The ecological condition of vermetid platforms affects the cover of the alien seaweed Caulerpa cylindracea

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Summary: The seaweed Caulerpa cylindracea Sonder is one of the most important invaders on Mediterranean rocky shores. However, many driving pressures affecting its spread are poorly understood and seem to involve the interactions between abiotic and biotic factors. We studied the invasiveness of C. cylindracea on two shallow vermetid platforms with a contrasting ecological status on which C. cylindracea was first detected simultaneously 15 years ago. The cover values of C. cylindracea and the other macroalgal species were assessed for one year, embracing the whole platform width. Caulerpa cylindracea cover was higher on the platform that had a low ecological status, especially during warmer months at the outer seaward margin. The ecological status of the overstory of native species seems to be a key point conditioning the success of C. cylindracea invasiveness on these platforms.

Keywords: rocky shores; phytobenthos; community composition; Caulerpa cylindracea; vermetid platforms; man-induced effects; Mediterranean.

El estado ecológico de las plataformas de vermétidos afecta la cobertura de la especie exótica Caulerpa cylindracea

Resumen: El alga Caulerpa cylindracea Sonder es una de las principales especies invasoras de las costas rocosas mediterráneas. Sin embargo, muchos condicionantes que afectan su proliferación son poco conocidos y parecen ser el resultado de la interacción entre factores bióticos y abióticos. Estudiámos la invasividad de C. cylindracea en dos plataformas de vermétidos que presentan un estado ecológico contrastado y en las que se detectó simultáneamente C. cylindracea hace 15 años. Los valores de cobertura de C. cylindracea y del resto de macroalgas fueron evaluados durante un año abarcando toda la anchura de la plataforma. La cobertura de C. cylindracea fue mayor en la plataforma que presentaba un pobre estado ecológico, especialmente durante los meses cálidos y en el margen externo y más expuesto de la plataforma. El estado ecológico del dosel, formado por las especies nativas, parece un condicionante clave en el éxito de la invasividad de C. cylindracea en estas plataformas de vermétidos.

Palabras clave: costas rocosas; fitobentos; composición de la comunidad; Caulerpa cylindracea; plataformas de vermétidos; efectos antropogénicos; Mediterráneo.

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INTRODUCTION

The Mediterranean Sea hosts over 80 introduced macrophyte species (Boudouresque and Verlaque 2002), so it is considered a hotspot for marine alien species (Rilov and Galil 2009). At least one-ninth of them are invasive, affecting food provision for human consumption, natural cycling of nutrients, diversity and
complexity of assemblages and cultural services such as recreational uses (Katsanevakis et al. 2014). The introduced species Caulerpa cylindracea Sonder has shown notorious effects (Montefalcone et al. 2015). Its vegetative propagation by fragmented thalli allows it to attach itself to anchors and disperse by drifting. Marinas and harbours are the putative focus from which it starts to expand locally (Verlaque et al. 2003, Cantasano et al. 2017), as has been observed for its conspecific invader Caulerpa taxifolia (Vahl) Agardh (Boudouresque et al. 1995). Moreover, the invasiveness from harbours and marinas to the neighbouring urban shores could be facilitated by the usually higher values of some human-induced stressors such as eutrophication and sedimentation, which also affect the native recipient assemblages (Connell et al. 2008), generating synergistic effects between the invader and the stressors mentioned above (Bulleri et al. 2010, Gennaro and Piazzì 2011, Airoldi et al. 2015). The invasion of C. cylindracea has serious effects on recipient communities, but assemblages with large canopy-forming species seem to dampen the effects of the invasion (Ceccherelli et al. 2002). Thus, the impact on recipient communities could be related to their state of health, degraded ones being more prone to invasion because of the increased supply of limiting resources such as nutrients (due to eutrophication), or light and space when recipient canopy-forming species decrease in cover, allowing the spread of the exotic ones (Hueneke et al. 1990, Marín-Guirao et al. 2015). Many studies have detected that unhealthy native communities usually show higher cover values of C. cylindracea than healthy ones with a good status of canopy-formers, either involving seaweeds and seagrasses (Ruitton et al. 2005, Ceccherelli et al. 2014, Bulleri et al. 2017) or gorgonians (Ponti et al. 2018). Furthermore, the homogenization effect on community composition and structure caused by the invasion could involve other processes such as impaired fish recruitment (Cheminée et al. 2016).

In the eastern Iberian Peninsula, C. cylindracea recently spreads over the coastal area between Catalonia (García et al. 2015) and Andalusia (Altamirano et al. 2014), where it shows a similar distribution pattern to that reported in other Mediterranean regions (Verlaque et al. 2003, Klein and Verlaque 2008). Thus, it thrives in shallow subtidal waters and in deep subtidal habitats beyond 30 m depth. It is more abundant on margins of Posidonia meadows or on dead Posidonia mat but also colonizes maerl bottoms and photophilous assemblages (Ruiz et al. 2011, Enguix et al. 2014, García et al. 2015).

The detection of C. cylindracea in vermetid platforms of the southeastern Iberian Peninsula (Pena-Martín et al. 2003) and its high cover values in some locations could shed light on the drivers fostering or hampering its invasiveness.

Vermetid platforms constitute a distinctive Mediterranean habitat, yet it has been highly neglected to the present day (Milazzo et al. 2016). These shallow systems are present in southeastern Iberian littoral shores (Templado et al. 2016) and other warm Mediterranean areas and subtropical seas (Laborel and Kempf 1965, Safriel 1975). Vermetid platforms are well developed in limestone rocks, and their assemblages show a distinctive zonal pattern. Thus, in non-degraded situations, an outer vermetid rim is followed by fucoid algae forming a continuous belt on relatively exposed shores. In less exposed situations, such as in the inner parts of such platforms, low stands of smaller algae flourish and include dictyotacean algae as an important group. Encrusting corallines with vermetids also dominate the innermost part. Vermetid platforms harbour many Mediterranean endemisms and contribute to the increase in regional diversity as a result of the environmental gradient generated over the platform (Milazzo et al. 2016). The shallowness of these platforms entails that these systems are subjected to many anthropogenic stressors (Ballesteros et al. 2007). Thus, the vermetid platforms in the eastern Mediterranean have been severely impaired in a few decades (Galil 2013, Badreddine et al. 2019). Putative reported drivers of this impoverishment are the rise in sea level, global warming, trampling, acidification and all factors linked to human activities, including water deterioration (Milazzo et al. 2004, 2014, Badreddine et al. 2019). As for bioinvasions, little direct information has been reported despite their likely effects on these platforms. The invasive red sea mussel Brachydontes pharaonis (Fisher, 1870) is colonizing the vermetid platforms in the eastern Mediterranean, spreading towards the west (Milazzo et al. 2016). This invasive species was considered an inferior competitor to the native ones, but by increasing the pool of recruits, it became dominant at the expense of other indigenous sessile species (Rilov et al. 2004, Didham et al. 2007). Little is known about the effects of C. cylindracea on these shallow systems. In vermetid platforms with undegraded macroalgal communities, C. cylindracea has been mainly reported in a patchy distribution within the vermetid platform, in most cases with low cover values. The alga grew intermingled with the thalli of other macroalgae without any clear relationship between the abundance values of C. cylindracea and those of the dominant macroalgae (Ramos-Esplá et al. 2008, Balistreri and Mannino, 2017). However, in the south of Alicante Bay, we detected high cover values of C. cylindracea on degraded vermetid platforms distinguished by their degraded macroalgal composition, which is attributable to the eutrophication of Alicante Bay (Aranda et al. 1994, Aguilar 2009). The C. cylindracea population of degraded vermetid platforms contrasts with the low cover values observed in the nearby location of Cabo de las Huertas, though both locations happen to be the first ones where this invasive species was detected in Alicante province 15 years ago (Pena-Martín et al. 2003, Terradas-Fernández et al. 2018). In order to understand whether the ecological status of vermetid platforms could be involved in the abundance of C. cylindracea, an annual survey was carried out in both locations, comparing the abundance of the macroalgal species forming overstory with the abundance of C. cylindracea. Environmental variables informative of anthropogenic affectation (sediment cover and nutrient concentration) were also measured. Hypotheses that could explain any differences regarding the cover of C. cylindracea and the ecological...
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status of the recipient macroalgal communities were discussed.

MATERIALS AND METHODS

Study site

The study took place in two ecologically contrasting locations with shallow vermetid platforms in Alicante, Spain, southwestern Mediterranean (Fig. 1). One location was Cabo de las Huertas, on the north side of Alicante Bay (38°21′10″N, 0°25″W), with no signs of severe alteration due to anthropogenic stressors (Terradas-Fernández et al. 2018), and the other was Aguamarga, located in the south of Alicante (38°18′06″N, 0°31′05″W).

Aguamarga is close to the port of Alicante and near the sewage outfalls of a waste treatment plant. The vermetid reefs are completely degraded, but some dead vestiges have been reported (Aranda et al. 1994 and references therein). According to Aranda et al. (1994), the main putative cause of this degradation is the high nutrient concentration attributed to eutrophication. Both locations are currently monitored to evaluate the ecological status at a regional scale to implement the European Water Framework Directive (WFD, 2000/60/FC). Several reports confirm the persistent contrasting ecological status of the two locations, Aguamarga being a “bad status spot” surrounded by rocky shores showing a better ecological status (Ramos-Esplà et al. 2011). Thus, we will consider Cabo de las Huertas henceforward as the non-degraded location and Aguamarga as the degraded one.

The invasive species C. cylindracea has occupied the shallow platforms of both locations for at least 15 years since it was first detected in the province of Alicante (Pena-Martín et al. 2003, Ramos-Esplà, pers. comm.).

Sampling and data collection

Three 10-m-long sites parallel to the shore and 20 m apart were chosen at each location. An exhaustive check was previously conducted throughout the platform system in order to find representative sites with similar platform widths between locations. Three zones parallel to the shore were established at each assigned site along the platform: a) the inner zone (ca. 2 m width), which was located in the innermost part of these platforms; b) the mid-platform zone, which occupied most of the platform (ca. 5 m width); c) and the exposed outer margin zone (the outer platform zone) in the seaward direction (ca. 1 m width) (Fig. 2).

The sampling was carried out on a flat, homogeneous platform, avoiding crevices, cuvettes or sloped surfaces. The study lasted for one year, and surveys were carried out approximately every month. In every survey, three random replicates were sampled in every zone at each site. Each sampled replicate had a surface area of 625 cm², wherein the cover of each taxon was calculated using a quadrat subdivided into 25 subquadrats, giving a score from zero to four on each one (Dethier et al. 1993). All zones were surveyed at their midpoint at each site. The platforms had similar widths at both locations (ca. 8 m). Sediment cover was measured using the same criteria as those applied to taxa cover (Terradas-Fernández et al. 2018).

Water-dissolved nutrients (phosphates, nitrates, nitrites and ammonia) were analysed just beyond the outer zone (0.3 m depth) at intervals of 1-2 months using two 50 mL plastic falcons per location to sample (n=2). The seawater was filtered using a Maroon PVDF Syringe Filter with a pore size of 0.45 µm and frozen. The analysis was carried out using an Automated Wet Chemistry Analyser (Skalar Analytical B.V., Breda, the Netherlands).
Data analysis

In order to test whether assemblages were significantly different throughout a year, a similarity matrix was generated on the basis of taxa cover values using the Bray-Curtis distance. The cover values were square-root transformed to lower the effects of the dominant taxa. A permutational multivariate analysis of variance (PERMANOVA) was performed to analyse the multivariate assemblage data using a four-way analysis to test the effects of location (a fixed factor with three levels: outer platform zone, mid-platform zone and inner platform zone) and location (a fixed factor with two levels: degraded and non-degraded), zone (a fixed factor with three levels: outer platform zone, mid-platform zone and inner platform zone) and date (a fixed factor with 12 levels: 12 surveys). Site (3 levels) was a random factor nested in location. A principal coordinate ordination (PCO) was performed to organize samples according to their assemblage composition, pooling replicates and sites by calculating distance between centroids. Another PCO without pooling was performed to visualize the vector overlay composition, pooling replicates and sites by calculating distance between centroids. Another PCO without pooling was performed to visualize the vector overlay composition, pooling replicates and sites by calculating distance between centroids.

Assemblages

With regard to species composition, there was a significant interaction effect between location, zone and date (Table 1A). Furthermore, pairwise tests show that the effect was maintained throughout the year among all levels of these fixed factors (Table 1B). The PCO shows that location was the main factor affecting the arrangement of the samples during the entire annual cycle (Fig. 4A). The most distinctive species of the degraded location were Ellisolandia elongata (Ellis and Solander) Hind and Saunders, Ulva laetevirens Areischou and Derbesia tenissima (Moris and De Notaris) Crouan and Crouan, whereas the “Laurencea complex” (mainly Palissada tenerrima (Cremades) Serio, Cormaci, Furnari and Boisset), Jania spp., Padina pavonica (Linnaeus) Thivy and Dictyota spp. (mainly Dictyota spiralis Montagne and Dictyota fasciola (Roth) Lamouroux) were the most distinctive ones of the non-degraded location. Turf species (germlings and small caespitose algae) were more abundant at the degraded location and on the inner margin of the non-degraded one. At the degraded location, most taxa included in this category were small green filamentous algae, Ceramium complex, Herposiphonia tenella (Agardh) and Erythrotrichiaceae, whereas at the non-degraded location that group was dominated by an eclectic component of Ceramiaceae and Rhodomelaceae (Ceramium spp., Spyridia filamentosa (Wulfen) Harvey; Herposiphonia secunda (C. Agardh) Ambroon; Lo-
Table 1. – A, summary of a four-factor PERMANOVA test (with location, zone, date and site nested in location) comparing all taxa cover values from all the samples. Lo, location; Zo, zone; Da, date; Si, site; (*) Monte Carlo p-value=0.001. B, pairwise tests for the term ‘Lo×Zo×Da’ for pairs of levels of factor ‘Location’ (Monte Carlo p-values).

| Source of variation    | df | SS     | MS     | Pseudo-F | p(perm) | Permutations |
|-----------------------|----|--------|--------|----------|---------|--------------|
| Lo                    | 1  | 6.04E+09 | 6.04E+09 | 252.46   | 0.093   | 10*          |
| Zo                    | 2  | 1.33E+09 | 6.66E+04 | 39.863   | 0.001   | 999          |
| Da                    | 11 | 2.48E+05 | 2.39E+04 | 13.457   | 0.001   | 997          |
| Si(Lo)                | 4  | 9.57E+03 | 2.39E+03 | 38.653   | 0.001   | 998          |
| Lo×Zo                 | 2  | 1.20E+09 | 5.99E+04 | 35.88    | 0.001   | 999          |
| Lo×Da                 | 11 | 1.95E+09 | 1.77E+04 | 10.583   | 0.001   | 999          |
| Zo×Da×Si(Lo)          | 22 | 1.59E+09 | 7.20E+03 | 5.654    | 0.001   | 998          |
| Zo×Si(Lo)             | 8  | 1.36E+03 | 1.67E+03 | 26.975   | 0.001   | 999          |
| Da×Si(Lo)             | 44 | 7.37E+03 | 1.67E+03 | 27.055   | 0.001   | 998          |
| Lo×Zo×Da              | 22 | 1.23E+09 | 5.57E+04 | 43.622   | 0.001   | 998          |
| Zo×Da×Si(Lo)          | 88 | 1.12E+09 | 1.27E+05 | 20.622   | 0.001   | 997          |
| Residual              | 432| 2.68E+09 | 6.19E+03 |          |         |              |

B, PAIRWISE TESTS for the term ‘Lo×Zo×Da’ for pairs of levels of the factor ‘Location’

| Date       | Inner zone | Mid-zone | Outer zone |
|------------|------------|----------|------------|
| 09/10/2016 | 0.001      | 0.004    | 0.003      |
| 08/12/2016 | 0.001      | 0.001    | 0.001      |
| 02/01/2017 | 0.006      | 0.001    | 0.001      |
| 25/02/2017 | 0.002      | 0.001    | 0.001      |
| 26/05/2017 | 0.003      | 0.001    | 0.001      |
| 03/05/2017 | 0.001      | 0.001    | 0.001      |
| 30/05/2017 | 0.001      | 0.001    | 0.001      |
| 04/07/2017 | 0.004      | 0.001    | 0.001      |
| 18/08/2017 | 0.006      | 0.002    | 0.001      |
| 30/09/2017 | 0.006      | 0.001    | 0.001      |
| 28/10/2017 | 0.003      | 0.001    | 0.001      |
| 18/11/2017 | 0.001      | 0.007    | 0.001      |

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phosphiponia spp., Polysiphonia spp.). Among all these taxa, Jania spp., the Laurencia complex, P. pavonica and Dictyota spp. at the non-degraded location and E. elongata, Jania spp. and U. laetevirens at the degraded one were the main overstory-formers.

The abundance pattern of overstory during an annual cycle in each zone differed by location and date according to the marginal interaction effect found between these fixed factors (p=0.051) (Table 2, Fig. 5). There was an increasing trend in overstory cover towards the outer margin (middle and outer zones), and the degraded location showed greater variability over time. This variability was dampened in the outer platform zone, where there was still a sharp drop in June and July 2017. Additionally, the non-degraded location had a higher turnover of overstory species, not only between zones but also over time, whereas in the degraded one that overstory role was mostly carried out by E. elongata, and to a lesser extent by Jania spp. (Figs 5, 6).

**Distribution pattern of C. cylindracea**

Caulerpa cylindracea abundance was also affected by the interaction between location, zone, and date.
Table 3. – A, summary of a four-factor PERMANOVA univariate test (with location, zone, date and site nested in location) comparing *Caulerpa cylindracea* cover values from all the samples. Lo, location; Zo, zone; Da, date; Si, site; (*) Monte Carlo p-value=0.001. B, pairwise tests for the term ‘Lo×Zo×Da’ for pairs of levels of the factor ‘Location’ (Monte Carlo p-values).

### A. four-factor PERMANOVA test

| Source of variation | df | SS   | MS   | Pseudo-F | p(perm) | Permutations |
|---------------------|----|------|------|----------|---------|--------------|
| Lo                  | 1  | 3468.1| 3468.1| 575.93   | 0.107   | 10*          |
| Zo                  | 2  | 519.49| 259.74| 7.25     | 0.024   | 999          |
| Da                  | 11 | 11400 | 1036.4| 50.43    | 0.001   | 999          |
| Si(Lo)              | 4  | 24.086| 6.0216| 0.196    | 0.944   | 999          |
| LoxZo               | 2  | 64.623| 32.312| 0.90     | 0.409   | 999          |
| LoxDa               | 11 | 10324 | 938.59| 45.671   | 0.001   | 998          |
| ZoxDa               | 22 | 8436.9| 383.49| 10.763   | 0.001   | 998          |
| ZoxSi(Lo)           | 8  | 286.71| 35.839| 1.1702   | 0.312   | 998          |
| DaxSi(Lo)           | 44 | 904.24| 20.551| 0.67     | 0.961   | 999          |
| LoxZoxDa            | 22 | 10177 | 462.6 | 12.98    | 0.001   | 998          |
| ZoxDaxSi(Lo)        | 88 | 31354 | 35.63 | 1.16     | 0.159   | 996          |
| Res                 | 432| 13231 | 30.627|          |         | 996          |

### B. PAIRWISE TESTS for the term ‘Lo×Zo×Da’ for pairs of levels of the factor ‘Location’

| Date       | Inner zone | Mid-zone | Outer zone |
|------------|------------|----------|------------|
| 09/10/2016 | 0.003      | 0.002    | 0.064      |
| 08/12/2016 | 0.061      | 0.067    | 0.029      |
| 02/01/2017 | -          | 0.082    | 0.155      |
| 25/02/2017 | 0.372      | 0.56     | 0.062      |
| 26/03/2017 | 0.266      | -        | 0.009      |
| 03/05/2017 | 0.357      | 0.3      | 0.2        |
| 30/05/2017 | 0.203      | 0.089    | 0.004      |
| 04/07/2017 | 0.012      | 0.047    | 0.004      |
| 18/08/2017 | 0.154      | 0.041    | 0.061      |
| 30/09/2017 | 0.433      | 0.259    | 0.408      |
| 28/10/2017 | -          | -        | 0.034      |
| 18/11/2017 | -          | 0.389    | 0.696      |

Fig. 5. – Temporal dynamics in the cover of overstory (black dots) and *C. cylindracea* (white dots) under non-degraded (white background) and degraded (grey background) conditions in the zones distributed along the shallow vermetid platforms. Data from a current survey being carried out at the degraded location (2019) are also shown (right column).
(Table 3A). It usually showed higher cover values in the degraded location and the outer platform zone, but cover values showed a temporal variability (Fig. 4B, Table 3B). At the non-degraded location, the cover values were low during an entire annual cycle, whereas at the degraded one there was a peak during June and July 2017 in the middle and outer platform zones, and another peak in October 2016 in the inner and middle platform zones (Fig. 5). These peaks always coincided with the low cover values of the overstory. The same pattern is shown in a current survey being carried out at the same degraded location. In this case, the July peak is not observed in the outermost zone, where overstory values remained high (Fig. 5).

DISCUSSION

In this study, the main differences in the composition of assemblages between locations are even greater than those within them along the entire platform width. Local drivers acting at the degraded location could explain the sharp differences found between locations. However, the specific causes driving a community shift in urban areas are still an open issue (Benedetti-Cecchi et al. 2001, Bertocci et al. 2017, Mancuso et al. 2018) and are far beyond the scope of this study. Even so, the correlation between urbanization and the replacement of fucoid algae and other phaeophycean groups by *E. elongata* is well known in the Mediterranean Sea (Pinedo et al. 2007, Mangialajo et al. 2008, Pinedo and Ballesteros 2019), pointing to eutrophication and sedimentation among the most essential drivers of change in anthropogenic-affected habitats (Munda 1993, Airoldi 2003, Pinedo et al. 2015). Moreover, these factors could interact synergistically, favouring the growth of turf algae that hampers the recruitment of other algal species (Gorgula and Connell 2004).

Being correlative, the results of this study do not reveal any cause-effect relationship between the low ecological status of the degraded location and its values in nutrient concentration and sediment cover. Furthermore, the high variability found leads to difficulties in interpreting the role of these variables at both locations, though at the degraded location there is a slight trend towards higher values of sediment cover and nutrient concentration.

The higher algal cover values found in the outer zones of each location could easily be related to the fact that their productivity potential (Steneck and De-thier 1994) is higher than that of the inner ones (Ter-
radas-Fernández et al. 2018) and to the lower effect of low sea level events (pers. obs.). There is a clear homogenization of assemblages at the degraded location, where *E. elongata* determines its annual dynamics. The decline episodes in these articulated algae could be related to natural stressors such as low sea level events, high light intensity and high temperatures, all of which could act together, intensifying this decline. These episodes have also been reported, especially during summer months, in other very shallow systems dominated by articulated corallines (Benedetti-Cecchi and Cinelli 1994, Guerra-García et al. 2011, Bertocci et al. 2012). On the other hand, at the non-degraded location, the greater diversity in species and their temporal replacement keep a high overstory cover in the outer margin zones throughout the year.

The lack of replacement of articulated corallines by other overstory species could act as a key point in determining the abundance of *C. cylindracea* at the degraded location. Thus, the low ecological status of the overstory could act as potential driver of the invasion (Piazzi et al. 2016 and references therein). This spread of *C. cylindracea* could be fostered in warmer months, when the decline of *E. elongata* coincides with the optimal growth temperature for *C. cylindracea* (Samperio-Ramos et al. 2015). Then, presumably, *C. cylindracea* could take advantage of both the free space generated by *E. elongata* decay and the “thermal opportunity window”. However, some competitive interaction between *E. elongata* and *C. cylindracea* cannot be ruled out. The lack of detection of *C. cylindracea* populations beyond the studied platforms suggests that the growth of *C. cylindracea* is due to a persistent resting stage rather than to propagule-recruitment processes (Üy et al. 2017), taking into account the unlikely sexual reproduction for *C. cylindracea* (Varela-Alvarez et al. 2012).

All in all, in this study our results indicate that *C. cylindracea* acts rather like an opportunistic species, taking advantage of the less persistent overstory at the affected location. Though competitive interactions cannot be ruled out, factors affecting the recipient degraded overstory seem to better explain the decay of this overstory than interactive processes with *C. cylindracea*. This decline, when abiotic conditions are optimal for *C. cylindracea* growth, would be harnessed by this alien species, in line with Bulleri et al. (2010). Thus, *C. cylindracea* would rather behave as a passenger of change on these degraded platforms (MacDougall and Turkington 2005). However, stressors such as sedimentation and eutrophication could also foster *C. cylindracea* establishment (Piazzi et al. 2005, Gennaro and Piazza 2011), and once established, *C. cylindracea* could enhance sediment accumulation, acting as a driver (Bulleri et al. 2010). Thus, the slightly higher values of both stressors at the degraded location makes their role as enhancers of *C. cylindracea* growth feasible. Owing to the high level of homogenization of the assemblages from the degraded and urbanized Mediterranean littoral fringe, the establishment and enhancement of *C. cylindracea* growth on other degraded Mediterranean vermetid platforms is plausible.

Further studies, especially long-term manipulative and correlative ones, are required to understand better how the ecological status of vermetid platforms affects the invasiveness of *C. cylindracea*. Possible future scenarios linked to global change are of particular concern: among others, the higher extremeness trend of disturbances such as storms and low sea level episodes, which could affect the overstory cover of the vermetid platforms (Sanz-Lázaro 2016, Zumir et al. 2018).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link:
http://scimar.icm.csic.es/scimar/supplm/sm04984esm.pdf

Table S1. – A, summary of a two-factor PERMANOVA univariate test (with location and date) comparing nutrient concentration (phosphates and nitrogen including ammonia, nitrates and nitrates) between samples. Lo, location; Da, date. B, pairwise tests for the term ‘Lo×Da’ for pairs of levels of the factor ‘Location’ (Monte Carlo p-values).

Table S2. – A, summary of a four-factor PERMANOVA univariate test (with location, zone, date and site nested in location) comparing sediment cover between samples. Lo, location; Da, date. B, pairwise tests for the term ‘Lo×ZoxD’ for pairs of levels of the factor ‘Location’ (Monte Carlo p-values).
Bathyal cumacean assemblages from the southern margin of the Cap Ferret Canyon (SE Bay of Biscay)

Jordi Corbera, Jean Claude Sorbe

Supplementary material
Table S1. – Vertical distribution of cumacean individuals in the near-bottom water layers (N1, 10-40 cm; N2, 45-75 cm; N3, 80-110 cm; N4, 115-145 cm above the seafloor) sampled by a suprabenthic sledge at 13 stations on the southern margin of the Cap Ferret Canyon. TS09 samples only partially studied due to bad conservation of material. –, 0; *, damaged specimens.

| Haul code | TS01 | TS02 | TS03 | TS04 | TS05 | TS06 | TS07 |
|-----------|------|------|------|------|------|------|------|
| Depth (m) | 346–347 | 399–383 | 425–437 | 485–484 | 523–522 | 568–611 | 660–714 |
| Net level | N1 | N2 | N3 | N4 | N1 | N2 | N3 |
| Family BODOTRIIDAE | | | | | | | |
| Bathycuma brevirostre (Norman, 1879) | | | | | | | |
| Cyclops longicaudatus Sars, 1865 | | | | | | | |
| Cyclaspis longicaudata Sars, 1865 | | | | | | | |
| Diastylis cornuta (Boeck, 1864) | | | | | | | |
| Diastylis tumida (Liljeborg, 1855) | | | | | | | |
| Diastylis bilicatus (GO Sars, 1865) | 4 | 1 | 1 | 1 | 22 | 1 | 2 |
| Diastylis serratus (GO Sars, 1865) | | | | | | | |
| Leptostylis longimana (GO Sars, 1865) | | | | | | | |
| Leptostylis macrura (GO Sars, 1870) | 10 | 7 | 7 | 47 | 2 | 25 | |
| Leptostylis sp.A | | | | | | | |
| Leptostylis sp.B | | | | | | | |
| Makrokylindrus (Adiastylis) anomalus (Bonnier, 1896) | | | | | | | |
| Makrokylindrus (Adiastylis) josephinae (GO Sars, 1871) | | | | | | | |
| Makrokylindrus (Adiastylis) longicaudatus (Bonnier, 1896) | | | | | | | |
| Makrokylindrus (Adiastylis) longipes (GO Sars, 1871) | | | | | | | |
| Makrokylindrus sp.* | | | | | | | |
| Venakylindrus hastatus (Hansen, 1920) | | | | | | | |
| Family LAMPROPIDAE | | | | | | | |
| Mesolamprops longipes (GO Sars, 1870) | 2 | | | | | | |
| Melaspis typicus (GO Sars, 1870) | | | | | | | |
| Platystylis orbicularis (Calman, 1905) | | | | | | | |
| Family LEUCONIDAE | | | | | | | |
| Endiella cf. parvula Hansen, 1920 | | | | | | | |
| ibyleucon corbora Becher, | | | | | | | |
| Leucon (Cymoleucon) tener Hansen, 1920 | | | | | | | |
| Leucon (Epipleucon) eritis (Bishop, 1881) | | | | | | | |
| Leucon (Epipleucon) pusillus (Bishop, 1881) | | | | | | | |
| Leucon (Leucon) affinis Fage, 1951 | | | | | | | |
| Leucon (Leucon) sp.* | | | | | | | |
| Leucon (Macrauloleucon) siphonatus Calman, 1905 | | | | | | | |
| Family NANNASTACIDAE | | | | | | | |
| Campylaspis gilba GO Sars, 1878 | 2 | | | | | | |
| Campylaspis laevigata Jones, 1974 | | | | | | | |
| Campylaspis nitens Bonnier, 1896 | | | | | | | |
| Campylaspis rostrata Calman, 1905 | | | | | | | |
| Campylaspis squamifera Fage, 1929 | | | | | | | |
| Camyplaspis sukata GO Sars, 1870 | 13 | 1 | 16 | | | | |
| Cumella (Cunelleta) diisca Jones, 1984 | | | | | | | |
| Cumella (Cunelleta) divisa | | | | | | | |
| Cumella (Cunelleta) purikin Calman, 1906 | | | | | | | |
| Cunelleta atlanticus Bacescu and Muradian, 1972 | | | | | | | |
| Procampylaspis armata Bonnier, 1896 | | | | | | | |
| Procampylaspis omnivora Jones, 1984 | | | | | | | |
| Schizocuma spinoculatum (Jones, 1984) | | | | | | | |
| Styloptospina gracillimum (Calman, 1905) | | | | | | | |
| Cumacea unidentified* | | | | | | | |
| Number of individuals | 31 | 0 | 1 | 0 | 31 | 0 | 0 |
| Number of species | 5 | 0 | 1 | 0 | 6 | 3 | 0 | 7 | 0 | 0 | 12 | 4 | 4 | 0 | 16 | 8 | 3 | 0 | 16 | 7 | 4 | 2 |
Table S1 (cont.). – Vertical distribution of cumacean individuals in the near-bottom water layers (N1, 10-40 cm; N2, 45-75 cm; N3, 80-110 cm; N4, 115-145 cm above the sea floor) sampled by the suprabenthic sledge at 13 stations on the southern margin of the Cap Ferret Canyon. TS09 samples only partially studied due to bad conservation of material. –, 0; *, damaged specimens.

| Haul code | TS08 | TS09 | TS10 | TS11 | TS12 | TS13 |
|-----------|------|------|------|------|------|------|
| Depth (m) | 714–708 | 740–754 | 791–790 | 923–924 | 1024–1043 | 1097–1099 |
| Net level | N1 | N2 | N3 | N4 | N1 | N2 | N3 | N4 | N1 | N2 | N3 | N4 | N1 | N2 | N3 | N4 | N1 | N2 | N3 | N4 |
| Family BODOTRIIDAE | | | | | | |
| Bathycuma brevirostre (Norman, 1879) | – | – | – | – | – | – | – | – | 3 | – | – | 2 | – | – | 6 | – | – | – | – |
| Cyclaspis longicaudata Sars, 1865 | – | – | – | – | 2 | 2 | – | 8 | – | – | 4 | 1 | – | 9 | – | – | – | – | – |
| Cyclaspoides sarsi Bonnier, 1896 | – | – | – | – | – | – | – | – | – | – | – | 3 | – | – | 5 | – | – | – | – |
| Iphinoe serrata Norman, 1867 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Family DIASTYLIDAE | | | | | | |
| Diastylis cornuta (Boeck, 1864) | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Diastylis tumida (Liljeborg, 1855) | – | – | – | – | 3 | 4 | – | 2 | – | – | – | – | – | – | – | – | – | – | – |
| Diastylis biplicatus (GO Sars, 1865) | – | – | – | – | – | 1 | – | 2 | – | – | – | – | – | – | – | – | – | – | – |
| Diastylis serratus (GO Sars, 1865) | 13 | 3 | 8 | – | – | – | 17 | 3 | 12 | 8 | 3 | 3 | – | – | – | – | – | – | – |
| Leptostylis longimana (GO Sars, 1870) | 9 | – | 1 | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – |
| Leptostylis sp.A | – | – | – | – | 6 | – | – | – | 5 | – | – | – | – | – | – | – | – | – | – |
| Leptostylis sp.B | – | – | – | – | 2 | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – |
| Makrokylindrus (Adiastylis) anomalus (Bonnier, 1896) | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Makrokylindrus (Adiastylis) josephinae (GO Sars, 1871) | 3 | – | 4 | – | – | – | 21 | 1 | – | – | – | – | – | – | – | – | – | – |
| Makrokylindrus (Adiastylis) longipes (GO Sars, 1871) | – | – | – | – | – | 3 | – | 4 | 1 | – | – | – | – | – | – | – | – | – | – |
| Makrokylindrus sp.* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Vemakylindrus hastatus (Hansen, 1920) | – | – | – | – | 2 | – | – | 3 | – | – | 14 | – | – | 17 | – | – | – | – | – |
| Family LAMPROPIDAE | | | | | | |
| Hemilamprops normani Bonnier, 1896 | – | – | – | – | 6 | 1 | – | 9 | – | – | 4 | – | 1 | 7 | – | – | – | – | – |
| Mesolamprops denticulatus Ledoyer, 1983 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Platysympus typicus (GO Sars, 1870) | 3 | – | – | – | – | 1 | – | 1 | – | – | 3 | – | – | – | – | – | – | – | – |
| Platytyphlops orbicularis (Calman, 1905) | – | – | – | – | 1 | – | 1 | – | – | 1 | – | – | – | – | – | – | – | – | – |
| Family LEUCONIDAE | | | | | | |
| Eudorella cf. parvula Hansen, 1920 | – | – | – | – | 1 | – | – | – | 22 | – | – | 1 | – | 1 | – | – | – | – | – |
| Bityleucon sorbeli Corbera, 2012 | – | – | – | – | – | – | – | – | 8 | 1 | – | 9 | – | – | – | – | – | – | – |
| Leucon (Crymoleucon) tener Hansen, 1920 | – | – | – | – | 2 | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – |
| Leucon (Epileucon) ensis (Bishop, 1981) | – | – | – | – | – | – | – | – | 8 | – | – | – | – | – | – | – | – | – | – |
| Leucon (Epileucon) pusillus (Bishop, 1981) | – | – | – | – | 8 | – | 10 | – | 51 | 1 | 1 | 16 | – | – | – | – | – | – | – |
| Leucon (Leucon) affinis Fage, 1951 | 2 | – | 1 | – | – | – | 8 | – | – | – | – | – | – | – | – | – | – | – | – |
| Leucon (Leucon) sp.* | – | – | – | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – |
| Leucon (Macrauloleucon) siphonatus Calman, 1905 | 5 | – | 3 | 1 | – | 3 | – | 11 | 1 | – | 3 | – | 1 | – | – | – | – | – | – |
| Family NANNASTACIDAE | | | | | | |
| Campylaspis glabra GO Sars, 1878 | 11 | – | 3 | 1 | 2 | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – |
| Campylaspis laevigata Jones, 1974 | 28 | – | – | 1 | – | 7 | – | – | – | 2 | – | – | – | – | – | – | – | – | – |
| Campylaspis nitens Bonnier, 1896 | 1 | – | 2 | – | – | – | – | 3 | – | – | – | – | – | – | – | – | – | – | – |
| Campylaspis rostrata Calman, 1905 | 74 | – | 1 | 7 | 1 | – | 4 | – | – | 2 | – | – | – | – | – | – | – | – | – |
| Campylaspis sulcata GO Sars, 1870 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Cumella (Cumella) divisa Jones, 1984 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Cumellopsis puritani Calman, 1906 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nannastacus atlanticus Basaeau and Muradian, 1972 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Procampylaspis armata Bonnier, 1896 | 37 | – | 1 | 1 | 16 | – | 8 | – | – | 5 | – | – | 7 | – | – | – | – | – | – |
| Procampylaspis omnion Jones, 1984 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Schizocuma spinoculatum (Jones, 1984) | 5 | – | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Styloptocuma gracillimum (Calman, 1905) | – | – | – | – | 5 | 2 | – | 1 | 2 | 4 | – | – | – | – | – | – | – | – |
| Cumacea unidentified * | – | – | – | – | – | – | – | – | 15 | 1 | – | 1 | – | – | – | – | – | – | – |

Number of individuals 201 5 2 1 167 17 2 90 11 1 108 4 0 217 5 5 4 169 10 7 4
Number of species 13 3 2 1 5 19 6 1 22 1 0 22 5 3 2 25 1 4 1