

# Habitat formed by the invasive macroalga *Caulerpa filiformis* (Suhr) Hering (Caulerpales, Chlorophyta) alters benthic macroinvertebrate assemblages in Peru

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## Research Article

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# Abstract

The green macroalga *Caulerpa filiformis* has been spreading on shallow soft sediment habitats along the Peruvian coast, colonizing previously unvegetated sediments to create monospecific meadows. We examined the nature of the impact of *C. filiformis* meadows on the density, taxonomic richness and assemblage structure of epifaunal and infaunal benthic macroinvertebrates. Specifically, we tested whether the spread of *C. filiformis* has resulted in different macroinvertebrate assemblages than those formed by the dominant native macroalgae (i.e., *Rhodymenia* spp.) and unvegetated sediments. Surveys were undertaken in two bays in each of two locations, in central and southern Peru, during winter 2017 and summer 2018. In general, our results show that macroinvertebrate assemblages were similar across all three habitats, although there were some differences, related to location and season, but with no clear patterns observed. Taxonomic richness and density was generally higher in the vegetated habitats than the unvegetated habitat, and where there were differences between the two vegetated habitats there was no consistent pattern of which habitat supported the highest richness or density. Given invading *C. filiformis* is primarily colonizing unvegetated habitats it would appear that this species is creating a new niche which supports similar assemblages, but higher taxonomic richness and density than unvegetated habitats. While our study suggests that *C. filiformis* is having a limited ecological impact we recommend that actions be put in place to limit the spread of this invasive species at the same time as increasing monitoring of the ecological impacts of this species as lags in the ecological impacts of invasive species are common.

# Introduction

Habitat-forming species are important to the structure and functioning of marine ecosystems as they often result in altered local environmental conditions and high levels of biodiversity (Teagle et al. 2016; Edwards et al. 2020). Many macroalgal species are considered habitat-formers, which have direct and indirect effects on associated communities by providing food (Schaal et al. 2009) and shelter (Teagle et al. 2016), modifying physical factors such as living space (Crooks 2002), light (Uribe et al. 2015) and water flow (Shelamoff et al. 2019), in addition to contributing to the cycling of energy and matter (Abdullah et al. 2017). As a result, habitat-formers and their associated communities strongly influence ecosystem processes, but these effects can vary among habitat types and times (Cvitkovic et al. 2017).

In many places throughout the world, habitat-forming macroalgae are being lost due to various, often local-scale stressors (Krumhansl et al. 2016). Persistent large-scale losses of native macroalgae have occurred in North America (Steneck et al. 2002), Europe (Airoldi and Beck 2007), Japan (Watanuki et al. 2010) and Australia (Connell et al. 2008; Coleman et al. 2008). Abiotic disturbances such as increased temperature, sedimentation, or eutrophication can often result in native macroalgae being replaced by smaller turf-forming algae (Airoldi and Beck 2007; Connell et al. 2008; Filbee-Dexter and Wernberg 2018). Alternatively, the bare space created by the loss of native macroalgae can provide an opportunity for colonization by invasive or non-native macroalgae (Valentine and Johnson 2003). Indeed, native turfing algae themselves can facilitate the colonization of other fast-growing invasive macroalgae such as

*Caulerpa* spp. (Voerman et al. 2017). Given that many invasive macroalgae are also habitat-formers the habitat complexity provided by these species potentially provide novel niches for native species (Dijkstra et al. 2017), which may in turn result in the development of non-analogue communities (Lubchenco et al. 1991; Zhang et al. 2014; Lanham et al. 2015; Suárez-Jiménez 2017).

Irrespective of whether opportunistic species are native or introduced, they can benefit from environmental change (Valéry et al. 2009; Carey et al. 2012). Green algae of the genus *Caulerpa* are common in lower intertidal and shallow subtidal regions along tropical and subtropical coastlines in both hemispheres (Cevik et al. 2012; Glasby et al. 2015; Maidanou et al. 2017). The genus is known for its opportunistic and rapid growth traits that have contributed to the genus, including *Caulerpa taxifolia* and *Caulerpa cylindracea* (Williams and Smith 2007), invading new locations globally. In some cases, the spread of *Caulerpa* spp. has been due to the colonization of previously unvegetated soft sediments (Glasby 2013), while in other cases they have colonized hard substrata (Montefalcone et al. 2015). The replacement of native habitat-forming species by *Caulerpa* spp. tends to occur in areas that are subjected to high levels of anthropogenic disturbances (Bulleri et al. 2011), consistent with the notion that *Caulerpa* spp. are often passengers of environmental change (Bulleri et al. 2011). Species of *Caulerpa* also tend to show a high tolerance to sedimentation (which tends to be greatest in heavily populated areas) compared to many other seaweeds (Piazzi et al. 2005; Glasby et al. 2005; Piazzi et al. 2007; Glasby et al. 2015).

*Caulerpa filiformis* (Suhr) Hering has been registered recorded in South Africa (Pillmann et al. 1997), eastern Australia (Pillmann et al. 1997; Glasby et al. 2015), southern Mozambique (Coppejans et al. 2005) and Peru (personal observation), inhabiting intertidal or shallow subtidal rocky shores and sandy sediments (Coppejans et al. 2005). Genetic differences between Australian and African populations suggesting these populations are native rather than introduced (Pillmann et al. 1997), while the provenance of Peruvian populations are unknown. *C. filiformis* was recorded (as *Caulerpa flagelliformis*) for the first time in 1907 on Lobos de Afuera Island (Howe 1914) and later on Piura region in northern Peru (Acleto 1986). Peruvian populations may therefore be native to Peru, however, molecular tests are necessary to determine this. There have been no formal surveys to track changes in the distribution and abundance of *C. filiformis* in Peru since it was first recorded, however, there are anecdotal reports that the alga has been spreading slowly southward. Over the past decades, *C. filiformis* has colonized shallow reefs and soft sediments in central and southern Peru, creating large monospecific meadows that were previously unvegetated, or dominated by native complex turf-forming red algae (e.g., *Rhodymenia* spp.). As such, *C. filiformis* could be considered an invasive species in these newly colonized areas.

Given a key objective in ecology is to understand how the presence of invasive species affects natural communities (Walsh et al. 2016), we quantified the density, species richness and community structure of epifaunal and infaunal benthic macroinvertebrates associated with habitats newly-formed by *C. filiformis* invasion on soft sediments on the Peruvian coast. Based on the model that invasion by *C. filiformis* would lead to a novel niche in turn leading to novel macroinvertebrate assemblages, we hypothesized that assemblages in habitats formed by *C. filiformis* would be significantly different over space and time from those in habitats formed by native species of *Rhodymenia* spp. and unvegetated soft sediments.

# Materials And Methods

## Study sites and habitat characteristics

This study was carried out in Paracas Bay and Samanco Bay located in southern and northern Peru, respectively (Fig. 1). Both bays are characterized by high levels of productivity, with large commercial fisheries for a range of fishes and invertebrates (i.e., bivalves, gastropods, cephalopods, crustaceans, echinoderms). There is also fish meal manufacturing and shellfish farming in both bays. The greatest wealth of benthic biota in both bays is found in an area of shallow water (to ~14 m depth; on sand, pebbles or split shell) with high abundance and coverage of polychaetes (i.e., *Diopatra* sp., *Chaetopterus* sp.), and extensive patches of red macroalgae *Rhodymenia corallina* and others species with reduced density such as *Rhodymenia* sp., *Ulva* sp. Collectively these species form a characteristic habitat henceforth named *Rhodymenia* spp. Since the late 2000s, large beds of *Caulerpa filiformis* have established in both bays, with the alga primarily colonizing the fine grain soft sediments and pebbles at depths 0.5 – 12 m (Personal observation) (Fig. 2).

## Sampling Design, Field Collections And Sample Processing

Diver (hookah system i.e. surface air feed) surveys of each bay were conducted to identify adjacent areas that were either unvegetated, dominated by *C. filiformis*, or dominated by *Rhodymenia* spp. Four locations were identified with adjacent patches of these three habitats. Two locations, Santo Domingo and Atenas, were situated in Paracas Bay, and two (La Bocana and El Polvorin) in Samanco Bay. All three habitats were sampled in all locations except Santo Domingo where only *C. filiformis* and unvegetated habitats were found. In each habitat, epibenthic organisms (those that were found on the surface of stones, gravel, mollusk shells and semi buried on a layer of sand less than 2 cm deep) and infaunal organisms (those that were found buried under the first 2 cm layer of sediment) were collected from three replicate quadrats on two occasions, September 2017 (winter/spring) and February 2018 (summer).

Epifauna were collected by hand from 0.25 m<sup>2</sup> quadrats with samples placed in labeled bags. In vegetated habitats, all macroalgae were carefully removed from each quadrat with a spatula whilst minimizing disturbance of the surrounding bottom, and placed in labeled bags. After the area was cleared, a PVC core of 10 cm diameter to 15 cm depth (approximately 628 cm<sup>3</sup>) was then used to sample the infauna, which was again placed in a labeled bag. In the boat, all samples were fixed with 10 % formalin for transfer to the laboratory. All samples were collected between 8 – 10 meters below chart datum where the two algal genera co-occurred.

In the laboratory, each sample was washed with freshwater and sieved through a 500 µm mesh. The epibenthic organisms were carefully detached from any substrate including macroalgae, shells, small stones, pebbles. Finally, benthic macroinvertebrates from each sieved sample were sorted and identified

under a stereomicroscope to the lowest possible taxonomic level with the aid of taxonomic keys. Epifauna was expressed as ind/0.25m<sup>2</sup> and infauna was expressed as ind/628 cm<sup>3</sup>.

## Statistical analysis

Univariate and multivariate analyses were used to test hypotheses about differences in epifaunal and infaunal macroinvertebrates between habitats using permutational ANOVA (PRIMER v.7 and PERMANOVA +b3 software, Anderson et al. 2008). Two separate designs were used to account for the fact that one habitat was missing from one of the locations (Santo Domingo). The first design compared three locations (Fixed), two times (fixed; summer or winter) and three habitats (fixed; *Caulerpa filiformis*, *Rhodymenia* spp. or unvegetated). Data from Santo Domingo were analyzed separately, comparing the factors Time and Habitat (*Caulerpa filiformis* or unvegetated). The tests were performed on square-root transformed data, to down weight the importance of numerically dominant species, prior to creating similarity matrices using the Bray-Curtis index. P-values were based on 9,999 permutations under a reduced model. Pairwise comparisons were used to identify the nature of any significant differences ( $\alpha = 5\%$ ). Univariate metrics included density and taxonomic richness. These metrics were compared using unrestricted permutations of raw data and Monte Carlo significance tests (due to small sample size) and based on a Euclidean distance matrix.

Non-metric Multidimensional Scaling (nMDS) ordinations built from Bray–Curtis distance similarity matrices of square root transformed data were used to visualize the dissimilarity/similarity of epifaunal and infaunal assemblages for the two time periods sampled. PERMANOVA was used to test for differences between macrobenthic assemblages inhabiting each habitat and between times within each locality. Finally, a SIMPER analysis was performed on significant data to determine which species were the principal contributors to the overall differences between habitats.

## Results

### Epifaunal and Infaunal Macroinvertebrate Assemblage Structure

For both infaunal and epifaunal assemblages there was a significant interaction between location, season and habitat type (Epifauna: Pseudo-F<sub>4,36</sub> = 1.36; P<0.05; Infauna: Pseudo-F<sub>3,36</sub> = 1.59, P<0.01) when compared across the three different habitat types (Table 1; Fig. 3). On the whole, *C. filiformis* supported similar assemblages to *Rhodymenia* spp. and unvegetated habitats across locations and seasons, however, epifaunal and infaunal assemblages did differ between *C. filiformis* and *Rhodymenia* spp. at La Bocana in summer. A similar pattern was observed in the summer at Atenas where epifaunal assemblages differed between *C. filiformis* and the other two habitats, which did not differ from each other. While not statistically significant (P=0.053) infaunal assemblages in *C. filiformis* and *Rhodymenia* spp. habitats were only marginally similar at Atenas in winter. With a few exceptions, epifaunal and

infaunal assemblage structure did not differ between seasons and was similar when comparing the same habitats from different locations (Fig. 3). Overall, the peracarids, such as Tanaidacea, Corophiidae, Ischyroceridae 1 and Photidae 2 were the principal drivers of dissimilarity of epifaunal assemblages amongst *C. filiformis* and other habitats (Table 2). Conversely, the principal drivers of dissimilarity of infaunal assemblages inhabiting *C. filiformis* were Nematoda, the Polychaeta Capitellidae and the mollusk *Caecum chilense* (Table 3).

Table 1

Permutational analysis of variance (PERMANOVA) examining differences in a) assemblage structure, b) richness and c) density of epifaunal and infaunal macroinvertebrates. Significant values are indicated in bold with a significance level of  $P < 0.05$

<b>a) Assemblage</b>	<b>Epifauna</b>				<b>Infauna</b>			
Source	df	MS	Pseudo-F	p	df	MS	Pseudo-F	p
Location (Loc)	2	14514	6.3085	0.0001	2	12077	4.7468	<b>0.0001</b>
Season (Sea)	1	4324.4	1.8796	0.0198	1	5211.7	2.0485	<b>0.0137</b>
Habitat (Hab)	2	12623	5.4864	0.0001	2	8784.7	3.4528	<b>0.0001</b>
Sea x Loc	2	4062.9	1.7659	0.0038	2	5517.1	2.1685	<b>0.0008</b>
Loc x Hab	4	6707.3	2.9153	0.0001	4	5914.3	2.3246	<b>0.0001</b>
Sea x Hab	2	4066.1	1.7673	0.0061	2	4097.5	1.6105	<b>0.0221</b>
Loc x Sea x Hab	4	3125.5	1.3585	0.0264	4	4052.2	1.5927	<b>0.0032</b>
Residual	36	2300.7			36	2544.2		
Total	53				53			
<b>b) Richness</b>								
Source	df	MS	Pseudo-F	p	df	MS	Pseudo-F	p
Location (Loc)	2	1.9396	6.4576	0.0041	2	4.7189	12.001	<b>0.0001</b>
Season (Sea)	1	3.6744	12.233	0.0015	1	0.71716	1.8239	0.1869
Habitat (Hab)	2	9.6843	32.242	0.0001	2	3.6743	9.3447	<b>0.0003</b>
Sea x Loc	2	2.08	6.925	0.002	2	0.25328	0.64414	0.5294
Loc x Hab	4	1.7372	5.7838	0.0004	4	0.85077	2.1637	0.0976
Sea x Hab	2	0.36352	1.2103	0.3022	2	0.85088	2.164	0.1344
Loc x Sea x Hab	4	0.74204	2.4705	0.0585	4	0.86673	2.2043	0.0868
Residual	36	0.30036			36	0.3932		
Total	53				53			
<b>c) Density</b>								
Source	df	MS	Pseudo-F	p	df	MS	Pseudo-F	p
Location (Loc)	2	16.809	13.395	0.0001	2	583.68	15.129	<b>0.0001</b>
Season (Sea)	1	1.8775	1.4962	0.2314	1	384.43	9.9643	<b>0.0034</b>
Habitat (Hab)	2	32.47	25.875	0.0001	2	108.89	2.8224	0.0705

<b>a) Assemblage</b>	<b>Epifauna</b>				<b>Infauna</b>			
Sea x Loc	2	5.4438	4.3381	0.0215	2	204.33	5.2962	<b>0.01</b>
Loc x Hab	4	4.4958	3.5827	0.0166	4	96.881	2.5111	0.0561
Sea x Hab	2	6.9287	5.5215	0.0069	2	72.595	1.8816	0.1646
Loc x Sea x Hab	4	0.33855	0.26979	0.8958	4	88.157	2.285	0.0696
Residual	36	1.2549			36	38.581		
Total	53				53			

Table 2

SIMPER analyses of epifauna based on Bray-Curtis similarity amongst *C. filiformis*, *Rhodymenia* spp. and unvegetated habitats.

	Av. Abund.	Av. Abund.	Diss./SD	Av. Diss.	Contrib.%	Cum.%
1) Group	<i>C. filiformis</i>	Unvegetated				
Average dissimilarity = 88.75						
Tanaidacea	33.71	6.45	9.75	1	10.98	10.98
Corophiidae	23.95	8.49	8.4	1.07	9.47	20.45
Ischyroceridae 1	29.6	1.67	6.92	0.54	7.8	28.24
Ostracoda	5.22	6.97	5.03	0.79	5.67	33.91
Nereididae	13.32	0.73	4.71	0.6	5.31	39.22
2) Group	<i>C. filiformis</i>	<i>Rhodymenia</i> spp.				
Average dissimilarity = 85.09						
Tanaidacea	33.71	2.21	5.98	0.73	7.03	7.03
Nereididae	13.32	12.86	5.72	0.98	6.72	13.75
Corophiidae	23.95	6.81	5.59	0.83	6.57	20.32
Ischyroceridae 1	29.6	1.22	5.55	0.5	6.52	26.84
Photidae 2	3.24	12.14	5.34	0.74	6.28	33.12
<i>Caecum chilense</i>	3.48	11.36	4.41	0.88	5.18	38.3
Actiniaria	3.52	11.08	4.26	0.7	5.01	43.31
3) Group	<i>Rhodymenia</i> spp.	Unvegetated				
Average dissimilarity = 90.41						
Photidae 2	0.56	12.14	7.4	0.76	8.18	8.18
Nereididae	0.73	12.86	6.95	0.96	7.69	15.87
Corophiidae	8.49	6.81	5.85	0.88	6.47	22.34
<i>Caecum chilense</i>	0.93	11.36	5.67	0.91	6.27	28.62
Actiniaria	0.08	11.08	5.65	0.72	6.25	34.87

Table 3

SIMPER analyses of infauna based on Bray-Curtis similarity amongst *C. filiformis*, *Rhodymenia* spp. and unvegetated habitats.

	Av. Abund.	Av. Abund.	Diss./SD	Av. Diss.	Contrib.%	Cum.%
1) Group	<i>C. filiformis</i>	Unvegetated				
Average dissimilarity = 87.35						
Nematoda	3.54	3.75	9.75	0.85	11.16	11.16
Capitellidae	3.71	1.7	7.52	0.71	8.61	19.77
Tanaidacea	2.03	1.46	6.08	0.79	6.97	26.74
<i>Caecum chilense</i>	2.82	2.29	5.82	0.6	6.66	33.4
Ostracoda	2.57	2.16	5.65	0.95	6.46	39.86
2) Group	<i>C. filiformis</i>	<i>Rhodymenia</i> spp.				
Average dissimilarity = 86.60						
Nematoda	3.54	6.21	11.39	1.04	13.15	13.15
<i>Caecum chilense</i>	2.82	3.06	5.8	0.61	6.69	19.84
Capitellidae	3.71	0.93	5.73	0.67	6.62	26.46
Caecidae	0.97	2.59	4.49	0.71	5.19	31.65
3) Group	<i>Rhodymenia</i> spp.	Unvegetated				
Average dissimilarity = 87.20						
<i>Caecum chilense</i>	2.29	3.06	6.63	0.54	7.6	22.13
Caecidae	0.83	2.59	5.19	0.76	5.95	28.08
Capitellidae	1.7	0.93	4.78	0.62	5.48	33.57
Ostracoda	2.16	0.68	4.44	0.73	5.1	38.67

At Santo Domingo there was a significant interaction between season and habitat for both epifaunal and infaunal assemblages (Epifaunal: Pseudo-F<sub>1,8</sub> = 8.18, P<0.01; Infauna: Pseudo-F<sub>1,8</sub> = 2.37, P<0.05). With the exception of infaunal samples collected in the winter, epifaunal and infaunal assemblages were significantly different between *C. filiformis* and unvegetated habitats. Assemblage structure also differed between seasons for both habitat types with the exception of infaunal assemblages associated with unvegetated habitats. Similar to other localities, SIMPER analysis indicated that the dissimilarity in assemblage structure between *C. filiformis* and unvegetated habitats was primarily driven by the abundance of peracarids and Nematoda in epifaunal and infaunal assemblages respectively.

# Richness

There were significant interactions between habitat type and location (Pseudo-F<sub>4,36</sub> 5.78, P<0.001) and location and season (Pseudo-F<sub>2,36</sub> 6.93, P<0.01) for epifaunal richness when comparing across the three habitat types (Table 1). Exploring the habitat type by location interaction, revealed that at El Polvorin *Rhodymenia* spp. habitats supported a higher number of species than *C. filiformis* habitats, with unvegetated habitats supporting the least number of species. At La Bocana, unvegetated habitats again support the lowest richness, but there was no difference between *Rhodymenia* spp. and *C. filiformis* habitats. At Atenas, all three habitats supported a similar number of species. There was also variability across locations with La Bocana supporting significantly more species in *C. filiformis* and unvegetated habitats compared to Atenas and El Polvorin, respectively. In contrast, richness was significantly higher at Atenas in *Rhodymenia* spp. habitats. In terms of the locality by season interaction, Atenas supported fewer species than the other two locations in winter and El Polvorin supported fewer species than the two other locations in summer. Atenas supported a similar number of species across the two seasons while richness differed between seasons at the other two locations (Fig. 4a-c).

Epifaunal richness showed a habitat by season interaction (Pseudo-F<sub>1,8</sub> 8.18, P<0.01) at Santo Domingo with *C. filiformis* supporting a greater number of species in the summer, while unvegetated habitats supported more species in the winter. Given this result it is perhaps unsurprising that richness was greater in winter in *C. filiformis* habitats and in summer for unvegetated habitats (Fig. 4d).

There were significant effects of habitat type (Pseudo-F<sub>2,36</sub> 9.34, P<0.001) and location (Pseudo-F<sub>2,36</sub> 12.00, P<0.001) when exploring infaunal richness across the three habitat types (Table 1). Post-hoc tests revealed that *C. filiformis* supported a greater number of species than *Rhodymenia* spp., with unvegetated habitats supporting the lowest number of species. Atenas supported a lower number of species than the other two sites, which were not different from each other (Fig. 4e-g). There was a significant interaction between habitat and season at Santo Domingo for infaunal richness with unvegetated habitats supporting a higher number of species than *C. filiformis* habitats in the summer. During the winter there was no difference between habitats types. Richness was greater in the summer in unvegetated habitats, while species richness was similar between the two seasons in *C. filiformis* habitats (Fig. 4h).

# Density

When comparing across the three habitat types there was a significant interaction between habitat and location (Pseudo-F<sub>4,36</sub> 3.58, P<0.05), habitat and season (Pseudo-F<sub>2,36</sub> 5.52, P<0.01) and season and location (Pseudo-F<sub>2,36</sub> 4.34, P<0.05) for epifaunal density (Table 1). Post-hoc tests revealed that at Atenas *C. filiformis* habitats supported a greater density of macroinvertebrates compared to the other two habitats, which were not different from each other. At El Polvorin, both *C. filiformis* and *Rhodymenia* spp. habitats supported greater densities than unvegetated habitats, but were not different to each other. At La Bocana *Rhodymenia* spp. habitats supported a greater density of individuals than *C. filiformis*, with

unvegetated habitats supporting the lowest densities. Epifaunal densities were greater in *C. filiformis* habitats at Atenas, but there was no difference between locations for the other habitat types or between *C. filiformis* habitats at El Polvorin and La Bocana.

Post-hoc tests for the habitat by season interaction suggested that across both seasons unvegetated habitats supported the lowest densities, however, *Rhodymenia* spp supported more individuals in winter, while *C. filiformis* supported higher densities in summer. Densities were highest in summer in *C. filiformis* habitats, while there was no difference in density between seasons across the other two habitats. Finally, Atenas generally supported a higher density of individuals in the summer, while there was no difference in macroinvertebrate density between locations in winter and there was no difference in density between seasons at the other locations (Fig. 5a-c).

At Santo Domingo there was a significant interaction between habitat and season for epifaunal density (Pseudo-F<sub>1,8</sub> 106.59, P<0.05). As with epifaunal richness, *C. filiformis* supported greater densities in winter, while unvegetated habitats supported greater densities in summer (Fig. 5d).

There was no main effect of habitat or an interaction between habitat and any of the other factors for infaunal density. There was, however, an interaction between location and season for infaunal density (Pseudo-F<sub>2,36</sub> 5.30, P<0.05) (Table 1). Infaunal density was significantly higher at Atenas compared to the other two locations in both winter and summer. There was no difference between infaunal density at Atenas and La Bocana between the two seasons, but at El Polvorin a significantly higher density of macroinvertebrates was found in winter compared to summer. As with epifaunal density there was a greater density found in unvegetated habitats in winter compared to *C. filiformis* habitats, while in summer there was no difference between habitats (Habitat x season: Pseudo-F<sub>1,8</sub> 9.83, P<0.05). There was also no difference between seasons in unvegetated habitats, but densities were higher in winter compared to summer for *C. filiformis* habitats (Fig. 5e-h).

## Discussion

The drivers underpinning the southern expansion of *C. filiformis* in Peru are currently unknown, however, observations by the authors and anecdotal evidence from artisanal fishermen suggest that the arrival of *C. filiformis* has coincided with the intensification of the commercial culture of the Peruvian scallop, *Argopecten purpuratus* (Kluger et al. 2016). Commercial culturing has recently commenced at two of our study locations (Paracas and Samanco Bay) where scallops are suspended on structures (long-line) and seabed farms. The industry wild-harvests juveniles from the north of Peru (Mendo et al. 2008), where *C. filiformis* has existed for some time, to stock these culturing facilities. Due to the lack of sanitary control, the juvenile scallops are translocated with attached epibiota, including *C. filiformis* fragments (R. Uribe, pers. Ob.). It is therefore highly likely that *C. filiformis* has arrived via shellfish aquaculture, a well-known vector of invasion (Williams and Smith 2007).

In order to generate management plans for the control of invasive species, it is important to identify the consequences of their expansion on the natural communities in which they have invaded (Cevik et al. 2012; Cvitkovic et al. 2017; Villaseñor-Parada et al. 2018). This is essential for ensuring the conservation of natural ecosystems (Camus 2005; Castilla and Neill 2009), with this being especially important in regions such as the northern Humboldt Current, which support high levels of biological diversity and endemism (Uribe et al. 2013; Tasso et al. 2018; Fernández and Hooker 2020), but have been little studied. Despite habitat forming invasive species, such as *Caulerpa* spp., supporting non-natural assemblages and different levels of diversity compared to native habitats around much of the world (Gallucci et al. 2012; Pusceddu et al. 2016; Cvitkovic et al. 2017), our results show that the differences in infaunal and epifaunal assemblage structure, richness and density between *C. filiformis*, *Rhodymenia* spp. and unvegetated habitats are context dependent. When comparing across the three habitats, in general similar assemblages were supported irrespective of seasons and site. Where differences did occur these were primarily between *C. filiformis* and *Rhodymenia* spp. habitats, but these differences were site and season specific. In contrast at Santo Domingo, where comparisons were between *C. filiformis* and unvegetated habitats, there was a clear difference in the assemblage structure between the two habitats (with the exception of infaunal assemblages in winter). Richness and organismal densities were generally greater in the vegetated habitats, although at Santo Domingo this depended on season. For the vegetated habitats there was some context dependency regarding which habitat supported the greatest richness or highest densities. Other studies have shown similar context dependency with Gallucci et al. (2012) finding meiofaunal communities associated with the invasive *C. taxifolia* and native seagrass and unvegetated habitats were influenced by location, with positive, negative and neutral effects of *C. taxifolia* on meiofaunal abundance and diversity.

While these results contradict many studies, which have shown that the arrival *Caulerpa* spp. can cause the total decline of biological diversity (Box et al. 2010; Zhang et al. 2014), our results should still be considered an ecological impact in the sense that it is a change from a natural state (Underwood 1991). While it is encouraging that the arrival of this invasive species has not resulted in a reduction in biological diversity or changes to the types of assemblages supported by vegetated habitats, the biggest differences in assemblage structure, richness and density was between *C. filiformis* and unvegetated habitats. This is particularly interesting because *C. filiformis* is not displacing the native vegetated habitat, which is generally found at lower depths than *C. filiformis*, but has occupied areas that were previously unvegetated (Fig. 2a). Assemblage structure was considerably different in Santo Domingo as well as epifaunal assemblages at Atena in summer, but perhaps more striking in general, *C. filiformis* supported high richness and densities than unvegetated habitats. The arrival of *C. filiformis* seems to have created a new niche for native macroinfauna and epifauna. Similar results have been observed for the invasive alga *Undaria pinnatifida*, which preferentially occupies vertical reef compared to native kelps that occupy horizontal slopes (Hesier et al. 2014; Epstein et al. 2019).

Our study may have only found a limited impact of *C. filiformis* on infaunal and epifaunal macroinvertebrates, however, this does not mean that negative impacts may not occur into the future. Lags in the response of native communities to invaders are not uncommon (Posey 1988; Neira et al.

2005) and likely a result of time since invasion meaning the population density or areal extent of the invader is not at a level that negatively affects native communities (Crooks 2005). It may also be the case that the impacts of the invasive species are subtle and the measures that we used were not able to detect such impacts. A number of studies have suggested that the invasive kelp *U. pinnatifida* has minimal ecological impacts (Epstein and Smale 2017; South et al. 2017), however, more recent experimental research has shown that this species does have subtle, but significant impacts on some components of the native community (Epstein et al. 2019).

Given the potential for a lag in the impacts of *C. filiformis* on native communities there is a need to propose management measures for monitoring the spread and impacts of this species, including the development of spread-prevention techniques. Moreover, our study purely focused on the macroinvertebrate assemblages associated with *C. filiformis* and two native habitats. Other studies have demonstrated that *Caulerpa* sp. invasions in other regions has resulted in changes in sedimentary dynamics through the baffling effect of their fronds (Gallucci et al. 2012). Changes to organic content and redox potential, which was linked to changes infaunal assemblages (Gallucci et al. 2012). Future work should therefore, in addition, to looking at the impacts on native biodiversity also examine changes in sediment size structure, organic matter build-up and changes in redox potential.

## Declarations

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### Author's contributions

SA contributed to the data collection and samples analysis, PJM contributed to the analysis, wrote the original draft and review the final manuscript, RUA contributed to the study conception, the data collection, analysis and wrote the original draft. All authors read and approved the manuscript.

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### Data Availability

Raw data will be made openly available following publication. All data will be made available in Dryad following publication.

## Conflicts of interest

The authors declare that they have no conflict of interest.

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## Figures

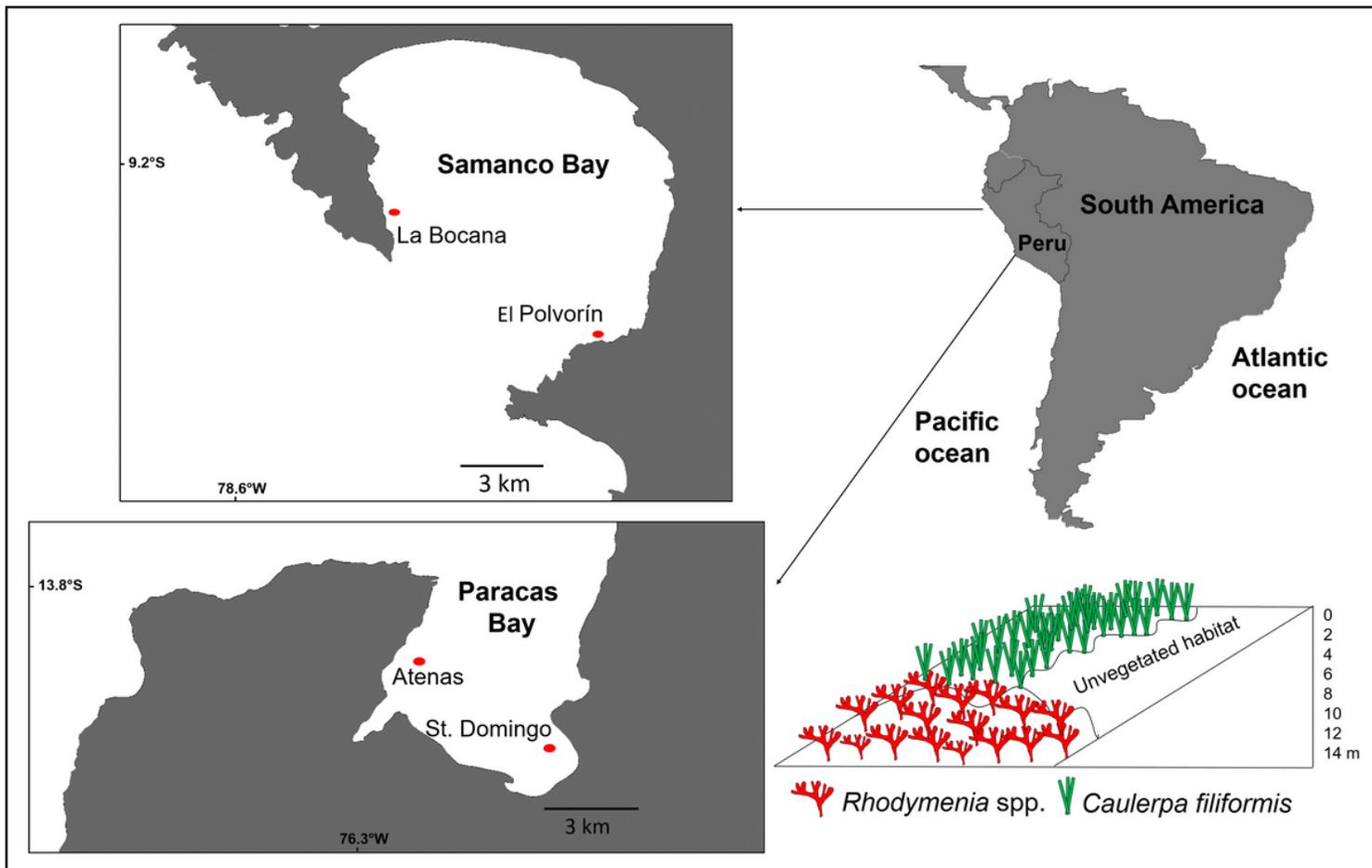


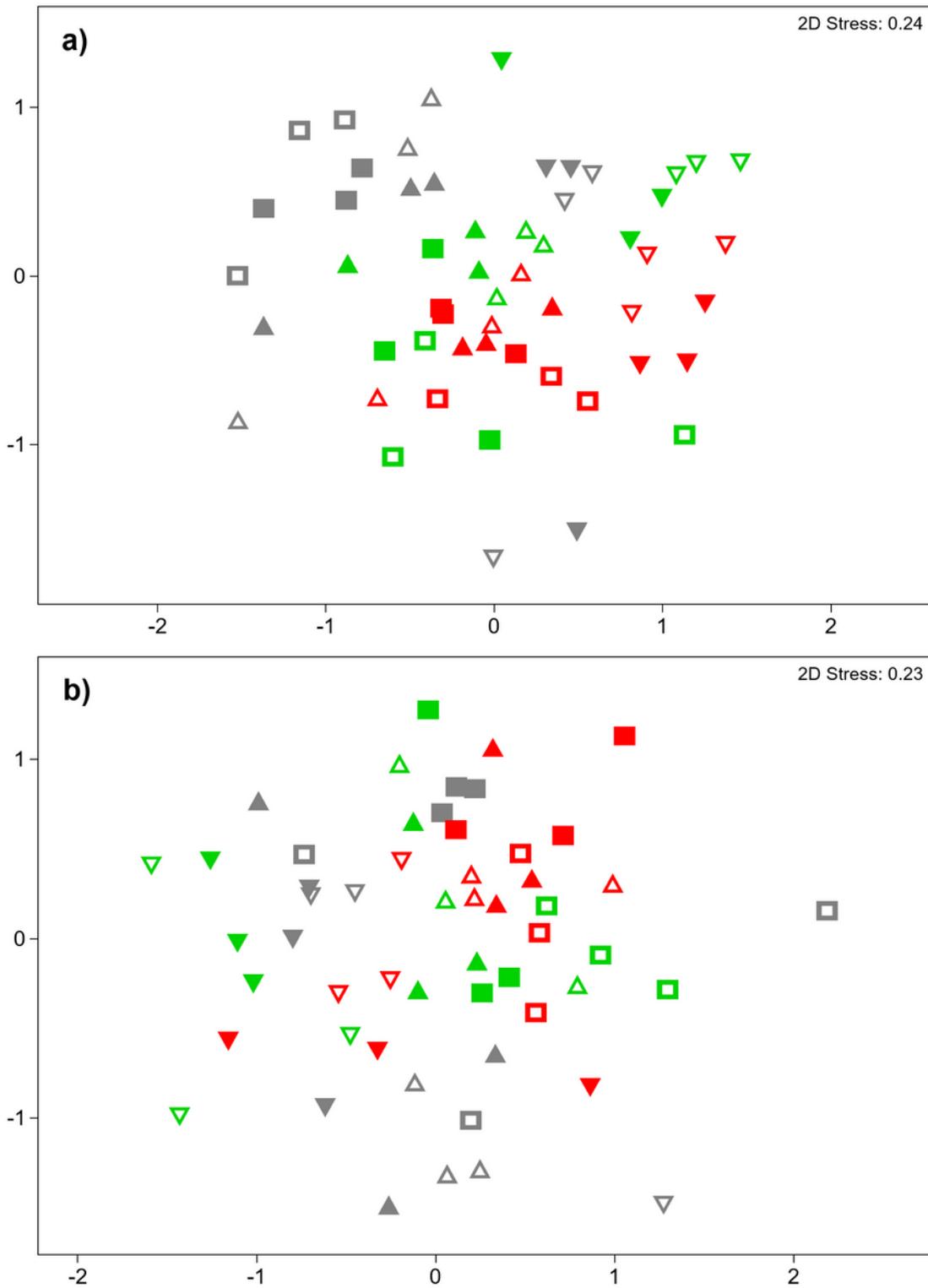
Figure 1

Map of Peru showing the embayments and the locations within the embayment that sampling was carried out. The schematic shows the bathymetric distribution of the three habitats in both bays.



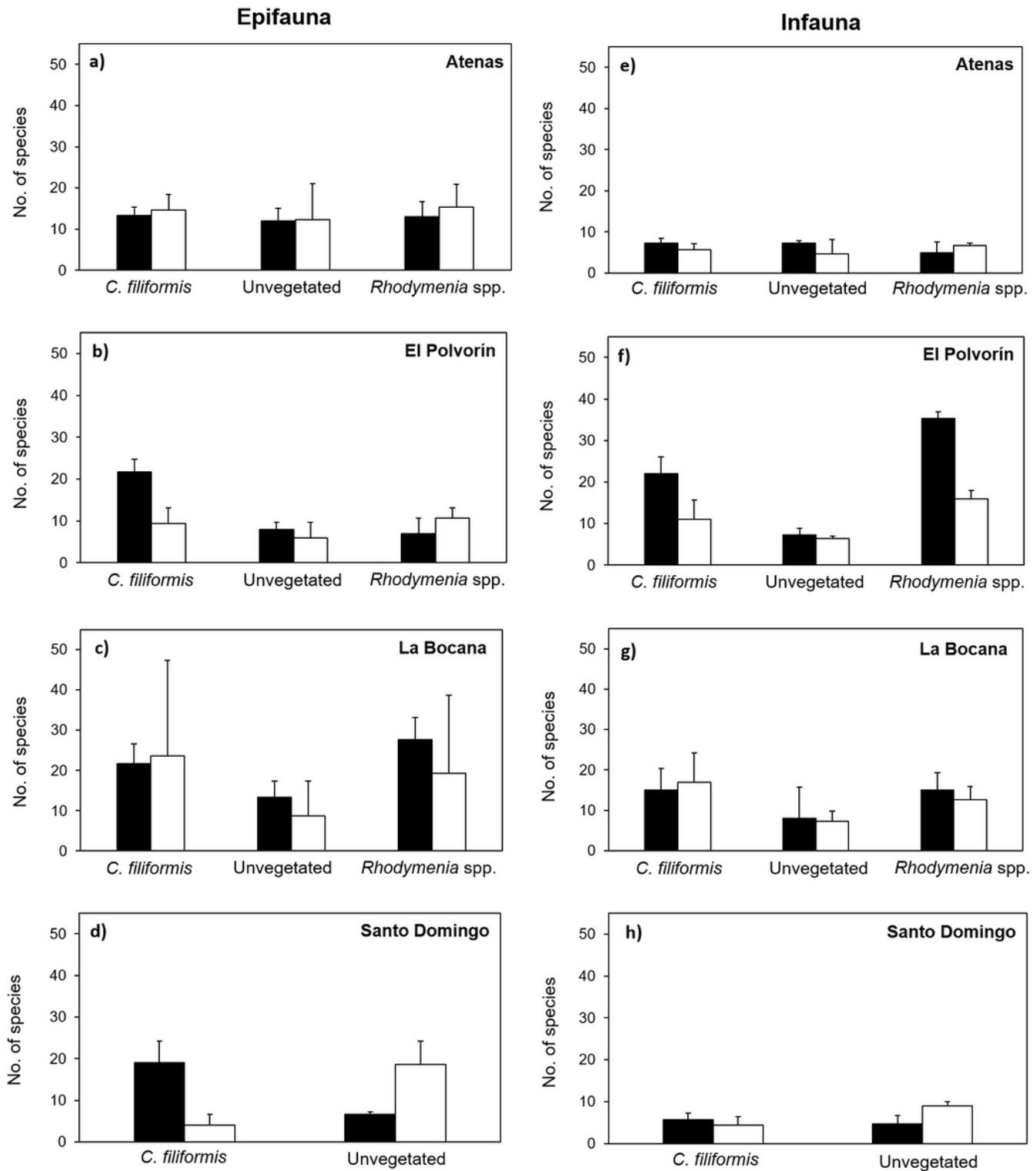
Figure 2

Photographs showing the limit between the habitat dominated by *Caulerpa filiformis* and unvegetated habitat (a) and habitat dominated by *Rhodymenia* spp. (b).



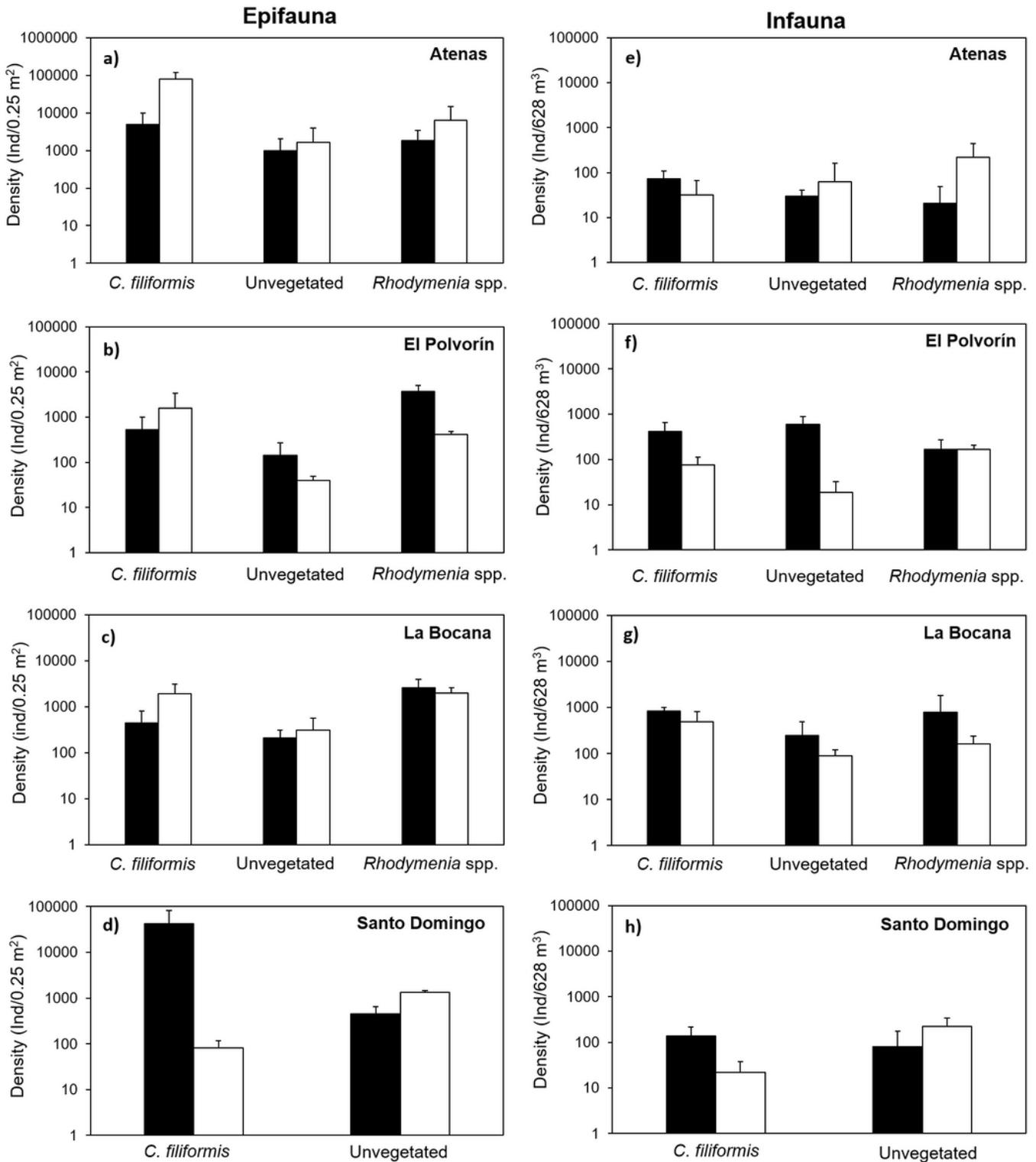
**Figure 3**

nMDS plots of a) epifaunal and b) infaunal assemblage structure across three habitats (*C. filiformis* (green), *Rhodymenia* spp. (red) and unvegetated (gray)) in the three localities (Atenas (inverted triangle), La Bocana (triangle) and El Polvorin (square)) during winter (filled symbols) 2017 and summer (unfilled symbols) 2018.



**Figure 4**

Mean (+ standard deviation) (a-d) infaunal (ind/0.25 m<sup>2</sup>) and (e-h) epifaunal (628 ind/cm<sup>3</sup>) richness found in three habitats (*C. filiformis*, unvegetated and *Rhodymenia* spp.) in Atenas, El Polvorin and La Bocana. In Santo Domingo only *C. filiformis* and unvegetated habitats were sampled. Samples were collected in winter 2017 (black bars) and summer 2018 (white bars).



**Figure 5**

Logarithm of the mean (+ standard deviation) density of epifaunal (ind/0.25 m<sup>2</sup>) (a-d) and infaunal (ind/628 cm<sup>3</sup>) (e-h) organisms found in three habitats (*C. filiformis*, unvegetated and *Rhodymenia* spp.) in Atenas, El Polvorin and La Bocana. In Santo Domingo only *C. filiformis* and unvegetated habitats were sampled. Samples were collected in winter 2017 (black bars) and summer 2018 (white bars).