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

Silvia Aguilar · Pippa J. Moore · Roberto A. Uribe

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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 time, 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.

Keywords *Rhodymenia* · Invasive species · Epifauna · Infauna · *Caulerpa* · Habitat-forming species

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 (Abdulrahah 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, turfing algae themselves can facilitate the colonization of other fast-growing invasive macroalgae such as Caulerpa spp. (Ceccherelli et al. 2002; Piazzi et al. 2003; Voerman et al. 2017, 2021). Given that many invasive macroalgae are also habitat-formers their habitat complexity potentially provides novel niches for native species (Dijkstra et al. 2017), which may in turn result in the development of non-analogue communities to those found in existing native marine vegetated habitats (Lubchenco et al. 1991; Zhang et al. 2014; Lanham et al. 2015; Suárez–Jiménez et al. 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 (M. Vahl) C. Agardh, 1817 and Caulerpa cylindracea Sonder, 1845 (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 (Ceccherelli et al. 2014), 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, 2007; Glasby et al. 2005, 2015).

Caulerpa filiformis (Suhr) Hering has been 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 suggest 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 Atuera Island (Howe 1914) and later on Piura region in northern Peru (Aceto 1973). Peruvian populations may therefore be native to Peru, however, there have clearly been recent range extensions of this species to areas where it has previously not been located. 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.

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
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that invasion by *C. filiformis* would lead to the creation of novel habitat in turn leading to altered macroinvertebrate assemblages, we predicted that assemblages in habitats formed by *C. filiformis* would be significantly different over space and time to 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 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 diversity 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 a high abundance and coverage of polychaetes (i.e., Diopatra sp., Chaetopterus sp.), and extensive patches of the red macroalgae Rhodymenia cf. corallina and at reduced densities species 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, including areas previously dominated by Rhodymenia spp. (Personal observation) (Figs. 1 and 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 (three replicates per habitat) on each of two occasions: September 2017 (winter/spring) and February 2018 (summer).

Epifauna were collected by hand from 0.25 m² quadrats. In vegetated habitats, all macroalgae were carefully removed from each quadrat with a spatula whilst minimizing disturbance of the surrounding bottom. After the area was cleared, a PVC core of 10 cm diameter to 15 cm depth (approximately 0.0078 m²) was then used to sample the infauna (e.g., Pacheco et al. 2013). In the boat, all samples were fixed with 10% formalin and transferred to the laboratory. All samples were collected between 8 and 10 m 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.

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 tested for the effects of the factors Location (three levels: La Bocana, El Polvorin and Atenas; random), Time (two levels: winter 2017 and summer 2018; random) and
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Habitat (three levels: *Caulerpa filiformis*, *Rhodymenia* spp. and unvegetated; fixed, crossed with all other factors). Data from Santo Domingo were analyzed separately, testing for the effects of 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 9999 permutations under a reduced model. Pairwise comparisons were used to identify the nature of any significant differences (α = 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.

Metric Multidimensional Scaling (MDS) 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

*Atenas, La Bocana and El Polvorín.*

For both infaunal and epifaunal assemblages there was a significant interaction between location, time and habitat type (Epifauna: Pseudo-$F_{4,36} = 1.363$; $P < 0.01$; Infauna: Pseudo-$F_{3,36} = 1.59$, $P < 0.01$). When compared across the three different habitat types, on the whole, *C. filiformis* supported similar assemblages to *Rhodymenia* spp. and unvegetated habitats across locations and time, however, epifaunal and infaunal assemblages did differ between *C. filiformis* and *Rhodymenia* spp. at La Bocana in summer (Table 1; Fig. 3). 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 sampling periods 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. Conversely, the principal drivers of dissimilarity of infaunal assemblages inhabiting *C. filiformis* were Nematoda, the Polychaeta Capitellidae and the mollusk *Caecum chilense*.

**Santo Domingo**

At Santo Domingo there was a significant interaction between time and habitat for both epifaunal and infaunal assemblages (Epifaunal: Pseudo-$F_{1,8} = 8.18$, $P < 0.01$; Infauna: Pseudo-$F_{1,8} = 2.37$, $P < 0.05$). With the exception of infaunal samples collected in the winter, epifaunal and infaunal assemblages were significantly different between *C. filiformis* and unvegetated habitats (Table 2). Assemblage structure also differed between times 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 (Table 3) and infaunal (Table 4) assemblages respectively.

Epifaunal and Infaunal Richness

*Atenas, La Bocana and El Polvorín*.

There was a significant interaction between location and time (Pseudo-$F_{2,36} = 6.92$, $P < 0.01$) and significant effect of habitat (Pseudo-$F_{2,36} = 4.96$, $P < 0.05$) for epifaunal richness (Table 1). While significant, post-hoc tests no significant difference at $P < 0.05$, between habitat types, but *Caulerpa* and *Rhodymenia* spp. assemblages tended towards being significantly different ($P = 0.06$). In terms of the location by time
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 time periods while richness differed between the two time periods at the other two locations (Fig. 4a–c). There were no significant effects across any of the factors of interest when exploring infaunal richness (Table 1; Fig. 4e–g).

Santo Domingo

Epifaunal richness showed a habitat by time interaction (Pseudo-F_{1,8} = 38.5, P < 0.01) (Table 2) 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 was a significant interaction between habitat and time at Santo Domingo for infaunal richness (Table 2) 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

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**Table 1** Permutational analysis of variance (PERMANOVA) examining differences in (a) assemblage structure, (b) richness and (c) density of epifaunal and infaunal macroinvertebrates for the sites Atenas, La Bocana and El Polvorín. Significant values are indicated in bold with a significance level of $P < 0.05$

| Source               | Epifauna | Infauna |
|----------------------|----------|---------|
|                      | df  | MS    | Pseudo-F | p  | df  | MS    | Pseudo-F | p  |
| (a) Assemblage       |     |       |          |    |     |       |          |    |
| Location (Loc)       | 2   | 14,514| 3.5724   | 0.0979| 2   | 12,077| 2.189    | 0.1615|
| Time (Tim)           | 1   | 4324.4| 1.0644   | 0.3712| 1   | 5211.7| 0.9446   | 0.4815|
| Habitat (hab)        | 2   | 25,245| 1.4618   | 0.2105| 2   | 8784.7| 1.2822   | 0.2545|
| Tim x Loc            | 2   | 8125.5| 1.7659   | 0.0004| 2   | 5517.1| 2.1685   | 0.0006|
| Loc x Hab            | 4   | 26,829| 2.146    | 0.0126| 4   | 5914.3| 1.4595   | 0.1371|
| Tim x Hab            | 2   | 8132.2| 1.3009   | 0.2649| 2   | 4097.5| 1.0112   | 0.4707|
| Loc x Tim x Hab      | 4   | 12,502| 1.3585   | 0.0258| 4   | 4052.2| 1.5927   | 0.004 |
| Res.                 | 36  | 82,826 |         |       | 36  | 2544.2|         |       |
| Total                | 53  | 53    |          |       | 53  | 53    |          |       |

(b) Richness

| Source               | Epifauna | Infauna |
|----------------------|----------|---------|
|                      | df  | MS    | Pseudo-F | p  | df  | MS    | Pseudo-F | p  |
| Location (Loc)       | 2   | 1.9396| 0.9325   | 0.4945| 2   | 4.7189| 18.631   | 0.1005|
| Time (Tim)           | 1   | 3.6744| 1.7665   | 0.3133| 1   | 0.7171| 2.8315   | 0.272 |
| Habitat (hab)        | 2   | 9.6843| 4.9632   | 0.0475| 2   | 3.6743| 2.6686   | 0.1393|
| Tim x Loc            | 2   | 2.08  | 6.925    | 0.0018| 2   | 0.2532| 0.64414  | 0.5391|
| Loc x Hab            | 4   | 1.7372| 2.3411   | 0.2158| 4   | 0.8507| 0.98159  | 0.5149|
| Tim x Hab            | 2   | 0.3635| 0.4898   | 0.6435| 2   | 0.8508| 0.98171  | 0.4547|
| Loc x Tim x Hab      | 4   | 0.74204| 2.4705   | 0.0592| 4   | 0.86673| 2.2043   | 0.0847|
| Res.                 | 36  | 0.30036|         |       | 36  | 0.3932|         |       |
| Total                | 53  | 53    |          |       | 53  | 53    |          |       |

(c) Density

| Source               | Epifauna | Infauna |
|----------------------|----------|---------|
|                      | df  | MS    | Pseudo-F | p  | df  | MS    | Pseudo-F | p  |
| Location (Loc)       | 2   | 19,110| 1.7768   | 0.3612| 2   | 583.68| 2.8565   | 0.2845|
| Time (Tim)           | 1   | 9045.7| 0.84104  | 0.5633| 1   | 384.43| 1.8814   | 0.2851|
| Habitat (hab)        | 2   | 15,475| 0.94689  | 0.5191| 2   | 108.89| 1.1627   | 0.4389|
| Tim x Loc            | 2   | 10,755| 14.126   | 0.0001| 2   | 204.33| 5.2962   | 0.0077|
| Loc x Hab            | 4   | 10,668| 2.2326   | 0.2116| 4   | 96.881| 1.0989   | 0.4623|
| Tim x Hab            | 2   | 10,721| 2.2436   | 0.2202| 2   | 72.595| 0.82347  | 0.4944|
| Loc x Tim x Hab      | 4   | 4778.4| 6.2758   | 0.0006| 4   | 88.157| 2.285    | 0.072 |
| Res.                 | 36  | 761.4 |         |       | 36  | 38.581|         |       |
| Total                | 53  | 53    |          |       | 53  | 53    |          |       |
species richness was similar between the two time periods in *C. filiformis* habitats (Fig. 4h).

Epifaunal and infaunal density

**Atenas, La Bocana and El Polvorín**

When comparing across the three habitat types there was a significant interaction between habitat, time and location (Pseudo-$F_{4,36} = 6.27$, $P<0.01$) 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.

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 time for infaunal density (Pseudo-F\textsubscript{2,36} = 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 time periods, but at El Polvorin a significantly higher density of macroinvertebrates was found in winter compared to summer (Fig. 5e–h).

**Santo Domingo**

At Santo Domingo there was a significant interaction between habitat and time for epifaunal density (Pseudo-F\textsubscript{2,36} = 12.1, P < 0.05). As with epifaunal richness, C. filiformis supported greater densities in winter, while unvegetated habitats supported greater densities in summer (Fig. 5d).

**Discussion**

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 system, 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 while there was some variability in responses across locations and between the different sampling periods, on the whole assemblage structure and species richness was similar across the three habitats at three of the four locations sampled. In Santo Domingo assemblage structure consistently differed between C. filiformis and unvegetated habitats.
Habitat formed by the invasive macroalga *Caulerpa filiformis* (Suhr) Hering (Caulerpales,…)

A more consistent pattern was found with regards to density of both infauna and epifauna which was higher in the vegetated habitats. There was, however, no difference in the density of macroinvertebrates between the two vegetated habitats. 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 of *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 in state through the arrival of a new novel habitat (Underwood 1991). While it is encouraging that the arrival of *C. filiformis* 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 were between *C. filiformis* and unvegetated habitats. This is particularly interesting because *C. filiformis* is not primarily 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 higher richness and densities than unvegetated habitats. The arrival of *C. filiformis* seems to have created a new habitat 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 (Heiser et al. 2014; Epstein et al. 2019a, b).

Table 3 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      |            |            |          |           |            |       |
| 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      |            |            |          |           |            |       |
| 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 |
| *Caecum chilense* | 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      |            |            |          |           |            |       |
| 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 |
| *Caecum chilense* | 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 |
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* spp. 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 to 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.

| (1) Group | Av. Abund. | Av. Abund. | Diss./SD | Av. Diss. | Contrib.% | Cum.% |
|-----------|------------|------------|----------|-----------|-----------|-------|
| *C. filiformis* | 3.54 | 3.75 | 9.75 | 0.85 | 11.16 | 11.16 |
| Unvegetated | 3.71 | 1.7 | 7.52 | 0.71 | 9.61 | 10.37 |
| Tanaidacea | 2.03 | 1.46 | 6.08 | 0.79 | 6.66 | 13.42 |
| *Caecum chilense* | 2.82 | 2.29 | 5.82 | 0.6 | 6.66 | 13.42 |
| Ostracoda | 2.57 | 2.16 | 5.65 | 0.95 | 6.46 | 20.58 |

Average dissimilarity = 87.35

| (2) Group | Av. Abund. | Av. Abund. | Diss./SD | Av. Diss. | Contrib.% | Cum.% |
|-----------|------------|------------|----------|-----------|-----------|-------|
| *C. filiformis* | 3.54 | 6.21 | 11.39 | 1.04 | 13.15 | 13.15 |
| *Rhodymenia* spp. | 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 |

Average dissimilarity = 86.60

| (3) Group | Av. Abund. | Av. Abund. | Diss./SD | Av. Diss. | Contrib.% | Cum.% |
|-----------|------------|------------|----------|-----------|-----------|-------|
| *Rhodymenia* spp. | 2.29 | 3.06 | 6.63 | 0.54 | 7.6 | 22.13 |
| Unvegetated | 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 |

Average dissimilarity = 87.20
Habitat formed by the invasive macroalga *Caulerpa filiformis* (Suhr) Hering (Caulerpales,…

Fig. 4 Mean (+ standard deviation) a–d infaunal (ind/0.25 m²) and e–h epifaunal (ind/core (0.0078 m²)) 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).
Fig. 5 Logarithm of the mean (+ standard deviation) density of epifaunal (ind/0.25 m²) a–d and infaunal (ind/core (0.0078 m²)) 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).
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Author contribution 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, wrote the original draft and review the final manuscript. 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.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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