher tolerance (Canning-Clode et al., 2011; Osborne and Poynton, 2019; Piola et al., 2009). This selective pressure can lead to differential resistance among populations of the same introduced species (Piola and Johnston, 2006) and has been observed to have an effect on populations separated by short distances (~ 100 m; Gauff et al., 2022a). Local adaptation as a response to such selective pressure, can however be impaired by larger scale pulse disturbances exerting identical pressure on the studied environments, favoring genotypes not linked to the original pressure which can homogenize the local populations (Colautti and Lau, 2015; Kawecki and Ebert, 2004). Anthropic pulse-disturbances in urban habitats like pulse-pollution (Johnston et al., 2002; Johnston and Keough, 2002, 2000) or marine heat waves (Castro et al., 2021; Smale et al., 2019, 2015) have been demonstrated to have drastic impacts on settled communities and together with introduced species are regarded as contributors to global homogenization of biodiversity (Firth et al., 2016; Mckinney and Lockwood, 1999; Waldock et al., 2018).

Previous studies showed that, in some harbors, pollution may be organized as gradient with maximal pollution in the inner parts of the harbor and less strong pollution at the entrance (Gauff et al., 2022a; Je et al., 2004; Kenworthy et al., 2018b; Ryu et al., 2011). Communities are organized along these gradients and display thus high intra-harbor variability, that can be greater than inter-harbor variability when comparing the same functional areas (Je et al., 2004; Kenworthy et al., 2018b; Ryu et al., 2011). In the present study we investigated, in a large Mediterranean harbor, how spatial variation of pollutants may drive the structure of the sessile community. In accordance with previous studies, we expected 1) a spatial variability of pollution with higher pollution at the inner part of the harbor associated to 2) a variability of community structure with 3) lower biodiversity at the inner location. Our experiment however coincided with unexpected extreme heat events, which could, as larger scale disturbance, reduce this observed variability.

Material and Methods

Study site

We focused on the Vieux Port de Marseille, a recreational marina with approximately 3200 boat moorings and zones dedicated to careening activities, artisanal fisher boats and short distance ferry transports. The high number of boats and the multiplicity of maritime activities renders this site a key example of human disturbance in anthropized habitats. Within this harbor three locations were chosen to show intra-harbor variability of the environment and the associated community. The locations were oriented on a hypothetic gradient of anthropic disturbance from the entrance to the inner part of the harbor (Fig. 1; Je et al. 2004; Kenworthy et al. 2018b).

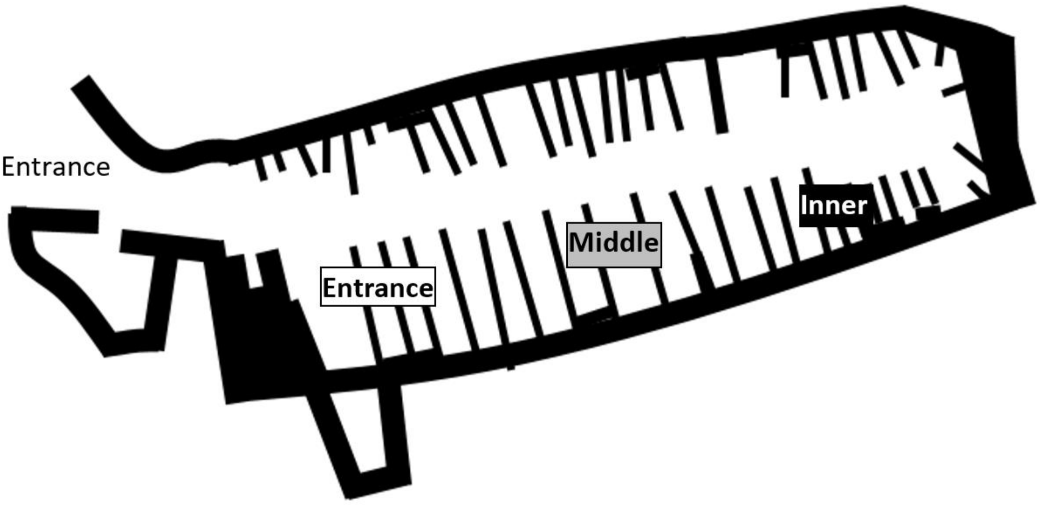

Fig. 1: Site of the Vieux Port de Marseille. The three study locations are indicated.

Environmental variables

Per location, three surface sediment samples (depth ranged from 3 - 7 m) of approximately 0.4 kg were taken for Persistent Organic Pollutant analysis, including PolyChlorinated Biphenyls (PCBs), Polycyclic Aromatic Hydrocarbons (PAHs) and the most frequent pesticides (see Table 1). Five more samples were sampled for quantifying Metallic Trace Elements (MTEs). Samples were frozen and lyophilized before analysis.

The PCBs and pesticides assessment method has been described in detail in the supplementary material of Gauff et al. (2022b) and in Wafo et al. (2006). We quantified 33 individual PCB congeners which include molecules targeted by the International Council for the Exploration of the Sea (ICES). The targeted pesticides can be seen in Table 1. PAH quantification of all 16 PAH targeted by the US Environmental Protection Agency (USEPA) priority list (Table 1, US EPA 2014), was conducted following Sarrazin et al. (2006), Ratier et al. (2018) and Dron et al. (2019) and is described in detail in the supplementary material of Gauff et al. (2022b).

Samples for Metallic Trace Elements (MTEs) quantification were dissolved in a three-acid solution (HCl, HNO_3, HF; all Suprapur grade). The analysis was conducted with a Sector Field Inductively Coupled Plasma Mass Spectrometry (SF-ICP-MS; ELEMENT XR, ThermoElement) as described in Jacquet et al. (2021). The spectrometer was calibrated with standard solutions and an external calibration method using Indium as internal standard. Dissolution procedure efficiency and SF-ICP-MS measurement quality were verified by the determination of concentrations of target elements in Certified Reference Materials (MESS-4, SLRS-5, SLEW-3 and CASS-5).

Water temperature at 1 m depth was logged at each location with a HOBO® (Onset®) TidbiT v2 Water Temperature Data Logger. We used a 15-minute measure interval for the whole duration of the experiment (135 days). We used the temperature data from the SOMLIT (Service d'Observation en Milieu Littoral; www.somlit.fr; consulted 30th Nov 2021) surveillance station at Marseille: Frioul (11) at surface level from mid-June to end of August for the years 1990 to 2021 as reference to compare our measurements. An extreme heat event would constitute any situation where temperatures exceed the 90th percentile of these 30 years of historic data ($T > 24.7°C$), potentially constituting a heat wave if the event lasts for at least 5 days (Hobday et al., 2016). We allowed for a slightly higher temperature in the marina and fixed the threshold at 25°C.

Experimental design

At each location, 10 Correx® Polyethylene panels (0.2 x 0.2 m) were placed horizontally at a constant depth of 1 m on the entirely shaded underside of floating pontoons in April 2019. The distance of the panels to the seafloor varied among locations, between 3 and 7 m. After two months (65 days, June 2019), allowing sessile communities to settle, 5 panels per location were randomly sampled. The stress on communities during handling was minimized as much as possible and all manipulations were done underwater and in shaded conditions. After two additional months (70 days more, August) the remaining 5 panels per location were sampled.

For both dates, the destructively sampled panels were analyzed in the laboratory. A 144-point grid was superimposed on the panels (stratified point design) and at each point all species were counted. This allowed for an optimal resolution for species contributing to at least 5% cover (~ 0.4 points cm^{-2}; Taormina et al., 2020). If one species overlapped with another, both were noted to account for epibionts as well as the different strata of the community. Species were identified to the lowest taxonomic level possible (Brunetti and Mastrototaro, 2017; Hayward and Ryland, 1995; Riedl, 1983; Zabala and Maluquer, 1988).

Statistical analyses

Contaminant data were compiled in a table with the individual contaminant name, its family, and its mean concentration for all three locations along with standard deviation. We used uniformly a Kruskal-

Wallis test (R version 4.0.3; R Core Team 2020) to test for significant differences between locations as conditions for parametric tests were not respected for all contaminants. As numerous contaminants were tested for differences between sites we adjusted the p-value for each contaminant category (MTEs, PAHs, PCBs, Pesticides) with a Benjaminji-Hochberg correction to avoid false positives. Reference values given by the Canadian sediment quality guidelines and by the US Environmental Protection Agency are indicated for all contaminants (CCME, 1999; US EPA, 2005). For MTEs an additional sediment quality category by Guerra-García et al. 2021 is indicated. To avoid problems arising from high multicollinearity, further analysis were conducted using latent variables (Dormann et al., 2013). The contaminant matrix was submitted to a CCA from the 'vegan' R package (version 2.4-6; Oksanen et al. 2018) and centroid coordinates were extracted. The centroid CCA1 value (Axis 1 explained 78% of variability) was computed into a 2-degree orthogonal polynomial for use as contamination weight (Cont.wt1, Cont.wt2).

All community data were analyzed in 'vegan'. The community matrix derived from the destructive sampling containing the multi strata cover of all present species for each panel was transformed into a Bray-Curtis dissimilarity matrix used in a nMDS comparing panels from the 3 locations in June and August. Multivariate homogeneity of groups (Date : Location) was verified via the 'betadisper' function of the R package 'vegan' (Oksanen et al., 2018). A PERMANOVA (10^5 permutations) tested for the effect of date, location as well as their interaction on community structure. A second PERMANOVA (10^5 permutations) was conducted by considering the previously computed contamination weight (Cont.wt) as quantitative variable replacing the categorical location. The model tested the effect of date, contamination weight, as well as their interaction for both polynomial degrees (see Table 3). A subsequent pairwise PERMANOVA (10^5 permutations) from the 'pairwiseAdonis' R package (version 0.3; Martinez Arbizu 2019) including a Benjamini-Hochberg correction was conducted to spatially and temporally compare individual locations (Benjamini and Hochberg, 1995). For each panel, species richness, the Shannon-Weaver index as well as the Pielou evenness were calculated. They were compared among locations at each date using a Dunn test from the 'FSA' R package (version 0.8.32; Ogle et al. 2021) accounting for the Benjamini-Hochberg procedure and they were compared between dates using a Kruskal-Wallis test. SIMPER analysis was conducted to determine the species' contribution to the observed temporal difference (Clarke, 1993). The percent cover of the species contributing more than 5% to contrasts between treatments in the SIMPER analysis was compared between June and August with a Kruskal-Wallis test.

Results

Contaminants

All contaminants, for which reference values were present, largely exceeded the Canadian sediment quality guidelines as well as concentrations at which 20% and 50% of sediments tested by the US Environmental Protection Agency would become toxic to model amphipods (Table 1; CCME 1999; US EPA 2005). PAHs in the sediments of the Vieux Port de Marseille were highly concentrated. Most notably, Benzo[*a*]pyrene, Benzo[*k*]fluoranthene and Phenanthrene were exceeding three to four times the concentration at which a 50% probability of toxicity is reached (Table 1, US EPA 2005). However, the only POP varying significantly between locations were total PCBs (K-W, $p < 0.05$), which exceeded quality thresholds by orders of magnitude.

Most tested MTEs had significant higher concentrations at the inner location compared to the entrance location (K-W, $p < 0.05$), however concentrations in the middle location were close to the inner concentrations. MTE concentrations were all above the Canadian sediment quality guideline and above the concentration of 20% probability of toxicity and fell within a sediment quality category of moderate for As and Cr and bad for Cu and Pb and Zn (Table 2; CCME 1999; US EPA 2005; Guerra-García et al. 2021). The Cu concentration in sediments even exceeded a 80% probability of toxicity at all locations (US EPA, 2005).

Table 1: Concentration of POP contaminants in the sediments of the three study locations. Mean values (µg.kg^{-1} = ppb) with standard deviation. Contaminants with significant differences between locations (Kruskal-Wallis test, $p < 0.05$) indicated by *. Reference values given by the Canadian Council of Ministers of the Environment (CCME 1999; ISQG: Interim Sediment Quality Guideline; PEL: Probable Effect Level); and the United Stated Environmental Protection Agency (US EPA 2005, Table 11; T20: probability of 20% of toxicity among samples; T50: probability of 50% of toxicity among samples). Bold font for reference values: threshold exceeded.

Polycyclic Aromatic Hydrocarbon (PAH) µg.kg^{-1}	**Site mean ± SD**			**K-W test**	**CCME**		**US EPA**	
	Inner	**Middle**	**Entrace**		**ISQG**	**PEL**	**T20**	**T50**
Acenaphthene	192 ± 64.3	230 ± 33.5	70 ± 21.4	ns	**6.71**	**88.9**	**19**	**120**
Acenaphthylene	96.8 ± 14.4	84.3 ± 13.2	37.1 ± 18.4	ns	**5.87**	128	**14**	140
Anthracene	660 ± 75.7	677 ± 21.3	389 ± 21.4	ns	**46.9**	**245**	**34**	**290**
Benzo[*a*]pyrene	1185 ± 170	1687 ± 230	590 ± 106	ns	**88.8**	**763**	**69**	**520**
Benzo[*a*]anthracene	1210 ± 115	1571 ± 221	838 ± 127	ns	**74.8**	**693**	**61**	**470**
Benzo[*g,h,i*]perylene	665 ± 35.3	509 ± 160	369 ± 48.8	ns			**67**	**500**
Benzo[*b*]fluoranthene	1184 ± 180	1184 ± 120	702 ± 4.6	ns			**130**	**1110**
Benzo[*k*]fluoranthene	1523 ± 275	1971 ± 242	953 ± 106	ns			**70**	**540**
Chrysene	103 ± 16	174 ± 77.1	62.9 ± 14.6	ns	**108**	846	**82**	650
Dibenzo[*a,h*]anthracene	1652 ± 272	2112 ± 313	1112 ± 98.6	ns	**6.22**	**135**	**19**	**110**
Fluorene	580 ± 31.5	1099 ± 716	290 ± 30.3	ns	**21.2**	**144**	**19**	**110**
Fluoranthene	486 ± 117	575 ± 128	207 ± 23.2	ns	**113**	1494	**120**	1030
Indeno[1,2,3-*c,d*]pyrene	570 ± 20.6	581 ± 142	494 ± 80.1	ns			**68**	**490**
Naphthalene	57.4 ± 15.3	78 ± 13	41.2 ± 12.4	ns	**34.6**	391	**30**	220
Phenanthrene	1233 ± 169	1691 ± 293	621 ± 42.9	ns	**86.7**	**544**	**68**	**460**
Pyrene	767 ± 46.3	962 ± 144	389 ± 65.2	ns	**153**	1398	**120**	**930**
Polychlorinated Biphenyl (tPCB) µg.kg^{-1}								
tPCBs	1252 ± 6.27	1395 ± 15.9	455 ± 7.61	*	**21.5**	**189**	**35**	**370**
Pesticides µg.kg^{-1}								
aldrin	2.74 ± 0.22	2.53 ± 0.14	5.32 ± 0.36	ns				
Trans_chlordane	1.57 ± 0.28	1.18 ± 0.05	2.42 ± 0.03	ns				
cis_chlordane	0.73 ± 0.22	0.11 ± 0.04	0.38 ± 0.21	ns				
tChlordane	2.3 ± 0.2	1.29 ± 0.08	2.81 ± 0.19	ns	**2.26**	4.79		
diazinon	4.3 ± 0.38	2.92 ± 0.65	2.09 ± 0.55	ns				
dieldrin	7.11 ± 0.09	11.3 ± 1.44	2.4 ± 0.26	ns	**0.71**	**4.3**	**0.83**	**2.9**
pp'-DDD	5.33 ± 0.55	12.3 ± 1.59	13.1 ± 1.46	ns	**1.22**	**7.81**	**2.2**	19
pp'-DDE	8.58 ± 1.39	15 ± 1.61	17.8 ± 1.96	ns	**2.07**	374	**3.1**	100
pp'-DDT	0.66 ± 0.19	1.82 ± 0.1	2.55 ± 0.16	ns	**1.19**	4.77	**1.7**	11
endosulfan-1	1.83 ± 0.44	3.74 ± 0.53	2.26 ± 0.1	ns				
endosulfan- 2	21.2 ± 0.94	13.8 ± 1.26	2.57 ± 0.17	ns				
heptachlor	6.09 ± 0.54	6.02 ± 0.43	3.89 ± 0.28	ns	**0.6**	**2.74**		
heptachlor_epoxide_a	23.9 ± 0.95	15.3 ± 2.67	5.8 ± 0.57	ns				
heptachlor_epoxide_b	1.6 ± 0.4	0.84 ± 0.14	0.47 ± 0.11	ns				
isodrin	5.68 ± 0.38	5.52 ± 0.43	8.45 ± 0.14	ns				
lindane	3.89 ± 0.34	3.83 ± 0.28	2.07 ± 0.4	ns	**0.32**	**0.99**		
methoxychlor	5.95 ± 0.48	15.7 ± 0.83	16 ± 1.03	ns				

Table 2: Concentrations of MTE contaminants in the sediments of the three study locations. Mean values (mg.kg^{-1} = ppm) with standard deviation. Contaminants with significant differences between locations (Kruskal-Wallis test) indicated by * $p < 0.05$. Reference values given by the Canadian Council of Ministers of the Environment (CCME 1999; ISQG: Interim Sediment Quality Guideline; PEL: Probable Effect Level); and the United Stated Environmental Protection Agency (US EPA 2005, Table 11; T20: probability of 20% of toxicity among samples; T50: probability of 50% of toxicity among samples). Quality category after Guerra-García et al. (2021) indicated. Bold font for reference values: threshold exceeded.

Metallic Trace Elements (MTE) mg.kg^{-1}	**Location mean ± SD**			**K-W test**	**CCME**		**US EPA**		**Quality category[1]**
	Inner	**Middle**	**Entrace**		**ISQG**	**PEL**	**T20**	**T50**	
Al27(MR)	12927 ± 3151	8400 ± 3829	5501 ± 1881	*					
As75(HR)	29.2 ± 5.95	31.5 ± 3.62	18.6 ± 2.78	*	**7.24**	**41.6**	**7.4**	**20**	Moderate
Co59(MR)	4.55 ± 1.65	4.82 ± 2.13	2.07 ± 0.2	*					Good
Cr52(MR)	68.6 ± 14.6	66.4 ± 9.42	27.8 ± 4.54	*	**52.3**	160	**49**	140	Moderate
Cu63(MR)	611 ± 111	545 ± 73.4	279 ± 103	*	**18.7**	**108**	**32**	**94**	Bad
Fe56(MR)	12881 ± 3158	12867 ± 1357	6859 ± 2341	*					
Mn55(MR)	164 ± 33.3	158.2 ± 13.2	126 ± 9.19	*					
Ni60(MR)	17.7 ± 2.76	17.3 ± 2.36	7.89 ± 1.49	*			**15**	47	Good
Pb208(LR)	299 ± 63.7	262 ± 26.2	136 ± 27.5	*	**30.2**	**112**	**30**	**94**	Bad
Ti47(MR)	1373 ± 301	1414 ± 251	723 ± 129	*					
V51(MR)	68.5 ± 16.7	70.8 ± 5.28	28.7 ± 1.65	*					
Zn66(MR)	665 ± 151	531 ± 85.8	198 ± 18.5	*	**124**	**271**	**94**	**240**	Bad

Temperature

The temperature curve of all three locations revealed a similar trend among locations with no striking temperature differences among locations. Taking into account the framework proposed by Hobday et al. (2016), between June and August two major heatwaves can be noted with temperatures exceeding 25°C during 13 and 7 days respectively, and a maximum temperature of 28°C, followed by a smaller heat spike (Fig. 2).

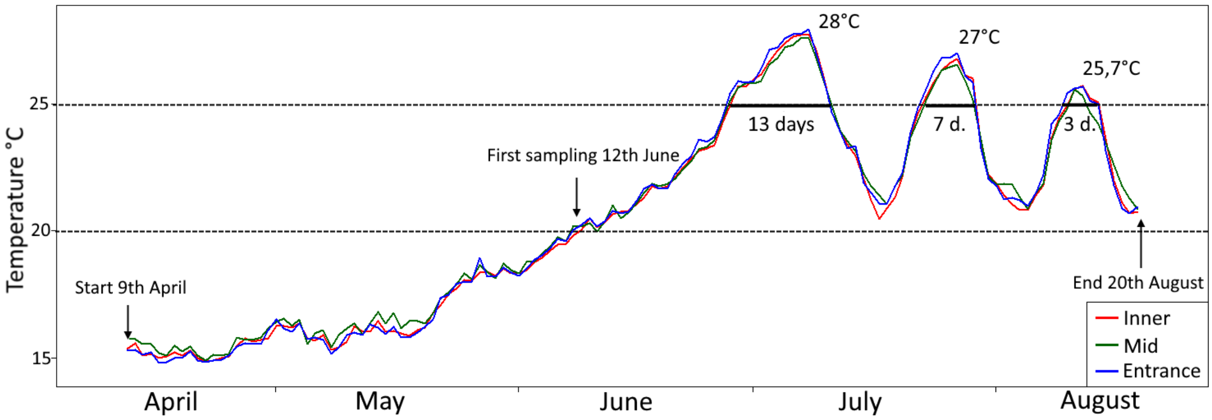

Fig. 2: Temperature curve for each location. Start and sampling dates as well as notable values are indicated.

Community

The analysis of community data derived from the laboratory analysis of panels in June and August showed a significant variability both in space and time (Fig. 3). Homogeneity of group dispersion was verified (Betadisper, F = 1.97, p = 0.12) allowing the application of a PERMANOVA showing a significant effect of location, date as well as their interaction (Table 3). This interaction indicated that the effect of location on community structure was unequal between both dates and may be attributed to the overall more similar communities in August compared to June, when higher differences between locations can be observed (Fig. 3). This was also observable when replacing location with contamination weight derived from the CCA centroids of the contaminant matrix. The PERMANOVA identified a significant effect of date, contamination weight and their interaction, for both polynomial degrees of contamination weight (Table 3). In both cases, interpretation of interaction terms required a subsequent pairwise comparison. The pairwise-PERMANOVA revealed a systematic difference for each of the three locations between June and August ($P_{adj.} < 0.05$, $R^2 > 0.75$; Table 3). All locations differed significantly from each other in June ($P_{adj.} < 0.05$; $R^2 > 0.54$; Table 3), while they were only significantly different between the inner and the middle location in August ($P_{adj.} = 0.02$, $R^2 = 0.44$; Table 3).

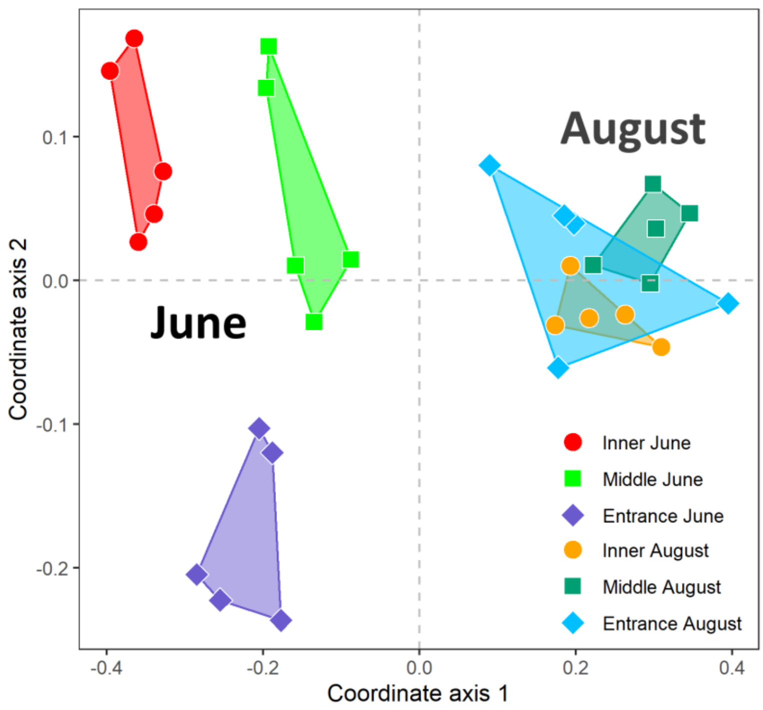

Fig. 3: Nonmetric Multidimensional Scaling (nMDS) of analyzed communities. Communities from a location are systematically different between June and August (PERMANOVA, p adj. < 0.05, $R^2 > 0.75$). Communities differ between locations in June (PERMANOVA, p adj. < 0.05, $R^2 > 0.54$). Inner and Middle different in August (PERMANOVA p adj = 0.02, $R^2 = 0.44$)

PERMANOVA results					
Overall Test with Location (Community structure ~ Date * Location)					
	Df	F.Model	R^2	Pr (>F)	
Date	1	117.55	0.65	< 0.001	***
Location	2	8.34	0.09	< 0.001	***
Date : Location	2	10.85	0.12	< 0.001	***
Residuals	24		0.13		
Overall Test with Contamination (Community structure ~ Date * Cont.wt1 + Date * Cont.wt2)					
	Df	F.Model	R^2	Pr (>F)	
Date	1	117.55	0.65	< 0.001	***
Cont.wt1	1	7.74	0.04	0.003	**
Cont.wt2	1	8.95	0.05	0.001	**
Date : Cont.wt1	1	7.38	0.04	0.003	**
Date : Cont.wt2	1	14.31	0.08	< 0.001	***
Residuals	24		0.13		
Pairwise PERMANOVA (Community structure ~ Date : Location)					
Within date June					
	Df	F.Model	R^2	Pr (>F)	
J E *vs* J M	1	9.22	0.54	0.012	*
J E *vs* J I	1	19.01	0.7	0.012	*
J M *vs* J I	1	16.7	0.68	0.012	*
Within date August					
	Df	F.Model	R^2	Pr (>F)	
A E *vs* A I	1	1.56	0.16	0.26	
A E vs A M	1	2.04	0.2	0.16	
A M vs A I	1	6.36	0.44	0.018	*
Between June and August					
	Df	F.Model	R^2	Pr (>F)	
J E *vs* A E	1	24.06	0.75	0.012	*
J M *vs* A M	1	45.74	0.85	0.012	*
J I *vs* A I	1	118.88	0.94	0.012	*

Table 3: Results from the PERMANOVA and the pairwise PERMANOVA on community structure. Cont.wt1: Contamination weight polynomial degree 1; Cont.wt2: Contamination weight polynomial degree 2; J: June; A: August; E: Entrance location; M: Middle location; I: Inner location. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

While a total of 28 species were identified during this study (Table 4), species richness per panel varied from 5 to 12 species. The average number of species per panel was 9.1 and remained constant between both studied periods (8.8 in June, 9.4 in August). Shannon index ranged from 1.09 to 2.58, and Pielou evenness ranged between 0.39 and 0.85. Significantly higher values of indices were detected in June (Dunn test, $p < 0.001$, Fig. 4), but not for species richness. For each date, no significant differences of diversity indices were found among locations (Dunn test). The polychaete annelids Serpulinae (Rioja, 1923), the serpulid worm *Simplaria pseudomilitaris* (Thiriot-Quievreux, 1965), the bryozoan *Bugula neritina* (Linnaeus, 1758) and the colonial ascidians *Botryllus schlosseri* (Pallas, 1766) and *Diplosoma listerianum* (Milne Edwards, 1841) accounted to over 85% of the contrast between June and August (Fig. 5). These species are also the five most abundant species with a mean cover of more than 5% at both dates. Most of these species suffered a significant reduction of their percent cover between June and August ($p < 0.01$, Fig. 6A) except the sub-family of the Serpulinae which significantly increased ($p < 0.001$, Fig. 6A). The latter is linked to a significantly increased total cover from June to August ($p = 0.002$, Fig. 6B). Significant differences of total cover between locations could only be identified in June between the middle and the entrance location ($P_{adj.} = 0.04$).

Table 4: Species list for the Marina. Non-Indigenous Species (NIS) and cryptogenic species (crypto.) are indicated with a respective source.

Annelida		**Status**	**Source**
Hydroides elegans	(Haswell, 1883)	NIS	(Langeneck et al., 2020)
Hydroides norvegica	Gunnerus, 1768		
Janua heterostropha	(Montagu, 1803)		
Jugaria granulata	(Linnaeus, 1767)		
Neodexiospira brasiliensis	(Grube, 1872)	NIS	(Hayward and Ryland, 1995)
Pileolaria berkeleyana	(Rioja, 1942)	NIS	(Langeneck et al., 2020)
Pileolaria militaris	(Claparède, 1870)		
Simplaria pseudomilitaris	(Thiriot-Quievreux, 1965)		
Serpula concharum	(Langerhans, 1880)		
Serpula vermicularis	(Linnaeus, 1767)		
Spirorbis marioni	(Caullery & Mesnil, 1897)	NIS	(Langeneck et al., 2020)
Spirorbis sp.	(Daudin, 1800)		
Arthropoda			
Perforatus perforatus	(Bruguière, 1789)		
Urochordata			
Ascidiella aspersa	(Müller, 1776)	NIS	(Zenetos et al., 2017)
Bortylloides sp.	(Milne-Edwards, 1841)		
Botryllus schlosseri	(Pallas, 1766)	Crypto.	(Zenetos et al., 2017)
Ciona intestinalis	(Linnaeus, 1767)		
Diplosoma listerianum	(Milne Edwards, 1841)	NIS	(Ulman et al., 2017)
Bryozoa			
Bugula neritina	(Linnaeus, 1758)	NIS	(Harmelin et al., 2016)
Bugulina simplex	(Hincks, 1886)		
Bugulina stolonifera	(Ryland, 1960)		
Cryptosula pallasiana	(Moll, 1803)		
Watersipora subatra	(d'Orbigny, 1852)	NIS	Gauff et al. in prep.
Cnidaria			
Laomedea flexuosa	(Alder, 1857)		
Obelia geniculata	(Linnaeus, 1758)		
Mollusca			
Crassostrea gigas	(Thunberg, 1793)	NIS	(Hayward and Ryland, 1995)
Parvicardium pinnulatum	(Conrad, 1831)		
Porifera			
Sycon ciliatum	(Fabricius, 1780)		

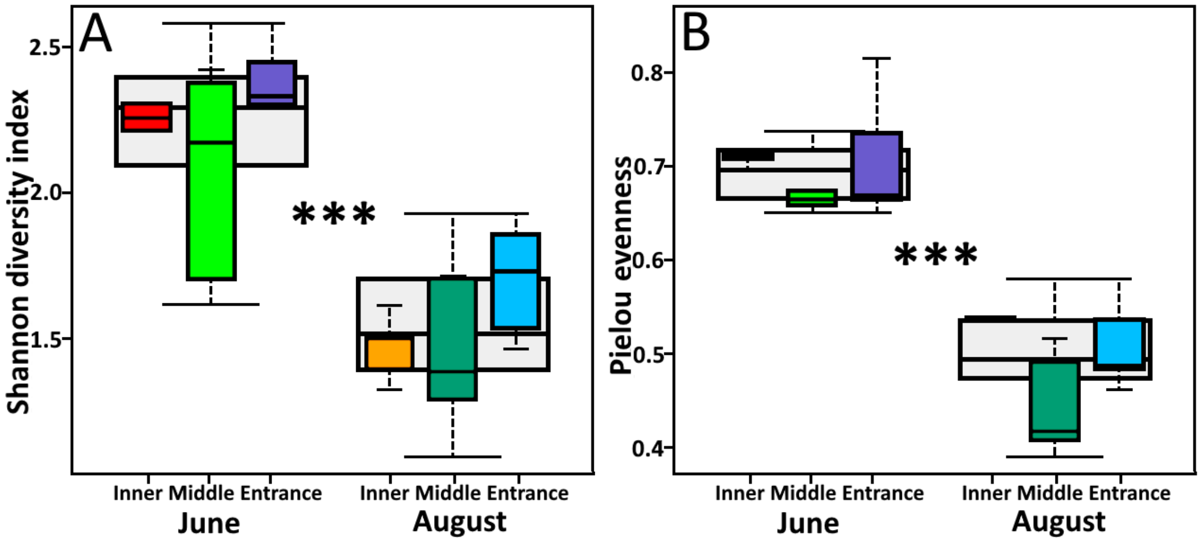

Fig. 4: Spatial and temporal variation of the Shannon-Weaver diversity index (A) and Pielou evenness (B). Significant differences between dates are indicated with big stars (Kruskal-Wallis test). No significant differences between locations within dates. *** p < 0.001

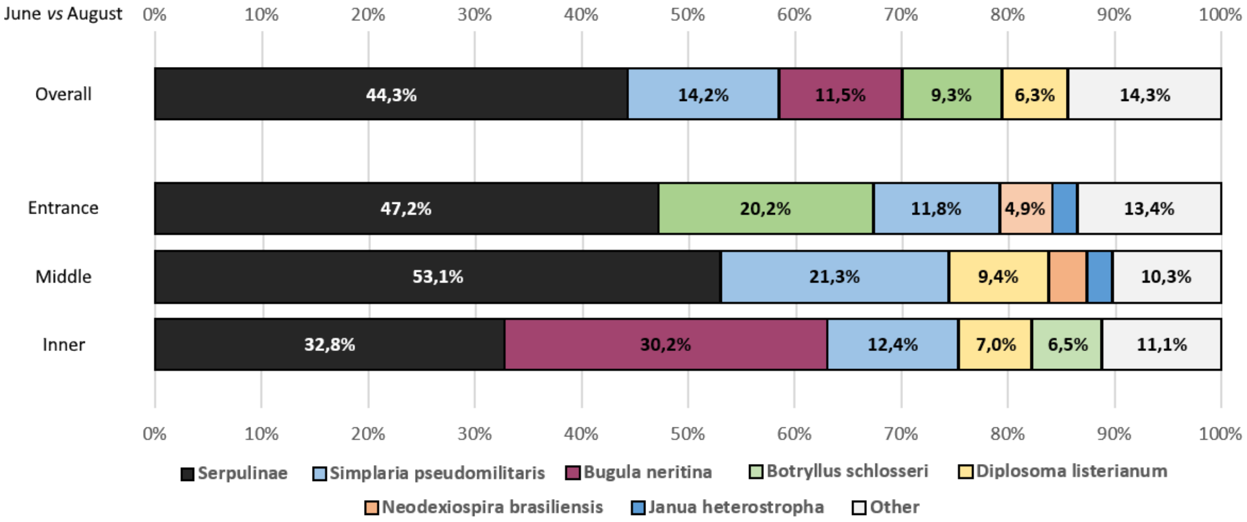

Fig. 5: SIMPER analysis showing the species that contribute the most to the temporal contrast among communities between June and August (percentage, SIMPER analysis)

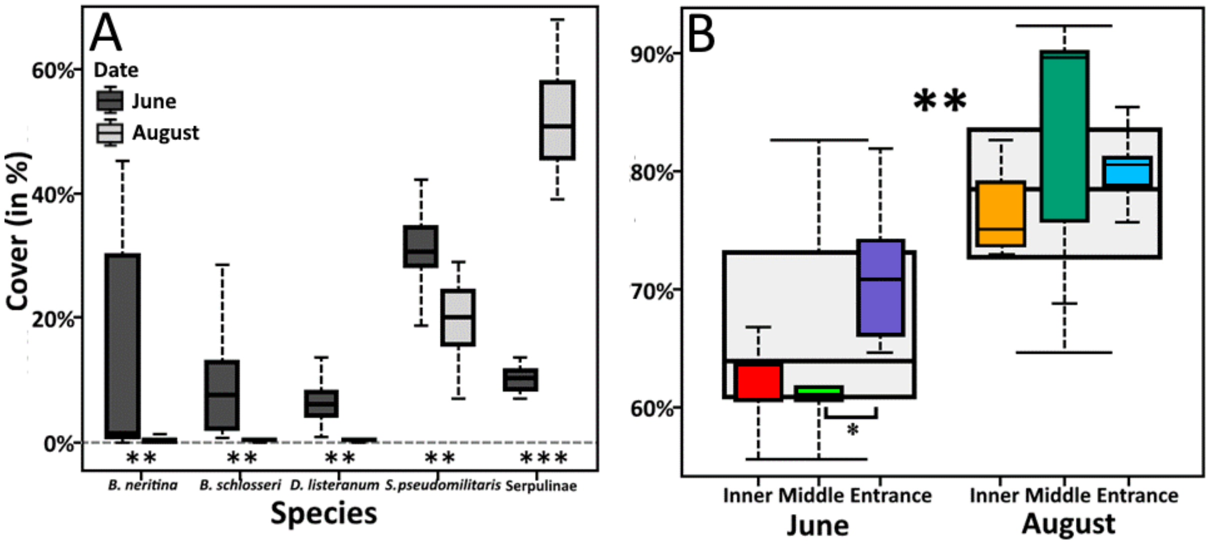

Fig. 6: Percent cover exerted by the A) five most abundant species (which are also the species, most contributing to the contrasts between June and August) between June (dark grey) and August (light grey) and the B) total community for each location and period Significant differences between dates are indicated with stars (Kruskal-Wallis test). Significant differences between locations are indicated by brackets (Dunn test). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Discussion

The present study aimed to describe how the sessile sciaphilic communities of the Vieux Port de Marseille are composed and how they vary in space. We hypothesized that different locations in the harbor have significantly different communities, associated to a local variation of pollution, as described in previous studies (Je et al., 2004; Kenworthy et al., 2018b; Rondeau et al., 2022; Ryu et al., 2011). In accordance with these studies, most contaminant concentrations and especially Metallic Trace Elements (MTEs) were minimal at the entrance of the harbor, where more exchange with the outer water masses occurs (Schiff et al., 2007). Conversely, we did not observe a clear pollution gradient, as concentrations in the middle and the inner parts of the harbor were similar which might be explained by local hydrodynamic conditions. Community structure was still significantly affected by location and by overall contamination.

While an expected community heterogeneity was observed among locations in June, it was in contrast strongly reduced in August with overall similar communities. In addition to this loss of spatial variability between locations in August, it was possible to observe a strong temporal shift of the communities between June and August. *Simplaria pseudomilitaris*, *Bugula neritina*, *Botryllus schlosseri* and *Diplosoma listerianum* had their cover significantly reduced. Conversely, calcareous worms of the

Serpulinae sub-family are the only group increasing their cover between both periods. We were not able to identify most Serpulinae species on the settlement plates, due to their small size making dissection impossible. Some species of this sub-family could however be identified: *Salmacina incrustans* Claparède, 1870, *Hydroides elegans* (Haswell, 1883), followed by *Serpula vermicularis* Linnaeus, 1767 were the most abundant identified Serpulinae while we noted the anecdotal presence of *Hydroides norvegica* Gunnerus, 1768 and *Serpula concharum* Langerhans, 1880.

The observed temporal decrease of the cover of most species (including the dominant ascidians and bryozoan) might be explained by the species' life cycles, biotic interactions among the organisms of the fouling community or by an abiotic factor leading to homogenization among the studied communities. Focusing on biotic interactions, ecological succession could explain our observations (Gardner and Wear, 2006; Loke et al., 2016; Raja, 1959) as it highly impacts community structure and biodiversity on settlement plates (Marraffini et al., 2017). The present case might reflect competitive exclusion due to the strong increase of the cover of Serpulinae (Hardin, 1960; Mayfield and Levine, 2010). However, while the total species cover increased between June and August, it reached 65%-90% in August with Serpulinae covering 39-68%, which would still leave enough space for other species to grow and thus limit competition for space. Furthermore, Serpulinae are mostly prone species forming calcareous tubes which should vastly limit spatial competition they could exert towards *B. neritina* an erect bryozoan. *B. neritina* could also simply overgrow the calcareous tubes. Equally, encrusting colonial ascidians *B. schlosseri* and *D. listerianum* are unlikely to be competitively excluded by Serpulinae. Both colonial ascidians can overgrow solitary animals such as serpulid worms due to their high competitive ability (Grosberg, 1981). The Spirorbinae serpulid *Simplaria pseudomilitaris* is the only major species that occupies a very similar ecological niche as Serpulinae and would be more likely to be competitively excluded by them. Yet, despite the reduction of its cover between June and August, this species seems to be the least affected one since it still covers 7-44% in August. Similar experiments with settlement plates conducted in another marina have shown to have constant community differences between the entrance and the inner part of a marina over a span of more than 4 years (Gauff et al., 2022a; Rondeau et al., 2022). These differences remained constant regardless of timing of panel deployment, or length between individual assessments (Rondeau et al., 2022), *i.e.,* regardless of successional state of the community. Thus, the observed differences between June and August might not be attributed to biotic interaction among fouling species or to succession, but rather to external abiotic factors impacting the communities at all three locations.

A possible explanation could be a larger scale environmental disturbance, leading to environmental homogenization of all locations of the harbor between June and August. The present Serpulinae could have a quicker recolonization rate due to their opportunistic nature and/or be more resistant to this disturbance than the other species (Diaz-Castaneda, 2000; Nishi and Nishihira, 1994; Pernet, 2001). Large scale climatic variation and extreme climatic events can affect local communities (Astudillo et al., 2016; Chang et al., 2018; Cascade J. B. Sorte et al., 2010). Water temperature has been subject to high variations between June and August with three successive phases of increased heat, the longest lasting 13 days over 25°C, and a thermal maximum of over 28°C. Two of this phases can be considered as heat waves as the 90th percentile threshold of historic temperature data at surface level in summer (24.7°C; SOMLIT) was exceeded for more than 5 days (Hobday et al., 2016). Research on the potential impacts of climate change shows a drastic impact of rising temperature on communities (Lejeusne et al., 2010; Smale et al., 2017, 2011; Sorte et al., 2010). Heat waves have particularly been shown to have severe consequences on marine communities, their physiology, and their ecosystem services (Britton et al., 2020; Garrabou et al., 2009; Lonhart et al., 2019; Pansch et al., 2018; Smale et al., 2019), with impacts potentially lasting long beyond the punctual time-scale (Gómez-Gras et al., 2021). High temperature events with surface temperatures reaching over 26.5°C in 1997, 1999 and 2003 have led to mass mortalities of multiple sessile species in the studied region (Garrabou et al., 2009; Lejeusne et al., 2010; Perez et al., 2000) and the concerned communities did not recover from this event (Gómez-Gras et al., 2021). Heat waves, as short term events, highly impact community composition in natural and artificial environments (Lonhart et al., 2019; Pansch et al., 2018; Sorte et al., 2010). Climate change and heat waves may also favor introduced species which might be more resistant to heat (Kelley, 2014; Kenworthy et al., 2018a; Lord, 2017). *Hydroides elegans*, one of the most abundant Serpulinae in our samples, has been shown to be highly resistant to temperatures up to 30°C and seems even to profit from higher temperatures due to faster development if this is not negated by other associated variables (Qiu and Qian, 1998, 1997).

Given the magnitude of the observed temperature anomaly, it constitutes a candidate for explaining the observed community shift and homogenization. We are here, however, not able to exclude all potential other factors and stochastic variation, or a simple correlational effect could still exist. It is important to note that contaminant concentrations measured in sediments integrate long-term tendencies of pollution and do not account for temporal variation which has been shown to strongly influence fouling community structure (Johnston et al., 2002; Johnston and Keough, 2002, 2000). A pollution spike could thus constitute an alternate explanation for our observations. However, it seems likely that such pollution spike may also be organized as a gradient of concentration. Increased vessel and tourist activity in the summer months might also constitute a potential explanation, it remains however difficult to quantify.

Loss of community variability

Here we showed a spatially organized community structure in the Vieux port de Marseille similar to previous studies (Gauff et al., 2022a; Kenworthy et al., 2018b; Rondeau et al., 2022), followed by an unexpected change in the community associated to a sharp decrease in biodiversity and a decline of most species except Serpulinae, eclipsing the effects of local variation of environmental factors and thus leading to the homogenization of the biodiversity within the harbor. Urbanization and climate change have led to the worldwide homogenization of ecosystems (Clavel et al., 2011; Magurran et al., 2015; Mckinney and Lockwood, 1999; Qian and Ricklefs, 2006). Heat waves are predicted to increase with climate change, both in frequency and intensity (Holl, 2009; Meehl et al., 2000; Stott, 2016), a trend which is particularly intense in Europe (Rousi et al., 2022). Regular heat waves might favor altered communities with highly opportunistic and/or species with high thermal tolerance, characteristics often described in introduced species (Kelley, 2014; Kenworthy et al., 2018a; Lejeusne et al., 2014; Sorte et al., 2010) and heat-stressed communities have been shown to have an increased invasibility (Castro et al., 2021). Here heat waves might constitute a potential explanation for the observed biodiversity homogenization. However, our experiment was originally not designed to study the effect of heat waves on marina communities and clear conclusions on the reason for the present homogenization are not possible. The temporal concomitance of the homogenization with the heat events remains, however, intriguing and illustrates that more research in this subject is needed. Further experiments with in situ heating structures that could simulate heat waves directly on the field (Gauff et al., 2022; Smale et al., 2017, 2011) would help to investigate the effect such events have on local communities and biodiversity to effectively understand them.

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