

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

Marc Terradas-Fernández¹, Miguel Valverde-Urrea¹, Nuria Casado-Coy¹, Carlos Sanz-Lazaro^{2,3}

¹ Departamento de Ciencias del Mar y Biología Aplicada, Facultad de Ciencias, Universidad de Alicante, Aptdo. Correos 99, 03080 Alicante, Spain.

(MT-F) (Corresponding author) E-mail: marcbentos@gmail.com. ORCID iD: <https://orcid.org/0000-0002-1916-5337>

(MV-U) E-mail: miguel_27692@hotmail.com. ORCID iD: <https://orcid.org/0000-0002-5708-5258>

(NC-C) E-mail: ncasadocoy@ua.es. ORCID iD: <https://orcid.org/0000-0003-4348-2225>

² Departamento de Ecología, Universidad de Alicante, P.O. Box 99, E-03080 Alicante, Spain.

³ Multidisciplinary Institute for Environmental Studies (MIES), Universidad de Alicante, P.O. Box 99, E-03080 Alicante, Spain.

(CS-L) E-mail: carsanz@ua.es. ORCID iD: <https://orcid.org/0000-0002-4431-1762>

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 verméticos 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. Estudiamos la invasividad de *C. cylindracea* en dos plataformas de verméticos 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 verméticos.

Palabras clave: costas rocosas; fitobentos; composición de la comunidad; *Caulerpa cylindracea*; plataformas de verméticos; 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 Piazzi 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 (Huenneke 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* matte 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-Esplà 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

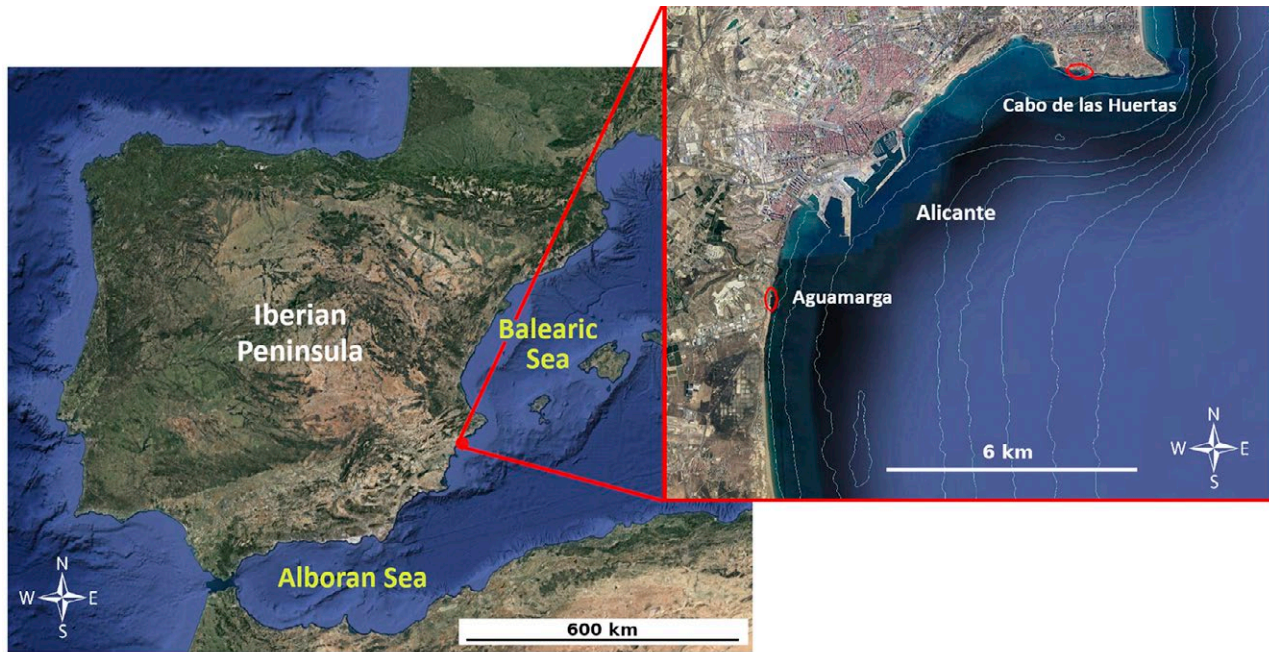


Fig. 1. – Study area showing the sampling locations: Cabo de las Huertas (the non-degraded location) and Aguamarga (the anthropogenic-degraded location). Isobath interval is equal to five metres. Modified from Google Earth.

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 ($38^{\circ}21'10''\text{N}$, $0^{\circ}25''\text{W}$), 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 ($38^{\circ}18'06''\text{N}$, $0^{\circ}31'05''\text{W}$).

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, 2000/06/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 cm^2 , 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 $0.45\ \mu\text{m}$ and frozen. The analysis was carried out using an Automated Wet Chemistry Analyser (Skalar Analytical B.V., Breda, the Netherlands).

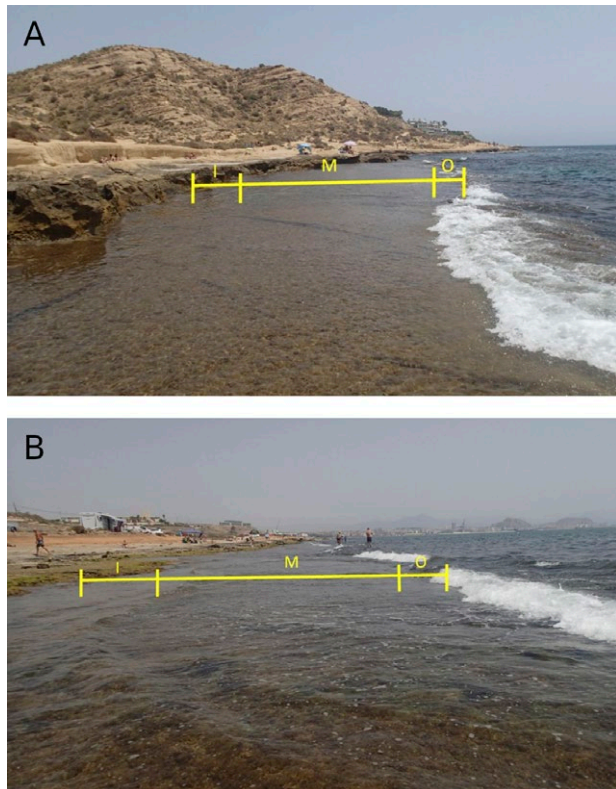


Fig. 2. – Zones surveyed at the non-degraded location (A) and the degraded location (B). Inner zone (I), mid-platform zone (M), outer platform zone (O).

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 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 of taxa with a correlation higher than 0.3 with the PCO axes.

The cover of *C. cylindracea*, sediment and over-story-forming taxa (that is, those taxa able to generate dense and conspicuous stands forming large patches or horizons) were assessed using a univariate PERMANOVA analysis through the same multivariate analysis design. Nutrient concentrations were assessed by two-way univariate PERMANOVA, considering *location* and *date* as fixed factors. Phosphates and total

nitrogen concentration (ammonia, nitrites and nitrates) were analysed separately.

Post-hoc tests were performed using pairwise comparisons when significant interactions were found. Univariate analyses were carried out from a Euclidean distance matrix instead of the Bray-Curtis one used in the multivariate case (Anderson et al. 2008). Analyses were performed using the PRIMER-E® v.7 + PERMANOVA package (Clarke and Gorley 2015, Anderson et al. 2008).

RESULTS

Environmental variables

Nutrient concentration showed high temporal variability (Fig. 3, Supplementary material Table S1). However, an interaction effect between *location* and *date* was detected. The degraded location usually showed a higher phosphate concentration, although a peak in phosphates was detected in the non-degraded one in August 2017. As for the total nitrogen concentration (total amount of ammonia, nitrates and nitrites), the pattern was analogous, but pairwise tests showed no significant differences between locations and dates.

There was also an interaction effect between *location*, *zone* and *date* regarding sediment cover (Fig. 3, Table S2). When significant, these differences were usually due to higher cover values in the degraded location. In both locations, the sediment cover showed a decreasing pattern from the inner zone to the outer one.

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* Areschoug and *Derbesia tenuissima* (Moris and De Notaris) Crouan and Crouan, whereas the “*Laurencia* 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) Ambronn; *Lo-*

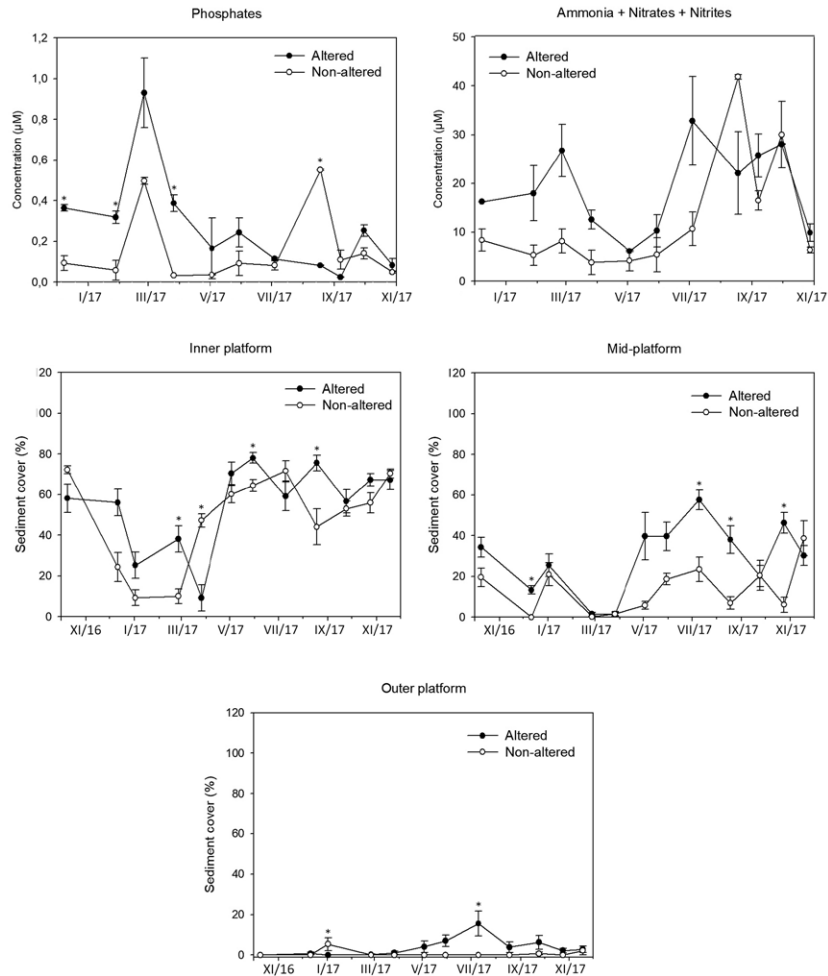


Fig. 3. – Values of nutrient concentration and sediment cover for each location (degraded and non-degraded). Vertical bars: standard error. Asterisks indicate significant differences between locations ($\alpha=0.05$).

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 'LoxZoxDa' for pairs of levels of factor 'Location' (Monte Carlo p-values).

A, four-factor PERMANOVA test						
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	2,25E+04	13.457	0.001	997
Si(Lo)	4	9574.1	2393.5	38.653	0.001	998
LoxZo	2	1,20E+09	5,99E+04	35.88	0.001	999
LoxDa	11	1,95E+09	1,77E+04	10.583	0.001	999
ZoxDaxSi(Lo)	22	1,59E+09	7220.00	5.654	0.001	998
ZoxSi(Lo)	8	13363.00	1670.4	26.975	0.001	999
DaxSi(Lo)	44	73715.00	1675.3	27.055	0.001	998
LoxZoxDa	22	1,23E+09	5570.4	43.622	0.001	998
ZoxDaxSi(Lo)	88	1,12E+09	1277.00	20.622	0.001	997
Residual	432	2,68E+09	619.23			

B, PAIRWISE TESTS for the term 'LoxZoxDa' 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
26/03/2017	0.003	0.001	0.001
03/05/2017	0.01	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

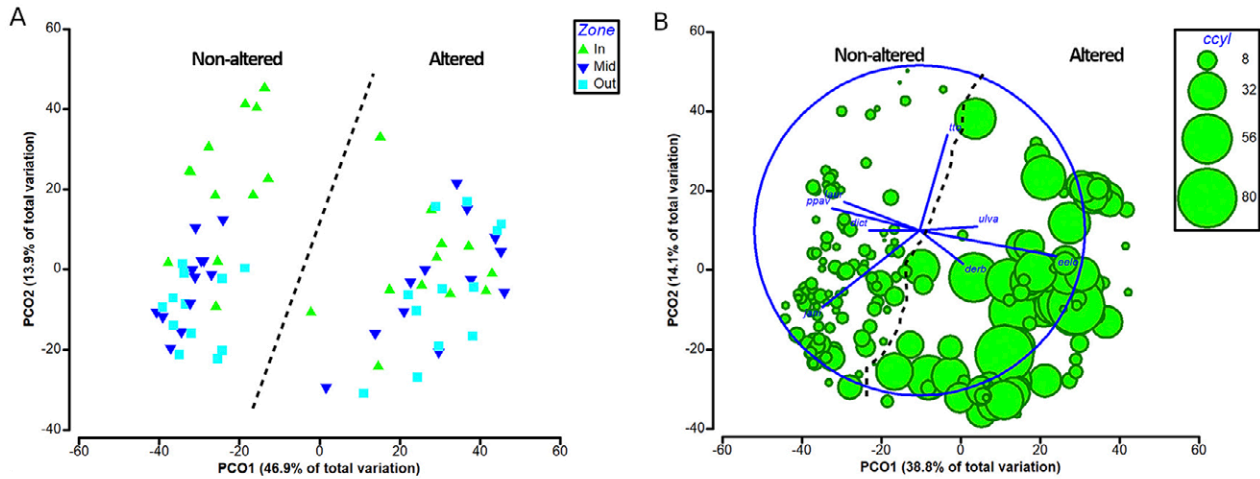


Fig. 4. – Principal coordinates ordination (PCO) of all inventories based on a Bray-Curtis similarity matrix of square-root transformed percent cover values of each taxa. Non-degraded location samples are separated from the degraded ones by a dotted line. A, PCO resulting from pooling replicates and sites by calculating the distance between centroids and showing zone adscription for each inventory. B, PCO without pooling showing the vector overlay of taxa with a correlation higher than 0.3 with the PCO axes. The percentage cover of *C. cylindracea* is also represented through a bubble plot. Taxa legend: *eelo*, *E. elongata*; *derb*, *D. tenuissima*; *dict*, *Dictyota* spp.; *jani*, *Jania* spp.; *laur*, *Laurencia* complex; *ppav*, *P. pavonica*; *tto*, turf-forming thalli; *ulva*, *U. laetevirens*.

phosiphonia 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 2. – A, summary of a four-factor PERMANOVA univariate test (with *location*, *zone*, *date* and *site* nested in *location*) comparing overstory 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 ‘LoxZoxDa’ 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	372.13	372.13	0.38018	0.672	10
Zo	2	254650	127330	103.63	0.001	999
Da	11	85737	7794.2	15.581	0.001	998
Si(Lo)	4	3915.3	978.82	4.8549	0.002	998
LoxZo	2	13204	6602.1	5.3732	0.033	998
LoxDA	11	89549	8140.8	16.274	0.001	999
ZoxDa	22	44416	2018.9	3.9575	0.001	999
ZoxSi(Lo)	8	9829.7	1228.7	6.0943	0.001	996
DaxSi(Lo)	44	22011	500.24	2.4812	0.001	998
LoxZoxDa	22	18902	859.19	1.6842	0.051	998
ZoxDaxSi(Lo)	88	44893	510.15	2.5303	0.001	999
Residual	432	87098	201.62			

B, PAIRWISE TESTS for the term ‘LoxZoxDa’ for pairs of levels of the factor ‘Location’			
Date	Inner zone	Mid-zone	Outer zone
09/10/2016	0.401	0.294	0.802
08/12/2016	0.093	0.019	0.984
02/01/2017	0.051	0.35	0.008
25/02/2017	0.002	0.042	0.035
26/03/2017	0.025	0.759	0.028
03/05/2017	0.951	0.179	0.489
30/05/2017	0.088	0.005	0.001
04/07/2017	0.054	0.065	0.134
18/08/2017	0.139	0.028	0.065
30/09/2017	0.206	0.527	0.391
28/10/2017	0.193	0.007	0.977
18/11/2017	0.344	0.078	0.003

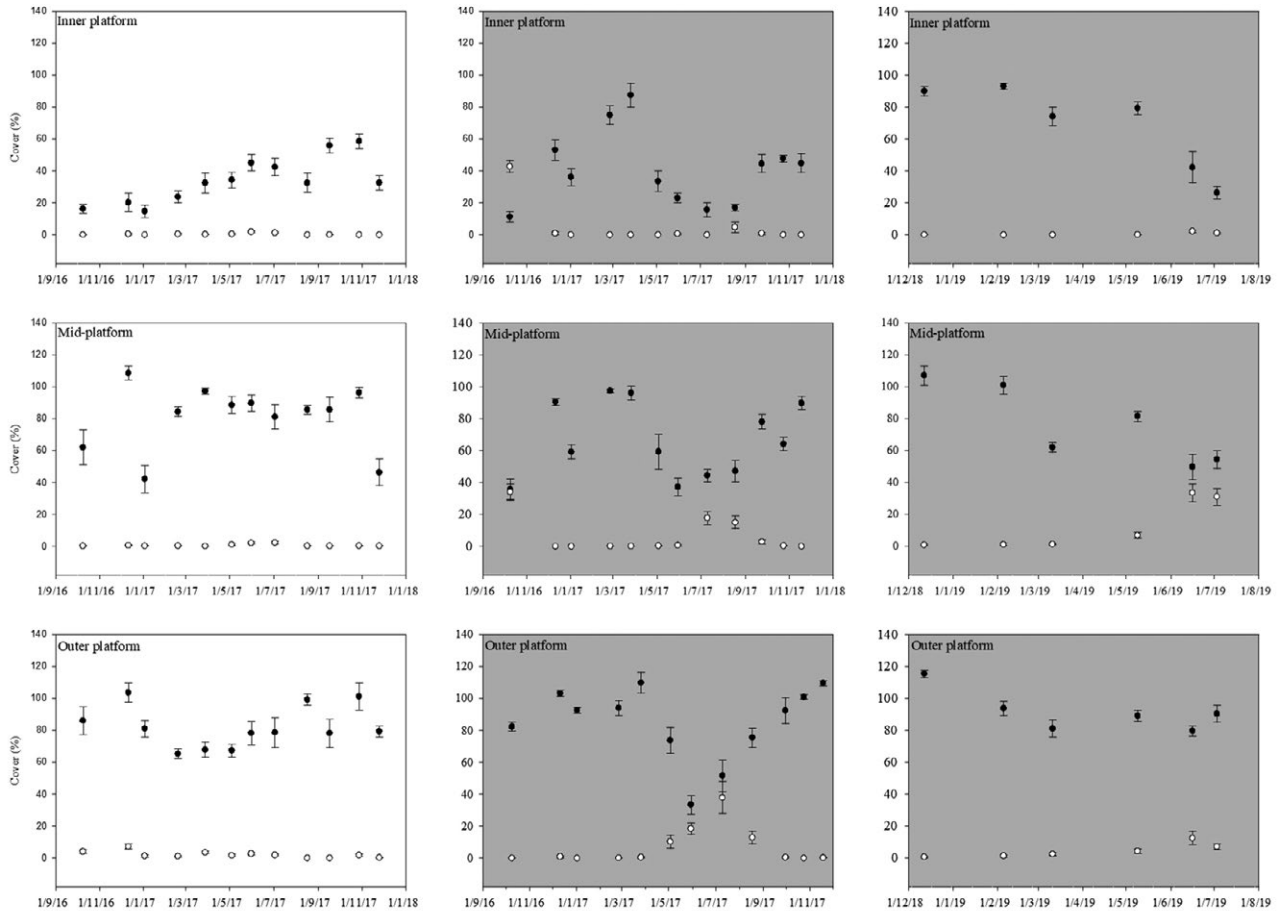


Fig. 5. – Temporal dynamics in the cover of overstory (black dots) and *C. cylindracea* (white dots) under non-degraded (white background) and degraded (grey background) conditions in the zones distributed along the shallow vermetid platforms. Data from a current survey being carried out at the degraded location (2019) are also shown (right column).

Table 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 'LoxZoxDa' 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			

B, PAIRWISE TESTS for the term 'LoxZoxDa' 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	0.661	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

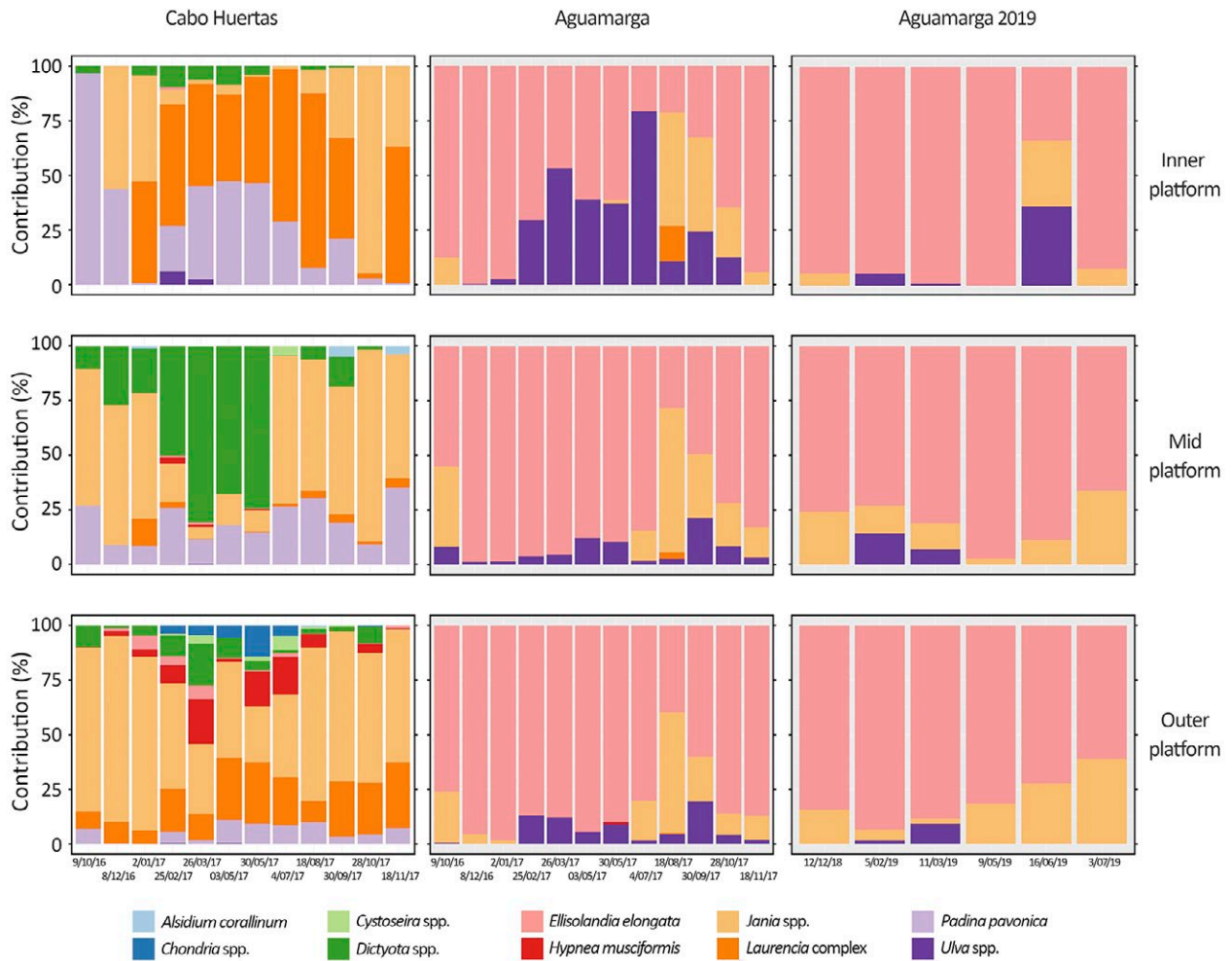


Fig. 6. – Stacked plots showing the proportion of each algae contributing to the total overstory cover in each survey. The graphics are arranged as in Figure 5.

(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 furoid algae and other phaeophyceyan 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 (Uyà et al. 2017), taking into account the unlikely sexual reproduction for *C. cylindracea* (Varela-Álvarez et al. 2012).

The higher stress occurring in the inner zones may hamper the invasiveness of *C. cylindracea* towards the inner parts of the platform. However, the high cover of *C. cylindracea* observed in the inner degraded zone in October 2016, coinciding with the low overstory cover, could be the result of high sea level episodes improving the growth of *C. cylindracea*. This scenario is likely to occur in late summer and autumn months, when the mean sea level is usually higher in the southeastern Iberian Peninsula (Soto 1987, Adloff et al. 2018).

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 Piazzi 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, Zamir 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 nitrites) between samples. Lo, *location*; Da, *date*. B, pairwise tests for the term 'LoxDa' 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 'LoXZoXDa' 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														
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4											
Family BODOTRIDAE																											
<i>Bathycuma brevirostre</i> (Norman, 1879)																											
<i>Cyclopsis longicaudata</i> Sars, 1865																											
<i>Cyclopsoides sarsi</i> Bonnier, 1896																											
<i>Iphinae serrata</i> Norman, 1867																											
Family DIASTYLIDAE																											
<i>Diasyllis cornuta</i> (Boeck, 1864)																											
<i>Diasyllis tumida</i> (Liljeborg, 1855)																											
<i>Diasylloides biplicatus</i> (GO Sars, 1865)																											
<i>Diasylloides serratus</i> (GO Sars, 1865)	4	1			1	1			22	1	2	1	4	1	2	1											
<i>Leptostylis longimana</i> (GO Sars, 1865)																											
<i>Leptostylis macrura</i> (GO Sars, 1870)	10				7				47	2	1		25			22											
<i>Leptostylis</i> sp.A																											
<i>Leptostylis</i> sp.B																											
<i>Makrokylindrus (Adiastylis) anomalus</i> (Bonnier, 1896)																											
<i>Makrokylindrus (Adiastylis) josephinae</i> (GO Sars, 1871)																											
<i>Makrokylindrus (Adiastylis) longicaudatus</i> (Bonnier, 1896)																											
<i>Makrokylindrus (Adiastylis) longipes</i> (GO Sars, 1871)																											
<i>Makrokylindrus</i> sp.*																											
<i>Vemakylindrus hastatus</i> (Hansen, 1920)																											
Family LAMPROPIDAE																											
<i>Hemilamprops normani</i> Bonnier, 1896																											
<i>Mesolamprops denticulatus</i> Ledoyer, 1983	2																										
<i>Platysympus typicus</i> (GO Sars, 1870)																											
<i>Platyphalops orbicularis</i> (Calman, 1905)																											
Family LEUCONIDAE																											
<i>Eudorella</i> cf. <i>parvula</i> Hansen, 1920																											
<i>Ithyleucon sorbei</i> Corbera, 2012																											
<i>Leucon (Crymoleucon) tener</i> Hansen, 1920																											
<i>Leucon (Epileucon) ensis</i> (Bishop, 1981)																											
<i>Leucon (Epileucon) pusillus</i> (Bishop, 1981)																											
<i>Leucon (Leucon) affinis</i> Fage, 1951																											
<i>Leucon (Leucon)</i> sp.*																											
<i>Leucon (Macrauloleucon) siphonatus</i> Calman, 1905																											
Family NANNASTACIDAE																											
<i>Campylaspis glabra</i> GO Sars, 1878	2																										
<i>Campylaspis laevigata</i> Jones, 1974																											
<i>Campylaspis nitens</i> Bonnier, 1896																											
<i>Campylaspis rostrata</i> Calman, 1905																											
<i>Campylaspis squamifera</i> Fage, 1929																											
<i>Campylaspis sulcata</i> GO Sars, 1870	13																										
<i>Cumella (Cumella) divisa</i> Jones, 1984																											
<i>Cumellopsis puritani</i> Calman, 1906																											
<i>Nannastacus atlanticus</i> Bacescu and Muradian, 1972																											
<i>Procampylaspis armata</i> Bonnier, 1896																											
<i>Procampylaspis ommidion</i> Jones, 1984																											
<i>Schizocuma spinoculatum</i> (Jones, 1984)																											
<i>Styloptocuma gracillimum</i> (Calman, 1905)																											
Cumacea unidentified*																											
Number of individuals	31	0	1	0	3	1	1	0	35	4	0	0	13	0	0	242	6	7	7	232	17	6	0	212	27	8	2
Number of species	5	0	1	0	3	1	1	0	6	3	0	0	7	0	0	12	4	4	4	16	8	3	0	16	7	4	2

