Aspectos ecológicos del fitobentos asociado a las plataformas de algas y mermétidos del SE ibérico

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"Aspectos ecológicos del fitobentos asociado a las plataformas de algas y vermétidos del SE ibérico"

Marc Terradas Fernández

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Los doctores Alfonso Ramos Esplá y Jose Jacobo Zubcoff Vallejo, del Departamento de Ciencias del Mar y Biología Aplicada de la Universidad de Alicante, certifican: que el Licenciado Marc Terradas Fernández ha realizado bajo su dirección la presente memoria por la cual opta al título de Doctor en Ciencias del Mar y Biología Aplicada, titulada “Aspectos ecológicos del fitobentos asociado a las plataformas de algas y vermétidos del SE ibérico”.

Fdo.

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AGRAÏMENTS

Aquesta tesi és una tesi típica del segle XXI: precarietat, incertesa, necessitat de publicar ràpid, i d'altres pressions "ruderalitzadores" que fan d'aquest "producte o tràmit" una cosa ben diferent de la idea de "tesi" que alguns tenim al cap. La oportunitat de fer-la, en aquest cas, també ha arribat una mica tard...en fi. Malgrat tot, els temes tractats han pogut ser, en gran mesura, els que volia i s'han pogut publicar.

En aquesta "batalla" haig d'agrair, en primer lloc, el suport dels pares, família, amics i amigues, els de veritat, que sabent que només poden perdre, t'ajuden igualment: sigui donant consells amb Grover (amb o sense mostassa), passejant per la part burgesa de Sabadell, fent escapades a Oporto, editant algun gràfic (o molts), ensenyant alguns trucs del SEASCAPE, anant a plaquejar per Sant Feliu de Guíxols, aixoplugant-te tot mirant spaghetti westerns amb gin-tonics, portant-te mascaretes a casa perquè acabis la tesi amb més tranquil·litat, fent trucades de Wassap grupals o individuals, passejant a Boira per Huertas, o empatitzant i *punto*!

Després vull agrair l' ajuda de molts i moltes estudiants caracteritzats per aquella il·lusió que se'ls hi pot girar en contra en aquest món de *tiburons*. També amb molts d'ells s'ha forjat una bona amistat. Carlos Botana i Miguel Valverde hi han estat des del primer moment. I en un segon moment, l' Aitor Navarro, la Cristina Nuñez, i Mari Paz Gallego fent feina de camp amb fred i calor. Rocío Huguet m'ha ajudat moltíssim per tirar endavant la quarta publicació. Leticia Asensio (en aquest cas professora) també ha estat des de el primer moment i amb el que fes falta. Ana Belén Jodar, que li encanta el mar, em va ajudar a fer molts inventaris i a trobar moltes parcel·les, com ho van fer Luís Enrique Alcaraz i Lotte Krüguer, sobretot, per tal de tirar endavant la segona publicació. En aquesta segona i quarta publicació Carlos Sanz i Nuria Casado, coautors, m'han presentat a moltes estudiants que també m'han ajudat moltíssim al camp: Lara Dreide, Leslie Stout, Lara Herrera, Iraide Saez, Natalia Sánchez i Laura Sempere. També alguns estudiants m'han volgut ajudar i han vingut alguns cops: Alejandro, Daverlyn, Paula i Lola. A tots ells, *muchos recuerdos*!!

A les campanyes de Tabarca, sempre que ha pogut, en Felio Quijada ha donat un cop de ma i Vicent Pardo va venir a moltes campanyes ajudant també a instal·lar les plaques.

Aquí haig de dir que la idea d'instal·lar les plaques no hagués sorgit sense l'ajuda de dos aventurers i escaladors, que ja fa varis anys, 14 anys de fet, em van instal·lar unes plaques que segueixo i que encara aguanten!! Joaquín Olmo i Juan Urquiza, un Abrazo!

Les campanyes per endinsar-me, a fons, en l'estructura i taxonomia dels esculls d'algues i vermètids han esdevingut un cul-de-sac, per ara. M'encantaria poder continuar explorant la biologia de les bioconstruccions mediterrànies que només he tocat, directament, en el tercer article d'aquesta tesi. Les campanyes de coralinàcies les vaig fer abans i durant la tesi, i m'han permès conèixer a algunes SUPERCRACKS de l'algologia. Viviana Peña em va introduir, en una setmana intensa, en el mon dels microscopis electrònics i de la taxonomia molecular crua i dura. Vaig poder conèixer a tots els seus companys, incloent alguns retrobaments universitaris. Em refereixo a l'àrea de botànica i al Grupo de Investigación *BioCost* (Universidade da Coruña). També vaig poder conèixer a Ignacio Barbara i a Javier Cremades juntament amb Pilar Díaz Tapia que em va clarificar que la "Neosiphonia ferulacea" no està gens clara. Continuant amb la taxonomía, vull agrair l'ajuda que he tingut de Carolina Pena, de la mateixa Universitat d'Alacant, així com de Jordi Rull i Amelia Gómez de la Universitat de Barcelona. Julio Afonso-Carrillo m'ha ajudat a la determinació d'algunes coralinàcies de la tercera publicació. I pensant amb les coralinàcies, no vull oblidar-me d'Andrés Izquierdo. Amb ell, a part de deixar-me dades de temperatura, ens hem recorregut tot el País Valencià buscant petites mostres per extreure el DNA. Aquesta història està inacabada.

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INTRODUCCIÓN GENERAL

Tal y como Kim *et al* (2017) enunciaron, es preciso conocer la resiliencia de las comunidades para cada hábitat específico. Esta necesidad de conocer a nivel de "hábitat", por supuesto, va más allá de la resiliencia que, a su vez, puede depender de múltiples factores extrínsecos e intrínsecos del mismo hábitat (de la intensidad y frecuencia de las perturbaciones, del estado de "salud o constitución" de las especies del propio hábitat, etc.). Al mismo tiempo, resulta esencial entender otras cuestiones, como la composición taxonómica, la dinámica y el valor patrimonial de cada hábitat. Así, se facilita aprovechar este conocimiento desde la perspectiva de la gestión. ¿Pero qué es un hábitat?

A pesar de ser un término ampliamente empleado en Ecología, su definición suele ser vaga (Hall *et al*., 1997; Mitchell, 2005). Según Mitchell (2005), varios conceptos, no excluyentes, suelen definirlo. El hábitat sería el lugar donde viven determinados organismos, el conjunto de factores abióticos que definen su "espacio vital", o aquel espacio con una serie de factores abióticos (físicos y químicos) que permiten su existencia en comunidad. La última acepción se aproxima a la de Hall *et al* (1997) definiendo hábitat como "el conjunto de recursos y condiciones presentes en un área que producen ocupación -incluyendo supervivencia y reproducción- para un organismo determinado". Sin embargo, las definiciones precisas se enfrentan con la dificultad de conocer la verdadera escala espacial y temporal que ocupa cada organismo, junto a las múltiples variables ambientales condicionantes de dicha distribución (Mitchell, 2005). Por todo ello, generalmente se imponen criterios operativos (Peters, 1991). Así, en la franja litoral, se generan horizontes fácilmente discernibles por las especies dominantes que los ocupan. Estos horizontes, indicadores de los condicionantes abióticos (muchas veces antrópicos), se utilizan para conocer el estado ecológico (Ballesteros *et al*., 2007) y para el cartografiado de hábitats operativos que permiten su gestión y conservación (Mariani *et al*., 2014).

Desde la perspectiva operativa, en el Sureste Ibérico se generan unas unidades paisajísticas que pueden categorizarse como hábitats específicos de este sector, y que forman parte de nuestro patrimonio natural a conservar: las plataformas de abrasión de vermétidos y algas calcáreas. El estudio de la ecología de estos hábitats (su estructura, dinámica, resiliencia), y en concreto de su fitobentos, es el objetivo de esta tesis doctoral. Esta tesis es, de hecho, la continuación del Trabajo fin de Máster previo en el que se caracterizaron las fitocenosis de estos sistemas a lo largo del Sureste Ibérico (Terradas-Fernández, 2014).

1. Las plataformas de abrasión de vermétidos y algas calcáreas en el contexto mediterráneo

Las plataformas de abrasión de vermétidos y algas calcáreas se desarrollan justo por debajo del nivel medio del mar, en lo que se correspondería con la franja litoral o con los primeros centímetros del infralitoral superior (Pérès y Picard, 1964). Su desarrollo es óptimo en rocas de fácil erosión, especialmente calcarenitas. Para la génesis de estas plataformas, parece clave el papel de la bioerosión junto al efecto protector del propio arrecife aunque este proceso no se entiende por completo (Safriel, 1975; Dalongeville, 1995; Laborel y Laborel-Deguen, 1996; Kelletat, 1997).

En la formación de estas plataformas en el Mediterráneo actual, aparte de la tipología de la roca, son necesarios otros factores: una temperatura relativamente elevada que permita el desarrollo del arrecife de algas y vermétidos; un nivel del mar relativamente estabilizado que permita el desarrollo del arrecife y de la plataforma; y aguas limpias con bajo contenido en nutrientes (oligotróficas) y con poca carga de sedimento. Así, tanto el principal vermétido constructor, perteneciente al género *Dendropoma* Mörch, 1861, como el alga calcárea principal *Neogoniolithon brassica-florida* (Harvey) Setchell et Mason, prosperan mejor en las zonas cálidas del Mediterráneo (Pérès y Picard, 1964). No es de extrañar que las plataformas vermetídicas actuales sean de origen reciente (holocénico), cuando el Mediterráneo se calentó, a la vez que la subida del nivel del mar se desaceleró (Antonioli *et al*., 1999; Milazo *et al*., 2016). De hecho, en la actualidad, encontramos su máximo desarrollo en la cálida cuenca oriental (Einav e Israel, 2007; Badreddine *et al*., 2019) donde se encuentran las plataformas vermetídicas más antiguas; mientras que en las cuencas central y occidental encontramos plataformas vermetídicas más recientes, relegadas a las partes más cálidas y meridionales de este sector (Antonioli *et al*., 1999).

La especificidad ambiental de estos sistemas, junto a su perdurabilidad, hacen de ellos buenos paleoindicadores para evaluar los cambios del nivel del mar y de la temperatura (Laborel, 1987; Antonioli *et al*., 1999; Silenzi *et al*., 2004). Además, la sensibilidad de los arrecifes vermetídicos frente a condicionantes antrópicos los hacen también buenos indicadores de la calidad del agua (Calvo *et al*., 1998; Donnarumma, 2014). Dada su naturaleza calcárea, estos arrecifes son sensibles a la acidificación del mar (Milazzo *et al*., 2014), y son destruidos para la recolección de cebos (Ramos *et al*., 2018); mientras que las comunidades algales, desarrolladas en la plataforma, responden negativamente al pisoteo (Milazzo *et al*., 2004). Por todo ello, estos sistemas, históricamente ignorados (Milazzo *et al*., 2016), empiezan a ser protegidos por ley a pesar de que se siguen priorizando especies individualizadas más que el hábitat o hábitats que las contienen (Terradas-Fernández, 2018).

Peculiaridades ecológicas de las plataformas vermetídicas

Tal y como ya apuntó Safriel (1975), las plataformas vermetídicas, debido a su escasa profundidad, presentan una falta substancial de los principales herbívoros mediterráneos: los erizos. Estos, tienden a refugiarse en grietas o cubetas relativamente profundas, dejando gran parte de la plataforma desprovista de los mismos. Solamente las lapas (Patellidae), quitones (Polyplacophora), bígaros y caracolas “peonza” (Littorinidae, Trochidae) suelen ser frecuentes en las plataformas, si bien su acción se limita principalmente al mediolitoral, donde contribuyen sustancialmente a la bioerosión (Kelletat, 1997). Otro grupo importante de omnívoros que pueden ser consumidores de algas, los cangrejos “corredores” (Grapsidae), parece que tienen una influencia muy localizada alrededor de sus madrigueras, en un diámetro de acción inferior a los 15 cm (Lipkin y Safriel, 1971; Safriel, 1975).

Otra peculiaridad y singularidad de estas plataformas es que, precisamente, por su poca inclinación, sus horizontes algales infralitorales, que constituyen parte de la franja litoral, presentan una amplitud muy superior a la habitual en otras regiones mediterráneas donde no existen tales sistemas (Chappuis *et al*., 2014; Mariani *et al*., 2014; Cefalí *et al*., 2016). Además, estos horizontes quedan fácilmente descubiertos en periodos de bajamar prolongados (Zamir *et al*., 2018). La escasa profundidad, junto a la posible baja presión por herbivoría, implica que estos sistemas estén posiblemente controlados por la disponibilidad de recurso (*bottom-up control*) y por las perturbaciones habituales (temporales y fluctuaciones del nivel del mar), aparte de las presiones antrópicas. Además, experimentan oscilaciones térmicas altísimas que superan los 20 grados de diferencia anual. Se han registrado temperaturas de 10ºC en invierno (obs. pers) que podrían ser incluso menores, en condiciones de bajamar; y temperaturas de 36ºC en condiciones de verano (Donnarumma, 2014).

Finalmente, la presencia del arrecife vermetídico también implica una serie de características singulares que no sólo afectan al arrecife sino a toda la plataforma. De entrada, el arrecife genera una diversidad notable. Al ser una bioconstrucción calcárea, es hábitat de multitud de especies que viven en su estructura, encontrándose más de 100 especies algales en una sola localidad (Mannino, 1992). Pero también existe una multitud de otros organismos: poliquetos, anfípodos, decápodos, sipuncúlidos, y otros como las esponjas perforadoras (Clionidae) y moluscos. Entre ellos, aparecen especies protegidas como el dátil de mar (*Lithophaga lithophaga*). De hecho, en estos arrecifes se han encontrado hasta 96 familias distintas de invertebrados (Chemello, 2009; Donnarumma, 2014; Donnarumma, 2018).

Los principales constructores del arrecife son el complejo *Dendropoma* y las algas calcáreas. Se ha visto que la especie de vermétido principal, *Dendropoma petraeum* (Monterosato, 1884) es en realidad un complejo de varias especies (al menos 4) cuya distribución mediterránea parece poco solapada: *D. lebeche* colonizaría la cuenca occidental, *D. cristatum* la parte central y *D. anguliferum* la cuenca oriental (Calvo *et al*., 2015; Templado *et al*., 2016). Sin embargo, las lagunas considerables que todavía existen en la taxonomía y en la cartografía de gran parte de la cuenca mediterránea podrían modificar el patrón descrito (Kelletat, 1997; Calvo *et al*., 2015; Milazzo *et al*., 2016).

Otro vermétido, *Vermetus triquetrus* (Bivona-Bernardi, 1832) vive en zonas más resguardadas y suele asociarse con algas calcáreas en la parte interna de la plataforma (Safriel, 1975; Ingrosso *et al*., 2018).

Por lo que respecta a las coralináceas contribuyentes a la generación del propio arrecife, también puede haber sorpresas. Clásicamente se ha considerado a *Neogoniolithon brassica-florida* (Harvey) Setchell et Mason como la principal alga mediterránea que se asocia al vermétido. Sin embargo, se ha visto que otras coralináceas la pueden sustituir en según qué condiciones. Así, Mannino (1992) observó que distintas especies de *Lithophyllum* pueden, al menos parcialmente, sustituir a *N. brassica-florida*. Barba *et al* (2008) observaron que el alga implicada en la conformación del arrecife vermetídico parecía tener un patrón geográfico a lo largo de la costa ibérica del mar de Alborán. Así, en la parte oriental de Andalucía, donde se siguen encontrando plataformas de abrasión bien desarrolladas, el alga constructora era *N. brassica-florida.* Sin embrago, en la costa central andaluza era sustituida por *Lithophyllum incrustans,* y finalmente, en la zona atlántica de la provincia de Cádiz por

L. byssoides. Con la colaboración de Viviana Peña Freire y Andrés Izquierdo Muñoz, observamos que también parece haber un patrón latitudinal desde el sureste ibérico hacia el norte, siendo dominante *N. brasica-florida* en las provincias de Almería, Murcia y Alicante, mientras que en la zona de Castellón y Sur de Catalunya (donde aparecen formaciones costrosas parecidas a las de Castellón con ausencia de plataformas vermetídicas desarrolladas) parecen dominar especies del género *Lithophyllum* (*Lithophyllum cf. pustulatum* y *Lithophyllum cf. papillosum*), aunque también aparece *N. brassica-florida*. Además, ambas especies, junto a *Phymatolithon lenormandii* (Areschoug) Adey también se han visto como principales constructoras en determinadas muestras recolectadas en la provincia de Alicante. Por lo tanto, aparte de un posible patrón latitudinal (¿regido por la temperatura?), no se pueden descartar patrones locales de distribución ligados a la ecología de las distintas algas (Huvé., 1962). Todo ello se debería abordar en futuros estudios.

Otra de las implicaciones de la presencia del arrecife colindante a tales plataformas es su papel amortiguador del oleaje. Esto implica que en estas plataformas se pueden encontrar especies de ambientes resguardados muy rarificados en costas desprovistas de las mismas. Además, el gradiente hidrodinámico generado incrementa la biodiversidad vegetal y animal (Milazzo *et al*., 2016). Asimismo, en periodos de bajamar prolongados, el arrecife vermetídico actúa de muralla contenedora del agua de la plataforma (Safriel, 1975). De este modo, las comunidades de la plataforma quedan algo protegidas frente a este tipo de perturbaciones.

Todo ello justifica, por lo tanto, tratar las plataformas vermetídicas como unidades paisajísticas cuyos componentes están interrelacionados y merecen, en este sentido, ser tratados también como hábitats a proteger y gestionar correctamente.

2. Las plataformas de vermétidos y algas calcáreas del Sureste Ibérico

Varios trabajos han tratado algunos aspectos ligados a las plataformas vermetídicas del Sureste Ibérico, tanto a nivel geomorfológico (Lillo-Carpio, 1980), como descriptivo (Cano *et al*., 1994; Ramos-Esplá *et al*., 2008), y fitocenológico o florístico (Barceló, 1987; Soto, 1987; Aranda *et al*., 1994; Pena-Martín, 2002). Sin embargo, desconocemos trabajos que traten las fitocenosis asociadas a estas plataformas como unidad de estudio. Por ello, de abril a junio de 2014, analizamos las principales fitocenosis asociadas a las plataformas de abrasión vermetídicas del Sureste Ibérico (de

Dénia al Cabo de Gata) (Terradas-Fernández, 2014). El estudio se centró en enclaves sin afectación antrópica y se hizo mediante inventarios visuales recolectando sólo especímenes dudosos o "manchas algales" no discernibles en el campo. Por lo tanto, sin ser un estudio florístico exhaustivo, nos permitió conocer el patrón de distribución de las algas dominantes, así como algunas singularidades florísticas. Los principales resultados, descritos parcialmente a continuación, ayudaron a conocer el patrón de distribución de los principales grupos algales, así como la elaboración de objetivos para la presente tesis.

Patrones de distribución de las fitocenosis algales en plataformas vermetídicas del Sureste Ibérico

Las especies algales dominantes en las plataformas vermetídicas son típicamente fotófilas y existe una presencia importante de elementos termófilos y de afinidad tropical. Estas características parecen generalizables a todos los sistemas de plataformas vermetídicas mediterráneas, lo que es esperable por su distribución en las zonas más cálidas y por su escasísima profundidad (Pérès y Picard, 1964; Lipkin y Safriel, 1971; Lakkis y Novel-Lakkis, 2000; Chemello, 2009; Badreddine *et al*., 2019). De entre estas especies termófilas destacamos *Anadyomene stellata*, *Penicillus capitatus*, *Sargassum vulgare*, *Digenea simplex*, *Neogoniolithon brassica-florida*, y *Neosiphonia ferulacea* cf[1]. Estas especies se rarifican o faltan en sectores más septentrionales (Chappuis et al., 2014).

También son frecuentes algunos endemismos como *Cystoseira algerienis*, *C. sauvageauana* y *Dictyota mediterranea*. El complejo *Laurencia* tiene varios representantes destacando el género *Palisada* por su abundancia (sobre todo en los márgenes externos y asociado al arrecife vermetídico). En cambio, el género *Osmundea* se rarifica, con escasos ejemplares encontrados de *O. truncata*, contrastando con la dominancia de *O. verlaquei* en la franja litoral de la Costa Brava catalana (Chappuis *et al*., 2014), que también se ha citado en el norte de la provincia de Alicante por Boisset y Aranda (bdb.cma.gva.es). Otras especies rarificadas o ausentes en las plataformas del Sureste Ibérico, comunes en sectores septentrionales, son: *Lithophyllum byssoides*

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[1] Esta especie, citada también en la cuenca oriental, no tiene todavía una posición taxonómica clara (Díaz-Tapia, com.pers)

(ausente), *Lithophyllum incrustans* (rarificada), *Ellisolandia elongata* (rarificada salvo en las zonas más expuestas), *Rissoella verruculosa* (ausente).

Aparecen, con relativa regularidad, tres especies algales exóticas. *Falkenbergia* stadio se encuentra regularmente en las zonas expuestas y algo esciáfilas de las plataformas; mientras que *Acrothamnion preisii* aparece con muy baja cobertura y ocasionalmente. *Caulerpa cylindracea* parece ser el alga exótica de mayor propagación. A pesar de su carácter invasivo en distintos enclaves mediterráneos (Piazzi *et al*., 2016), su presencia en las plataformas estudiadas parece moderada (Terradas-Fernández, 2014), aunque se ha extendido por todo el sector del SE ibérico. En situaciones de poca alteración, nunca se observan grandes manchas de esta alga que, por norma, se entremezcla laxamente con las especies típicas de la plataforma. Este patrón es similar al de otras plataformas de vermétidos con poca alteración antrópica (Balisteri y Mannino, 2017).

Por lo que respecta a la vegetación dominante, ésta se distribuye en todo el sector del Sureste Ibérico acorde a un patrón regular. Así, como ya hemos comentado, se generan horizontes dominados por especies concretas que son de una anchura muy superior a la habitual cuando faltan estas plataformas (Terradas-Fernández, 2018) (Fig.1).

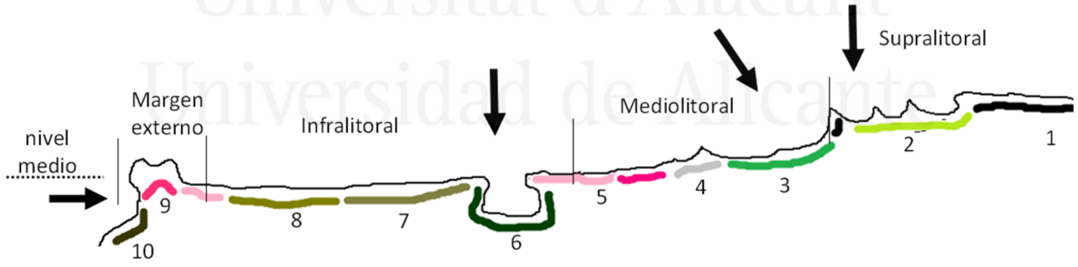

Figura 1. Perfil idealizado de una plataforma de abrasión con arrecife de vermétidos y algas calcáreas del Sureste Ibérico. Las flechas indican las zonas de erosión y bioerosión más activas. (1) Comunidad supralitoral de *Echinolittorina punctata*, (2) Comunidad de cubeta supralitoral con cianobacterias, (3) Comunidad de cubeta mediolitoral con ulváceas, (4) Comunidad mediolitoral de *Chthamalus* spp. y rivulariáceas, (5) Comunidad de *Vermettus triquetrus* y *Neogoniolithon brassica-florida*, (6) Comunidad de cubeta de plataforma con dictiotáceas y fucales de modo calmo, (7) Comunidad de *Padina*, (8) Comunidad de *Dictyota* spp., (9) Arrecife de *Dendropoma lebeche* y *Neogoniolithon brassica-florida*, (10) Comunidad de fucales de modo expuesto o de algas esciáfilas (según el grado de desarrollo del *notch*). Figura extraída de Enseñanza de las Ciencias de la Tierra, 2018 (26.2) – 145, con permiso del editor.

Empezando desde la parte más alejada del mar, en el margen interno, normalmente encontramos un horizonte supralitoral relativamente empobrecido, salvo en las cubetas y grietas generadas en el lapiaz supralitoral, ocupadas, mayoritariamente, por tapetes de cianobacterias. Este empobrecimiento obedece a la fuerte amortiguación del oleaje causado por la plataforma y el arrecife (Terradas-Fernández, 2018). El horizonte mediolitoral puede presentar cierta inclinación desarrollándose un enclave o *notch* en algunos casos. En la parte inferior de este margen interno suele aparecer un cinturón costroso de vermétidos y algas calcáreas (generalmente *N. brassica-florida* y *D. lebeche*) muchas veces acompañado de rodomeláceas (*Palisada* spp., *Polysiphonia* spp., *Lophosiphonia* spp.). También son importantes muchos moluscos que contribuyen a la bioerosión ya descritos previamente. Este horizonte se continúa, en la superficie aplanada de la plataforma, con costras de *V. triquetrus* y algas calcáreas (no siempre bien desarrolladas) y luego ya suelen vislumbrarse horizontes conspicuos de macroalgas erectas. Generalmente, el horizonte más interno está dominado por *P. pavonica,* siendo sustituido por un horizonte de *Dictyota* spp. (*D. spiralis* y *D.fasciola*) en la zona media de la plataforma. A medida que nos acercamos al margen más expuesto suelen aparecer algas fucales que pueden llegar a formar horizontes evidentes. Generalmente, encontramos primero un cinturón de *Cystoseira humilis*, o en zonas más resguardadas, de *C. sauvageauana* (sobre todo en depresiones o cubetas). En la zona media también se desarrolla, en algunos casos, un horizonte poco denso de *Sargassum vulgare*. Cerca del margen externo suele dominar *C. algeriensis*. Finalmente, justo antes del horizonte de *Dendropoma* y *Neogoniolithon* también suele reaparecer el horizonte de *V. triquetrus* y *Neogoniolithon* (muy desdibujado). El arrecife no suele sobrepasar los 20 cm de altura (incluso menos en muchas localidades) pero suele formar bandas continuas de varios metros, con pequeñas discontinuidades entre ellas (Fig. 2). En la zona externa, suele haber una pendiente abrupta, a veces con un *notch* desarrollado. A flor de agua, suele desarrollarse un último cinturón denso y expuesto de *C. amentacea*. Todos estos horizontes de fucales también pueden aparecer en cubetas de cierto desarrollo en la plataforma, cuyo tipo de fucal dominante depende del grado de exposición de la propia cubeta.

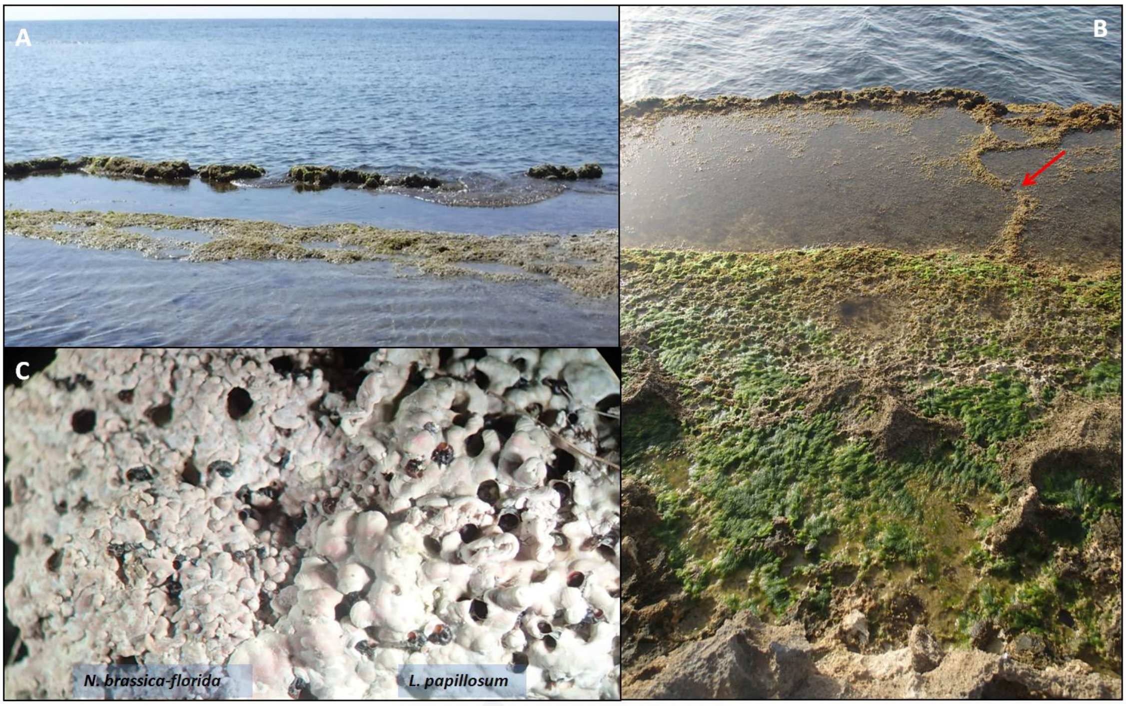

Figura 2. Plataformas de algas calcáreas y vermétidos. A. Cornisa del margen externo del arrecife (Cabo de las Huertas). B. Plataforma en la que se observa bien los horizontes: Ulváceas del mediolitoral y una comunidad dominada por *P. pavonica* colindante con la cornisa externa del arrecife de algas y vermétidos. La flecha indica "cordones" de bioconstrucción, menos desarrollados que en la cornisa (Cabo de las Huertas). C. Bioconstrucción con vermétidos y algas calcáreas donde dos especies algales contribuyen a la generación de la misma: *Neogoniolithon brassica-florida* y *Lithophyllum papillosum* (Fotografía realizada en Xàbia). Más explicación en el texto. Las fotografías se realizaron en bajamar (nótese en B, cómo el agua queda contenida en la plataforma dónde cierta inclinación hacia la parte interna, junto a la propia cornisa de algas y vermétidos, parecen contribuir a tal contención).

En muchos casos, también aparecen horizontes mixtos con codominancia de varias algas fotófilas (*Padina pavonica*, *Halopteris scoparia*. *Alsidium corallinum*, *Dascycladus vermicularis*, etc…).

Debido a estos patrones en la distribución de las algas en lo ancho de la plataforma, formando horizontes de constitución parecida que se suceden zonalmente, la variabilidad local (a escala de pocas decenas de metros) parece mayor que la encontrada a escala regional (en todo el sector estudiado del Sureste Ibérico; Terradas-Fernández, 2014). Este patrón parece general, a escala regional, cuando no hay barreras biogeográficas importantes o condicionantes locales específicos (Cruz-Motta, 2007; Chappuis *et al*., 2014). Así, teniendo en cuenta que el patrón de distribución algal parece general, los condicionantes de este patrón también lo deben ser.

OBJETIVOS GENERALES

Por lo comentado anteriormente, se generan varias dudas a considerar, entre ellas:

1. Habiendo realizado el muestreo en primavera, ¿qué ocurre con la dinámica anual de estas plataformas?, ¿es equivalente a la observada en otras comunidades del infralitoral superior, a pesar de las peculiaridades descritas para estos enclaves?, ¿qué condicionantes abióticos y bióticos pueden ser responsables de la dinámica anual?, ¿las fases de diversificación y producción descritas para el Mediterráneo Noroccidental (Ballesteros, 1992) encajan con el ciclo anual de estas plataformas?

2. Habiendo llevado a cabo el muestreo en situaciones de bajo impacto, ¿qué ocurre en situaciones claramente antropogenizadas?, ¿las especies invasoras, como *Caulerpa cylindracea*, presentan el mismo patrón, en abundancia y dinámica, en plataformas que difieren por su estado ecológico?

3. ¿Cuál es la resiliencia de estos sistemas?, ¿influye la afectación antrópica en la misma?

A partir de estas cuestiones se han generado 4 artículos científicos (3 ya publicados y el cuarto en revisión) que forman el cuerpo de esta tesis por compendio de publicaciones.

Primera publicación: Terradas-Fernández, M., Botana Gómez, C., Valverde Urrea, M., Zubcoff, J., Ramos-Esplá, A.A., 2018. The dynamics of phytobenthos and its main drivers on abrasion platforms with vermetids (Alicante, Southeastern Iberian Peninsula). Mediterranean Marine Science. 19, 58–68. https://doi.org/10.12681/mms.14143.

En esta publicación se estudia la dinámica de las fitocenosis de plataforma en un ciclo anual. Principales hipótesis consideradas:

1. Existe una dinámica anual en la composición algal de las plataformas que presenta variaciones en un patrón zonal vinculado al potencial productivo.

2. La variabilidad en la composición se rige por una serie de variables bióticas (abundancia de herbívoros) y abióticas (inclinación, distancia al margen externo, cantidad de sedimento, rugosidad, profundidad, temperatura y fotoperiodo).

3. Podría existir una fase de diversificación (medida a través de la diversidad α y β) ligada a un proceso de decaimiento en los meses de mayor estrés térmico y lumínico (verano-otoño), seguida de una fase de producción durante los meses más aptos para el

desarrollo algal (invierno-primavera) tal y como ocurre, en gran medida, en la franja litoral del Mediterráneo Noroccidental.

Segunda publicación: Terradas Fernández, M., Valverde-Urrea, M., Casado-Coy, N., Sanz-Lázaro, C. 2020. The ecological condition of vermetid platforms affects the cover of the Alien Seaweed *Caulerpa cylindracea*. Scientia Marina 84 (2). https://doi.org/10.3989/scimar.04984.06A

En esta publicación se realizó un estudio comparativo de la composición y dinámica de las comunidades algales de plataformas en dos localidades con un estado ecológico diferente: Cabo de las Huertas, con un estado ecológico bueno (acorde con la composición específica y la constitución de las comunidades algales); y Aguamarga, con un estado ecológico alterado. Además, se tuvo en cuenta que ambas localidades fueron las primeras en las que se detectó, prácticamente al mismo tiempo, la presencia del alga exótica *Caulerpa cylindracea,* hace más de 15 años (Carolina Pena Martín y Alfonso Ramos Esplá, com.pers). Debido a la abundancia con que esta alga se presentaba en la situación alterada, justo antes de empezar el muestreo (agosto del 2016), decidimos evaluar si existía alguna propiedad en la comunidad receptora que permitiese explicar las diferencias en abundancia de dicha alga entre ambas localidades. Principales hipótesis consideradas:

1. La condición de alteración se mantiene durante todo el ciclo anual siendo la composición específica diferente en Aguamarga, respecto a Cabo de las Huertas, durante todo el año.
2. Algunos condicionantes ligados a las zonas urbanas, como la eutrofización y la sedimentación, podrían explicar el cambio de fase entre ambas localidades.
3. La cobertura de las especies formadoras de dosel y su estabilidad, a lo largo del año, podrían explicar la diferencia en la abundancia de *C. cylindracea* entre ambas localidades.
4. Debido al gradiente ambiental a lo ancho de la plataforma y con un potencial productivo mayor en el margen externo, se genera un patrón zonal en la abundancia de especies formadoras de dosel que repercute en la abundancia de *C. cylindracea.*

Tercera publicación: Terradas-Fernández, M., J. Zubcoff & A. Ramos-Esplá, 2019. Early succession patterns in a Mediterranean vermetid reef. Journal of Sea Research 152: 1-15. https://doi.org/10.1016/j.seares.2019.101768

En esta publicación se querría evaluar la resiliencia, tras una pequeña perturbación, del arrecife de vermétidos mediante el empleo de placas de colonización. De este modo, se simuló un clareo de área pequeña sin afectar las propiedades importantes para la recuperación de la comunidad (como la disponibilidad de reclutas y la estructura poblacional previa). Tampoco quedó afectado el arrecife al usarse discontinuidades del mismo para la instalación de las placas.

Según la velocidad del proceso, y del grado de colonización por parte del vermétido y del alga calcárea, se podría plantear la utilidad del método de colonización, mediante placas, como método de restauración para casos determinados. Principales hipótesis consideradas:

1. La sucesión se verá influenciada por el momento de instalación debido a la distinta fenología de las especies del arrecife, repercutiendo en su capacidad de reclutar y colonizar.

2. Se espera que las diferencias iniciales, ligadas al momento de la instalación, remitan a lo largo de un proceso de convergencia en donde las especies ingenieras principales (*Dendropoma lebeche* y *Neogoniolithon brassica-florida*) ganen importancia cuantitativa.

Cuarta publicación (en revisión en Hydrobiología): Terradas-Fernández, M., N. Casado-Coy, R. Huguet-Sánchez, C. Sanz-Lázaro. Response to small pulse disturbances of phytobenthos on vermetid platforms with distinct ecological status.

En esta publicación se quería evaluar la resiliencia de los principales horizontes algales que habitan a lo largo de la anchura de la plataforma, a partir de pequeños clareos artificiales que simulaban pequeñas perturbaciones. En este sentido, se trata de una continuación de la tercera publicación pero focalizada en otras comunidades (las que, cuantitativamente, son las principales ocupantes de dichas plataformas). También se consideraron aquellas situaciones de alteración donde las especies dominantes (nitrófilas y tolerantes al estrés) diferían de aquellas de las situaciones de no alteración. Por estas razones, algunas de las hipótesis son coincidentes con las de la tercera publicación. Principales hipótesis consideradas:

1. La sucesión se verá influenciada por el momento del clareo debido a la distinta fenología de las especies que colonizan la plataforma.

2. La sucesión se verá afectada por el gradiente ambiental que se genera a lo ancho de la plataforma y que repercute en el potencial productivo (menor en la zona interna y mayor en la zona externa).

3. La sucesión se verá afectada por el estado ecológico de la localidad.

4. Se espera un proceso de convergencia a medida que transcurra el tiempo, siempre que no haya efectos prioritarios (*priority effects*) ligados a especies que tengan una capacidad de ocupación parecida y sostenida en el tiempo.

Research Article

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The dynamics of phytobenthos and its main drivers on abrasion platforms with vermetids (Alicante, Southeastern Iberian Peninsula)

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Abstract

Abrasion platforms with vermetids shape unique seascapes and biotic assemblages that characterize several of the warm Mediterranean coasts. The composition, structural and seasonal dynamics of the platforms' phytobenthos were examined at two Southeast Iberian locations through non-destructive sampling. The patterns observed were linked with environmental variables and grazers' coverage, and we assessed their possible influence. Structural descriptors α-diversity and β-diversity were applied, pointing that depth and season-related variables were the major influencing drivers. Higher α-diversity and β-diversity values during winter and spring coincided with the production optimum of the community. A greater average water depth influences the abundance of both midlittoral and infralittoral taxa. The strong resemblance between the phytobenthos of these vermetid platforms and that on similar platforms in the Eastern and Central Mediterranean Sea suggests that these are affected by the same structuring mechanisms.

Keywords: Seasonality, Community structure, Environmental factors, Species diversity, Benthos.

Introduction

Abrasion platforms with vermetids are characteristic seascapes of warm Mediterranean rocky coasts composed of limestone. Vermetid reefs of several decimetres wide are frequently found at their outer margin, contributing to the platform development (Lillo-Carpio, 1980; Laborel, 1987; Antonioli *et al*., 1999) and playing an important role as habitat engineers (Milazzo *et al*., 2016). Such reefs host a variety of species (Mannino, 1992; Donnarumma *et al*., 2014) and buffer water movement over the platform, creating favourable conditions for the establishment of communities which are characteristic of calmer, more sheltered, conditions (Cano *et al*., 1994), increasing thus shoreline biodiversity (Safriel, 1975; Chemello, 2009; Milazzo *et al*., 2016).

Nonetheless, these systems have been poorly studied from an ecological and phycological perspective (Milazzo *et al*., 2016). In the Iberian Peninsula, shallow systems with well-developed vermetid platforms are found from the north of the province of Alicante south to that of Almería (Molinier & Picard, 1956; Ramos-Esplá, 1985; Ramos-Esplá *et al*., 2008; Templado *et al*., 2016) (Fig. 1). Data on the structure and dynamics of the phytobenthic communities inhabiting such platforms are scarce (Soto, 1987; Pena-Martín, 2002; Terradas-Fernández, 2014).

The zonation pattern is easily recognizable in the whole platform. An initial sloping midlittoral algal belt dominated by Corallinaceae is followed by an upper infralittoral zone occupying a large portion of the platform,

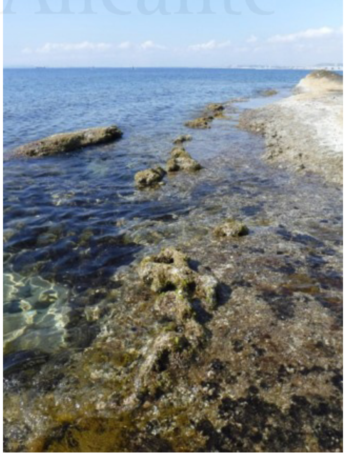

Fig. 1: Abrasion platform with vermetids at Cabo de las Huertas (Alicante). Seascapes of this type are well developed along rocky limestone shores in the Southeast Iberian Peninsula.

dominated mainly by Dictyotaceae. The exposed outer margin normally hosts Corallinaceae formations with vermetids, along with leathery algae. These platforms are very shallow in depth (≤ 40 cm), and are characterized by intermediate temperature and nutrient conditions when comparing to those found along the adjacent Iberian coasts (cooler and somewhat more eutrophic) and those in the Eastern Mediterranean (more oligotrophic and warmer) (Bosc *et al*., 2004; Coll *et al*., 2010). Such characteristics suggest that their dynamics may also be different from other comparable shallow phytobenthic assemblages, in both Iberian (Ballesteros, 1992) and Eastern Mediterranean Sea (Lipkin & Safriel, 1971; Lundberg & Olsvig-Whittaker, 1998).

The focus of this study is to explore the structure, composition and seasonal dynamics of the phytobenthic communities on abrasion platforms with vermetids and to identify the main influencing drivers of these assemblages. The results are compared with those of other analogous studies in shallow systems of the Western and Eastern Mediterranean Sea.

Material and Methods

Sampling and data collection

Two previously typified locations (Isla de Tabarca and Cabo de las Huertas) (Terradas-Fernández, 2014) were chosen. These sites present no pollution source or other visually anthropogenic disturbances. Tabarca is located at 38.16701º N, 0.48498º W and Cabo de las Huertas at 38.35340º N, 0.42053º W (Fig. 2). Three permanent transects perpendicular to the shore (3 to 6 m in long) were established at each location including: a) a proximal midlittoral zone; b) an infralittoral zone; and c) an exposed outer margin adjoining its seaward 'wall' (Fig. 2, Electronic appendix Fig. S 1, Fig. S 2). Each transect was sampled monthly for one year (June 2015–May 2016), using contiguous 625 cm^2 pre assigned squares separated by 5 cm. Sampling squares were sampled monthly along each transect.

The coverage of visually distinguishable sessile taxa was calculated using the Braun-Blanquet scale (1979) (Díez *et al*., 2003; Chappuis *et al*., 2014). 6 cover-categories were used: <5% cover (1), 5–25% (2), 25–50% (3), 50–75% (4), and >75% (5). A 0.1% value (6) was used for taxa with insignificant coverage. Taxa impossible to identify *in situ* were collected for subsequent identification in the laboratory. Inconspicuous taxa with less than 0.1% coverage in all zones and seasons were excluded from the analysis (see Electronic appendix Table S 1).

For each sampled square, 6 environmental variables were measured or estimated: i) the *substrate slope*, ii) the *distance from the outer margin* (platform seaward limit), iii) the *grazers' coverage*, iv) the *sediment coverage*, v) the *topographic complexity*, and vi) the *depth*, as follows:

i) Substrate slope angle, from 0 up to 4: (0) horizontal surface; (1) 15-30º slope; (2) 30º-45º slope; (3) 45º-90º slope; (4) >90º slope.

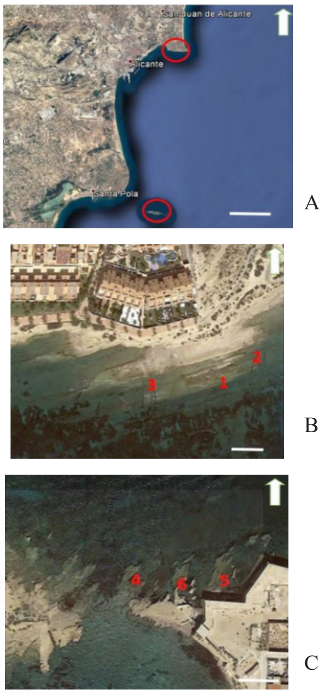

Fig. 2: Sampling locations. A. Geographic location of both areas (northern circle indicating Cabo de las Huertas, and southern circle indicating Isla de Tabarca); scale bar = 5 km. B and C. Transect locations at Cabo de las Huertas and Isla de Tabarca respectively (scale bar = 30 m). Modified from Google Earth.

ii) Distance from the outer margin in cm for each transect square (Gil *et al*., 2008; Balistreri *et al*., 2015).

iii) Grazers' coverage, using the Braun-Blanquet (1979) scale in line with Chappuis *et al*. (2014), integrating all grazers' taxa.

iv) Sediment coverage followed the criteria suggested by Díez *et al*. (2003), keeping the same Braun-Blanquet categories used for phytobenthos coverage: (1) <5% coverage, (2) 5–25%, (3) 25–50%, (4) 50–75%, and (5) >75%.

v) Topographic complexity followed the methods of Graziano *et al*. (2009) employed by Balistreri *et al*. (2015), but using the same 625 cm2 sampling squares for the calculation. Thus, the inverse ratio of the sums of the perimeter and the diagonals with regard to the measurement adjusted to the rocky substrate were calculated for each square.

vi) Depth, defined as the water-column height above each square, measured with a vertically placed ruler, resulting in an average value for each sampled square during the year. The average depth was incorporated as a variable. The reason for using the average instead of empirical value was its considerable variability even on the same day (pers. obs.).

In addition, each day's photoperiod was taken into account based on information provided by the National Astronomical Observatory of Spain (http://www.fomento.gob.es). Finally, temperature data were obtained by CIMAR Research Station at Cabo de Santa Pola at 0.5 m depth at 9 AM over a similar abrasion platform to those studied, situated close to both sampling locations. The maximum algal canopy height of each plot was also measured with a ruler and used as a surrogate to estimate the productivity potential (Steneck & Dethier, 1994).

Data analysis

The coverage values of each phytobenthic taxon, sediment and grazers were determined by using a transformation of the Braun-Blanquet scale data, considering the median points of each interval as new values (Díez *et al.*, 2003; Guinda *et al.*, 2012). The coverage values of the taxa were square root transformed for the multivariate analyses, and a similarity matrix was generated based on them using the Bray-Curtis distance.

To assess whether there were significant differences between zones and seasons, a permutational multivariate analysis of variance (PERMANOVA) was performed (Anderson *et al.*, 2008). The analysis consisted of a two-way crossed model in which *zone* and *season* were treated as fixed factors. Sums of squares type III were employed to account for unbalanced design (Anderson *et al.*, 2008). Pairwise *post-hoc* comparisons were made to test for significant differences. The taxa that contributed most to the differences were identified using similarity percentages (SIMPER) (Clarke & Gorley, 2006).

To test the potential influence of each variable within the community structure, a distance-based linear model routine (DistLM) was applied to the previously generated Bray-Curtis matrix. The stepwise selection procedure was used with the R^2 criterion. Environmental variables were normalized: *grazers' coverage* was previously square-root transformed as it presented a right skewed distribution. Spearman correlations were used to test the relationship between the abundance of the algal taxa and the variables that contributed most to the DistLM analysis. Finally, a distance-based redundancy analysis (dbRDA) was performed to visualize the relationships between algal assemblages and environmental variables, based on the above multivariate regression model (DistLM analysis).

Furthermore, *α*- and *β*-diversity were used as indicators of structural complexity (Ballesteros, 1991; Simboura & Zenetos, 2002; Martí *et al.*, 2005; Mangialajo *et al.*, 2008; Balata & Piazzi, 2008; Casas-Güell, 2016). Shannon index was applied for calculating *α*-diversity, where "N" is the overall taxa coverage of a given sampled square and "ni" is the coverage of each of taxon for the same square:

$$H' = -\sum (ni/N) \log_2 (ni/N)$$

In order to determine whether there were significant differences between *α*-diversity values depending on the *season* and *zone*, a second PERMANOVA was applied from a similarity matrix using the Euclidean distance (Anderson *et al.*, 2008).

For calculating *β*-diversity, the criteria suggested by Anderson *et al.* (2008, 2011) were followed, here construed as the acceptance defined by the degree of variability within a community, calculated from the variability between different samples thereof. Thus, on the basis of the taxa composition in each square, a Jaccard similarity matrix was calculated and the homogeneity of the dispersions for *zone* and *season* (PERMDISP) was tested using the average distance to centroid as the measure of *β*-diversity.

All statistical analyses were performed using the PRIMER--E® v.6 + PERMANOVA package (Clarke & Gorley, 2006; Anderson *et al.*, 2008), except for the information graphics for α-diversity (Fig. 3) and Spearman correlations between taxa and environmental variables, which were performed using R software version 3.2.2 (R Development Core Team, 2011) and gggplot2 package (Wickham, 2009).

Results

Through the overall annual survey, 970 square samples were studied and over than 100 taxa were identified (see Electronic appendix Table S 1). Some commonly found species in our study areas appear to be more rare or absent in the Northeast Mediterranean Iberian Peninsula (Chappuis *et al.*, 2014), e.g. *Cladophoropsis membranacea* and *Cystoseira algeriensis*. Additionally, *Neosiphonia ferulacea* and *Chaetomorpha pachynema* were present in our infralittoral sampling squares, but neither species seems to have been reported previously in the Iberian part of the Mediterranean (Gallardo *et al.*, 2016), although C. pachynema has been reported from the Balearic Islands (Cremades, 1989).

Differences in community configuration attributable to season and zone factors

Both season and zone affiliation were significant in the configuration of the phytobenthic assemblages (Table 1). The pairwise test showed that these differences remained when comparing season effects within each zone, except the midlittoral zone between summer and autumn (P (perm) = 0.058).

The results of the SIMPER two-way crossed analysis based on *season* and *zone* factors are shown in Table 2 with a cut-off percentage of 90% accumulated similarity. In the midlittoral zone, the major contributors to similarity were the crustose Corallinaceae, *Jania* spp., *Dendropoma lebeche,* Rivulariaceae and *Ulva* spp. In the platform's infralittoral zone, along with *Jania* spp., the role of Dictyotaceae was significant (contributions over 10%). Finally, at the outer margin, the main similarity contri-

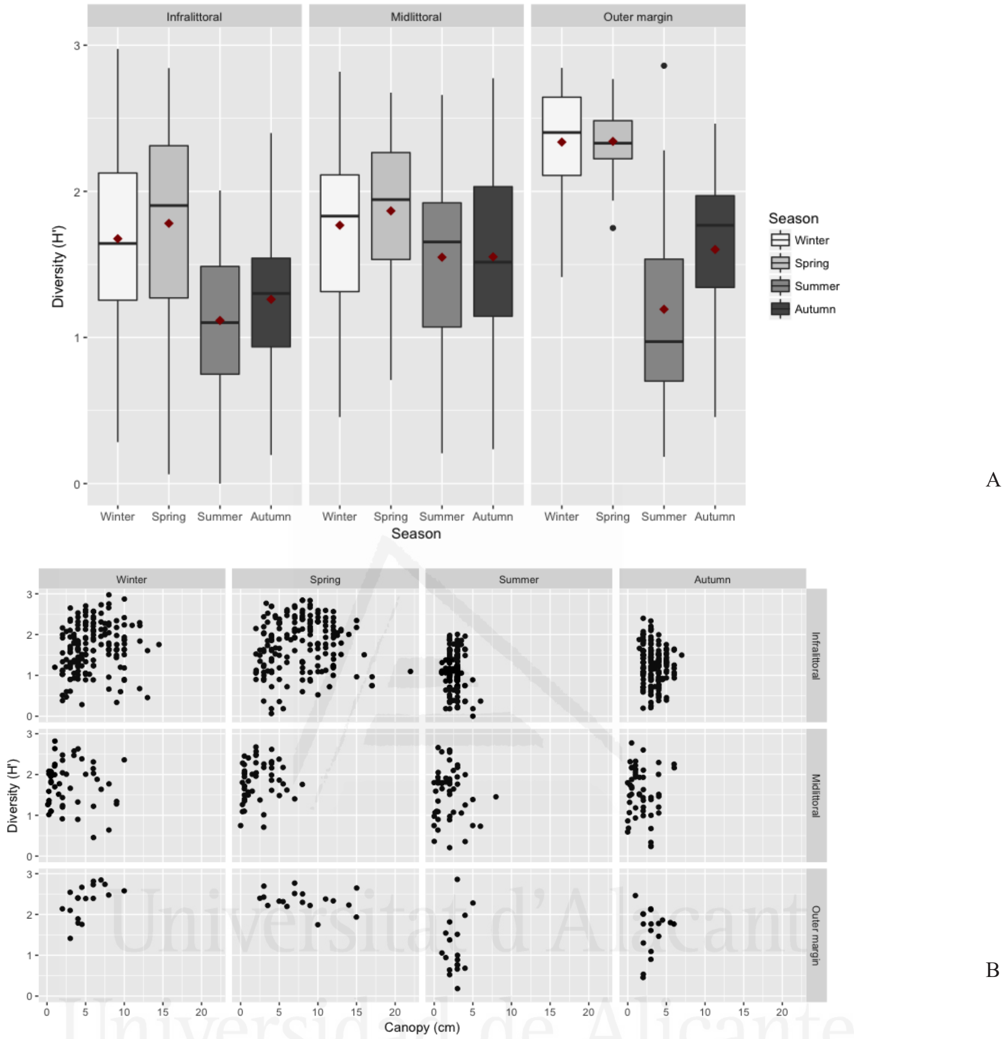

Fig. 3: A. Shannon diversity values (H') per *season* for all studied zones. B. Canopy height values per *season*, *zone* and Shannon diversity.

bution was made by a mixed group of infralittoral and midlittoral taxa. As in the infralittoral case, *Jania* spp. were the main contributors followed by *Padina pavonica* and the crustose Corallinaceae group (all with contributions above 10%). *Dictyota* spp. and *Cystoseira* spp. were found below 10%. *Ellisolandia elongata* and *Caulerpa cylindracea* contributed around 1% in the outer margin zone, while their contribution was near-zero in the midlittoral and infralittoral zones (data not shown).

The proportion of each taxon to SIMPER similarity varied highly according to season. In summer and autumn, *Jania* spp. contributed to similarity with a high percentage (over 50% in both seasons), followed by *Padina pavonica* with 34.8% in summer and 19.3% in autumn. In winter and spring, *Jania* spp. contribution progressively decreased (35% in winter and 8% in spring). On the other hand, Dictyotaceae (*P. pavonica* and *Dictyota* spp.) showed the inverse pattern, with a total 47.2% in winter and up to 63% in spring. Other algae with strong seasonality included *Cystoseira compressa* and *Halopteris scoparia* (with spring contributions of 10.6% and 7% respectively).

α-diversity

α-diversity showed a significant seasonal pattern associated with zone (Fig. 3 and Table S 2). A greater diversity phase during winter and spring was observed, which coincided with a higher algal canopy, but a lesser diversity during summer and autumn with a lower canopy height. This pattern was observed in each zone, being greater at the outer margin and lesser in the midlittoral zone.

Table 1. Distance-based permutational two-way PERMANOVA comparing all the samples taxa inventories using *zone* and *season* as fixed factors (A). Results of pairwise analyses (B). Se, *season*; Z, *zone*; df, degrees of freedom; SS, sums of squares; MS, mean squares; Pseudo-F, pseudo-*F* ratio; t, pseudo-*t* statistic; P(perm), permutation *P*-value.

A

Source of variation	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Se	3	102800	34267	28	0.001	996
Z	2	504190	252100	209	0.001	998
SexZ	6	52706	8784	7	0.001	999
Res	959	1155600	1205			
Total	970	1959900				

B

Pairwise analysis within levels of factor 'Z'	**Midlittoral**		**Infralittoral**		**Outer margin**	
Groups	**t**	**P(perm)**	**t**	**P(perm)**	**t**	**P(perm)**
Spring, Summer	2.97	0.001	12.22	0.001	3.99	0.001
Spring, Autumn	3.78	0.001	11.66	0.001	3.45	0.001
Spring, Winter	1.62	0.026	6.02	0.001	1.94	0.001
Summer, Autumn	1.48	0.058	6.16	0.001	1.82	0.004
Summer, Winter	2.79	0.001	7.75	0.001	2.69	0.001
Autumn, Winter	3.43	0.001	5.77	0.001	2.04	0.001

Table 2. Main taxa contributions to SIMPER two-way similarity (*season* and *zone*). Contrib. %: Percentage of contribution to group similarity. Cut-off for low contributions: 90%.

Species	**Midlittoral Contrib%**	**Infralittoral Contrib%**	**Outer margin Contrib%**	
Cladophora spp.	3.38			
Corallinaceae	39.86		15.74	
Cystoseira compressa / humilis		3.09	4.68	
Dendropoma lebeche	10.28		1.46	
Dictyota spp.		13.76	5.74	
Jania spp.	16.43	43.39	46.28	
Padina pavonica		31.81	17.3	
Palisada spp.	2.57			
Rivulariaceae	12.91			
Ulva spp.	5.95			
	Spring	**Summer**	**Autumn**	**Winter**
Species	Contrib%	Contrib%	Contrib%	Contrib%
Corallinaceae	4.87			5.46
Cystoseira compressa / humilis	10.56			
Dictyota spp.	21.95		11.37	21.31
Halopteris scoparia	6.95			3.03
Jania spp.	7.93	57.93	59.87	34.98
Padina pavonica	41	34.81	19.34	25.99

β-diversity

β-diversity results can be found in Table 3. The midlittoral zone had the highest *β*-diversity, with related samples showing a Jaccard average distance to centroid of 47.46 ± 0.52%. The outer margin showed a 45.62 ± 0.79% value. Lastly, the infralittoral zone showed a value of 41.2 ± 0.35%. Based on the homogeneity of multivariate dispersions test (PERMDISP) (Table 3 A), pairwise comparisons indicated that the differences between the infralittoral and the other zones were significant. Nevertheless, the midlittoral and outer margin did not differ significantly (P (perm) = 0.09).

Comparing seasons, winter and spring had higher values of average distance from the centroid with respect to the whole platform (both slightly over 48%), while summer and autumn had lower values (40% and 42% respectively). There were no significant differences between winter and spring, or between summer and autumn, but the rest of the cross-season comparisons were significantly different (P (perm) < 0.05; Table 3 B).

The role of environmental variables

The multivariate regression model generated by the DistLM analysis showed that the matrix of environmental variables explained a significant proportion of the multivariate variation in the structure and composition of the studied communities (Table 4). On the basis of the sequential test using the step-wise selection procedure and

Table 3. *β*-diversity values and test for homogeneity of multivariate dispersions. A) Zones**;** B) Seasons (for the whole platform); t, pseudo-*t* statistic; P(perm), permutation *P*-value; Average, average Jaccard distance-to-centroid; SE, standard error.

A

PAIRWISE COMPARISONS	**Group factor:** ***Zone***		
Groups	t	P(perm)	
(Midlittoral, Infralittoral)	8.8876	0.00	
(Midlittoral, Outer margin)	1.8551	0.09	
(Infralittoral, Outer margin)	3.9516	0.00	
MEANS AND STANDARD ERRORS			
Group	Size	Average	SE
Midlittoral	204	47.46	0.51911
Infralittoral	695	41.25	0.3461
Outer margin	72	45.62	0.78543

B

PAIRWISE COMPARISONS	**Group factor:** ***Season***	
Groups	t	P(perm)
(Spring, Summer)	8.06	0.00
(Spring, Autumn)	6.66	0.00
(Spring, Winter)	0.44	0.73
(Summer, Autumn)	1.82	0.13
(Summer, Winter)	7.78	0.00
(Autumn, Winter)	6.35	0.00

MEANS AND STANDARD ERRORS			
Group	Size	Average	SE
Spring	243	48.77	0.64
Summer	243	39.94	0.89
Autumn	243	42.08	0.77
Winter	242	48.37	0.62

R^2 criterion, *depth* was the variable explaining the greatest proportion of the variation for the model. The next-best variables to add in order to increase R^2 were respectively: *photoperiod*, *water temperature*, *distance from outer margin*, *topographic complexity*, *slope*, *sediment coverage* and *grazers' coverage*. Total variability, defined by the selected environmental variables, was 44%.

In the dbRDA analysis (Fig. 4), *depth* was negatively correlated with the first axis while the *distance from outer margin* was positively correlated to it, along with *topographic complexity*, *grazers' coverage* and *slope* (with a lesser correlation). The variables that correlated best with the second axis were the *photoperiod* (negatively) and *temperature* (positively). Both axes accounted for 79% of the fitted variation (35% of total variability).

Crustose Corallinaceae, Rivulariaceae and *Dendropoma lebeche* were positively correlated with the first axis, while *Padina pavonica*, *Dictyota* spp. and *Cystoseira compressa* were negatively correlated to it. As for the second axis, crustose Corallinaceae and Rivulariaceae showed near-zero correlations, Jania spp. was clearly positively correlated, and the rest of the taxa showed negative correlations.

When it comes to Spearman correlations between environmental variables and taxa coverages (Table 5), it was observed that depth still showed a greater correlation with the majority of taxa. Correlation was positive with typical infralittoral species, excepting *Padina pavonica,* whereas it was negative with midlittoral taxa (Rivulariaceae, *Ulva* spp., crustose Corallinaceae).

Photoperiod only displayed a high and negative correlation value with *Jania* spp.. Crustose Corallinaceae and Rivulariaceae did not show significant correlations, while the rest of the infralittoral taxa generally showed positive correlations.

Most taxa showed negative correlations with *temperature*, coinciding with winter and spring conditions. Only *Padina pavonica*, with high coverage during summer, showed a clearly positive correlation. *Jania* spp., which develops in summer and autumn, showed a near-zero correlation.

Taxa showing a higher negative correlation with *distance from outer margin* were the *Jania* spp. and *Padina pavonica*. Conversely, Rivulariaceae was the group with the highest positive correlation.

Sediment coverage showed a moderate and positive correlation (0.3) with *Dictyota* spp., and slightly lesser with *Padina pavonica* and *Dasycladus vermicularis. Halopteris scoparia* presented near-zero values. The rest of the taxa displayed a negative correlation. As for the crustose Corallinaceae, their abundance in highly sediment-covered areas may have been underestimated.

Grazers' coverage, *slope* and *topographic complexity* showed a generally positive correlation with midlittoral taxa, being negative with those dominating in the other zones. Nonetheless, the midlittoral *Ulva* spp. presented a negative correlation with *slope*.

Patellidae, Trochidae, Lepidochitonidae, and Littorinidae were the main grazer families represented in the midlittoral zone. In the infralittoral, the most common visible groups were instead Columbellidae, Cerithidae, Paguroidea and Plakobranchidae, always with lower coverage values than midlittoral taxa, and barely detectable visually.

Discussion

Floristic aspects

The abrasion platforms with vermetids studied at both locations (Tabarca and Cabo de las Huertas) share the main taxa with other Mediterranean vermetid platforms (Lipkin & Safriel, 1971; Mannino, 1992; Lakkis & Novel-Lakkis, 2000). The alien alga *Caulerpa cylindracea*, despite commonly found along the entire platform, it grows better on the outer margin, generating conspicuous patches, mostly in spring. The higher coverage of this alien species on the eutrophicated Aguamarga platforms

Table 4. Results of DistLM (distance-based linear model routine). Sequential test for relationships between environmental variables and taxa coverage (considering all environmental variables and using the step-wise procedure and R^2 selection criterion) determining the variance explained by predictor variables when fitted sequentially.

SEQUENTIAL TEST				
Variable	**Pseudo-F**	**P**	**Prop.**	**Cumul.R^2**
Depth	239.87	0.001	0.20	0.20
Photoperiod	65.39	0.001	0.05	0.25
Water temperature	118.97	0.001	0.08	0.33
Distance	48.14	0.001	0.03	0.36
Topographic complexity	51.91	0.001	0.03	0.40
Slope	32.63	0.001	0.02	0.42
Sediment	21.21	0.001	0.01	0.43
Grazers	17.49	0.001	0.01	0.44

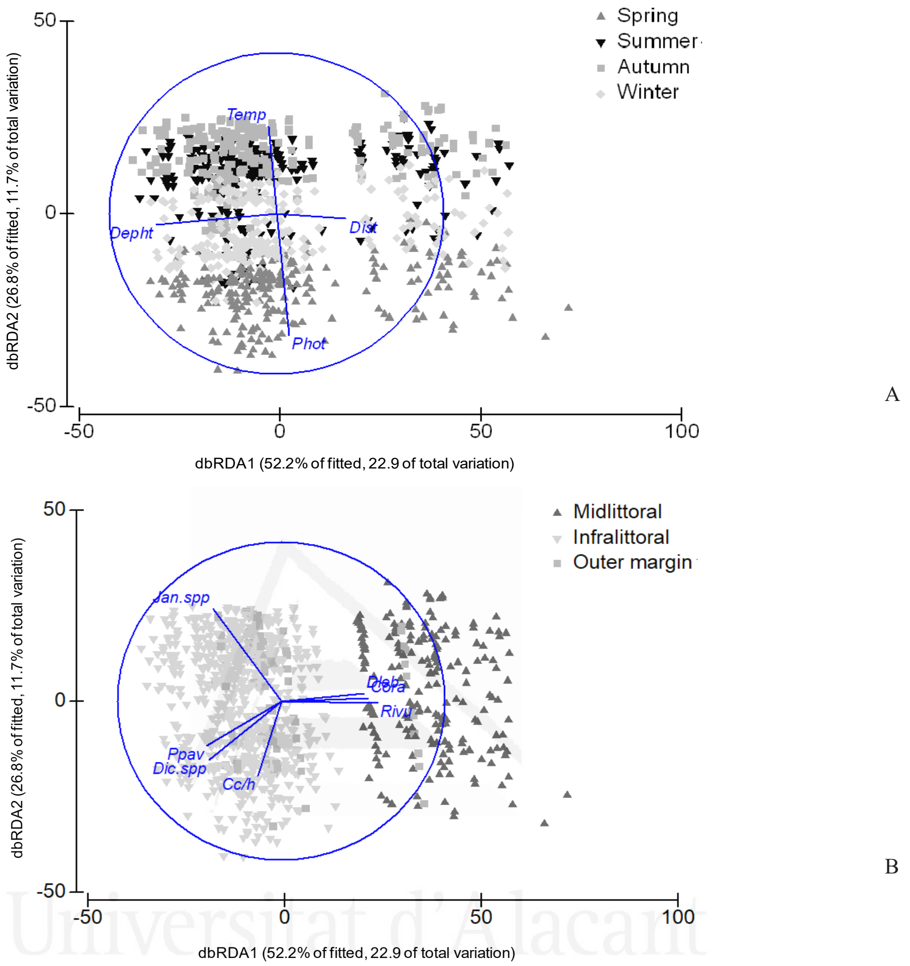

Fig. 4: Distance-based redundancy analysis (dbRDA). A. Relationships between the ordination of samples, based on taxa coverage and environmental variables (four variables that explain most of the variability in the data cloud are shown, according to the step-wise procedure and R2 criterion). Abbreviations: Temp = water temperature, Dist = Distance from outer margin, Phot = photoperiod. B. Direction of increasing coverage of the most abundant taxa with Spearman correlations over 0.4. Abbreviations: Cora = Corallinaceae, *Cc/h* = *Cystoseira compressa/humilis, Dleb* = *Dendropoma lebeche, Dic.*spp = *Dictyota* spp., *Jan.*spp = *Jania* spp., *Ppav* = *Padina pavonica, Rivu* = *Rivulariaceae.*

(a place close to Alicante, being under the influence of sewage), could indicate that this alien species thrives better in the most productive locations along these platforms, with the increased water motion and/or eutrophication being the two important factors enforcing its growth. Similarly, experimental studies indicate that this alga is favoured by eutrophic conditions (Gennaro & Piazzi, 2011).

The role of resource availability in the phytobenthos structure of the platform

The variables determining productivity potential, i.e. contributing to the maximum possible rate of biomass production (Steneck & Dethier, 1994), appear to exert the major role as drivers of the phytobenthic communities growing on vermetid platforms. Some of these variables are non-seasonal (*depth* and *distance from outer margin*), while others show a seasonal variability (*photoperiod*, *temperature*).

Low-canopy taxa (such as encrusting calcareous algae and *Padina* taxa) are followed by larger-sized taxa (such as *Dictyota* and *Cystoseira* taxa) according to the increase in depth and/or water motion, the latter variable being more important when the distance from the outer margin diminishes.

Regarding the seasonal cycle, the canopy height rises during winter and spring, coinciding with the photoperiod increase. This is because larger erect algae (*Dictyota*

Table 5. Spearman correlations between the coverage of the most abundant taxa and the environmental variables studied. Shaded results indicate correlations over 0.3. Significant results ($P < 0.05$) were marked with an asterisk (*). Abbreviations: *Top.comp* = *Topographic complexity.*

Variables	***Depth***	***Distance***	***Grazers***	***Photoperiod***	***Sediment***	***Slope***	***Top.complexity***	***T°***
Corallinaceae	-0.43*	0.14*	0.31*	-0.06	-0.24*	0.29*	0.40*	0.11*
C. compressa/ humilis	0.10*	-0.24*	-0.14*	0.28*	0.13*	-0.09*	-0.095 *	-0.16*
D. vermicularis	0.50*	-0.07*	-0.09*	-0.09*	0.17*	-0.16*	-0.16*	-0.13*
Dictyota spp.	0.57*	-0.21*	-0.10*	-0.11*	0.31*	-0.17*	-0.09*	-0.38*
H. scoparia	0.32*	-0.09*	-0.14*	0.25*	0.02	-0.06	-0.17*	-0.02
Jania spp.	0.23*	-0.33*	-0.32*	-0.40*	-0.27*	-0.04	-0.21*	0.03
P. pavonica	-0.32*	-0.42*	-0.30*	0.27*	0.29*	-0.29*	0.11*	0.11*
Rivulariaceae	-0.54*	0.49*	0.41*	0.06	-0.24*	0.22*	0.28*	-0.05
Ulva spp.	-0.32*	0.27*	0.05	0.07*	-0.18*	-0.01	-0.11*	-0.11*

and *Cystoseira* taxa) increase in coverage. On the other hand, articulated calcareous algae (*Jania* spp.) are more abundant during summer and autumn when photoperiod shortens. This pattern fits with the productive cycle observed in shallow Northwest Mediterranean phytobenthic communities, where the production phase coincides with high nutrient concentrations (Ballesteros, 1989).

The scarcity of grazers' coverage in the outer margin and infralittoral platform zone suggests that their impact is limited as drivers of the macroalgae thriving in these zones. This suggests that bottom-up processes seem to be the main structuring mechanisms of at least a large portion of these shallow platforms. The importance of bottom-up processes and disturbances has already been examined in other works related to Mediterranean vermetid platforms; radiation intensity, wave strength, emersion periods and temperature appeared to be significant drivers for macroalgae thriving in these systems (Lundberg & Olsvig-Whittaker, 1998; Einav *et al.*, 1998; Einav & Israel, 2007; Gil *et al.*, 2008; Chemello, 2009).

The response found in several studies performed on Mediterranean infralittoral bottoms, where grazing pressure was experimentally modified (Verlaque, 1987; Sala, 1996; Hereu *et al*., 2008), is similar to that found with increasing depth in our grazer-deficient system. In the first case, larger algae tend to thrive more as grazing decreases. In the second case, larger algae tend to thrive more in line with the rise in water depth. Both responses fit with Steneck & Dethier (1994) predictions on the dominance of different morphological groups according to their production potential and degree of disturbance. Crustose and calcified thalli withstand the disturbances and stress better, while the more complex thalli (large and rather internally complex) are more developed in situations showing greater productivity potential and stability.

Diversity pattern

A positive correlation between α-diversity and β-diversity was found for the production phases (winter and spring). The α-diversity shows the opposite pattern compared to that of several Mediterranean littoral rocky benthic communities (Soto, 1987; Rull-Lluch & Gómez-Garreta, 1990; Ballesteros, 1991; Rodríguez-Prieto *et al*., 2013), where production phases are accompanied by a lower α-diversity. Instead, our observed α-diversity pattern is similar to that of other infralittoral rocky shallow systems, where diversity values may be uncorrelated or positively correlated with the production phases (Garrabou *et al*., 2002; Martí *et al*., 2005). These differences appear to be caused by the dominance of relatively persistent habitat engineering species, which thrive in disturbance-free systems in high productivity conditions. The quantitative importance of these species affects the diversity values of the whole community (Wernberg & Goldberg, 2008). On the other hand, under stress conditions (whether by lack of water movement or light), or under a high disturbance degree (herbivory), the persistent species dominance seems to be hindered. In such cases, the seasonal production peak may not coincide with a diversity decrease, but rather the opposite (Martí *et al*., 2005). This would be the case of the majority of the communities on the surveyed platforms. Thus, their relatively buffered hydrodynamics and especially the lack of enough depth would limit the community's productivity, hindering the establishment of persistent taxa with high coverages, such as Cystoseira taxa, which may lower the α-diversity values during the productive phase.

The lower annual *α*-diversity fluctuations in our midlittoral zone platform could be caused by a lesser fluctuation in taxa coverage due to stress caused by low average depth and water motion deficit. In contrast, the wide environmental variation in this midlittoral zone results in a relatively high heterogeneity between midlittoral sampling squares, making for maximum β-diversity values, although close to those observed on the platform's outer margin.

In conclusion, the main drivers of the studied vermetid abrasion platforms seem to be bottom-up in their influence, water availability (depth) and seasonal factors being the most important. These results contrast with those obtained in other infralittoral systems, which are apparently under more intense grazing pressure (Verlaque, 1987; Hereu *et al*., 2008). Diversity is positively linked to the production cycle of the phytobenthos inhabiting these platforms, due to the lack of a persistent dominant group able to reduce diversity at its peak productivity.

Eutrophication and extreme climatic events (Sanz-Lázaro, 2016), such as unusual long emersion periods or strong storms, are other important factors not directly considered in this study. They should be taken into account in future research in order to widen our knowledge of these scarcely studied seascapes, typically found in the warm parts of the Mediterranean, along with their possible interaction with the current global warming scenario.

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Supplementary Data

The dynamics of phytobenthos and its main drivers on abrasion platforms with vermetids (Alicante, Southeastern Iberian Peninsula)

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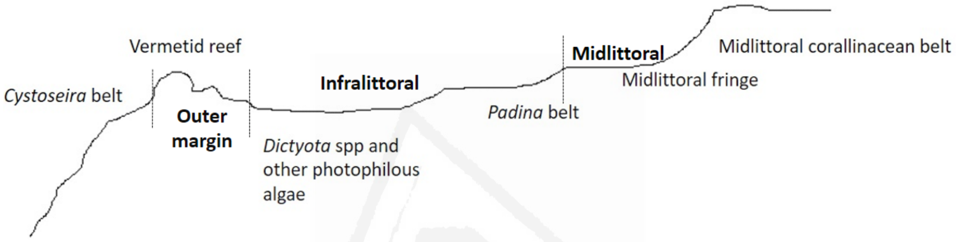

Figure S1: Schematic representation of the main belts found in the abrasion platforms at 10 locations in the Southeastern Iberian Peninsula (according to the present work and Terradas-Fernández, 2014). The outer wall (beyond the outer margin), usually having a significant presence of Fucales and/or articulated Corallinaceae, was not sampled in this study. The main zones were typified following Pérès & Piccard (1964).

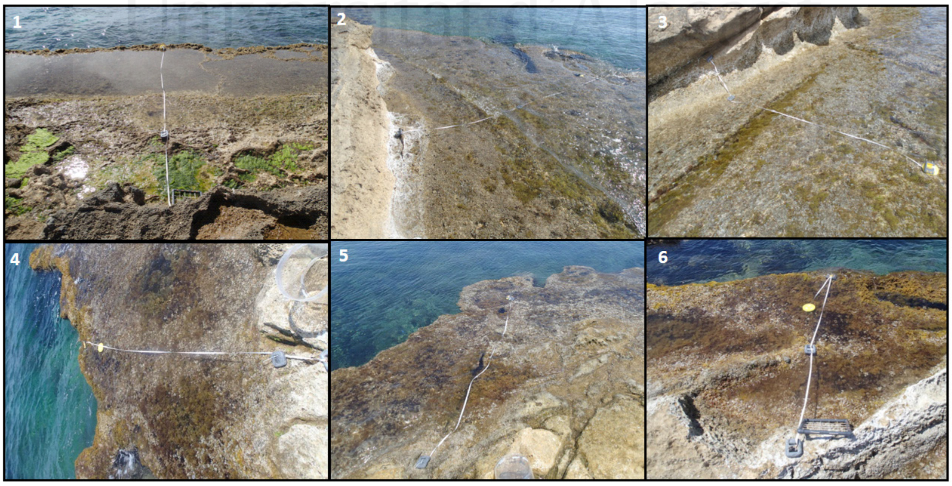

Figure S2: Areas where the six transects were performed. Numbers indicate each specific transect. The first three transects were performed at the Cabo de las Huertas location. The last three transects were performed at Isla de Tabarca. Exact positions of each transect are as follows:

Transect 1: 38.35319º N, 0.42089º W. Transect 2: 38.35340º N, 0.42053º W.
Transect 3: 38.35323º N, 0.42156º W. Transect 4: 38.16701º N, 0.48498º W.
Transect 5: 38.16702º N, 0.484240º W. Transect 6: 38.166990 º N, 0.48450º W.

Table S1. Taxa found in all the zones studied at Cabo de las Huertas and Isla de Tabarca during an entire year: A, midlittoral; B, infralittoral; C, platform outer margin. Results are shown based on the seasonal average coverage (%). Some taxa were identified at genus or other higher taxonomic levels. Only taxa in bold were quantified. The remainder of taxa were identified in the laboratory from collected samples and adjoined at higher taxonomic categories easier to detect in the field. Standard deviation (σ) is also shown.

A Midlittoral zone

SEASON	**Spring**		**Summer**		**Autumn**		**Winter**	
LOCATION	**Huertas**		**Huertas**		**Huertas**		**Huertas**	
TAXA	%	σ	%	σ	%	σ	%	σ
***Anadyomene stellata* (Wulfen) C. Agardh**	0	0	0	0	0	0	0	0
Asparagopsis sp - tetrasporophyte	0	0	0	0	0	0	0	0
***Ceramium* s.l.spp.**	0.4	0.8	0	0	0	0	0.1	0.2
Ceramium ciliatum (J.Ellis) Ducluzeau	-	-	-	-	-	-	-	-
Cerithiidae	0.1	0.3	0	0	0.1	0.2	0.1	0.2
***Chaetomorpha linum* (O.F.Müller) Kützing**	0.8	1.7	0	0	0	0	0.1	0.2
***Chondria* sp.**	0.2	0.3	0	0	0	0	0	0
***Chondria capillaris* (Hudson) M.J.Wynne**	0.6	0.8	0.6	1.1	0.2	0.3	0	0
***Chthamalus* spp.**	7.8	3.6	8.5	3.2	5.7	2.1	6.4	2.7
***Cladophora* spp.**	15.1	5.5	8.1	14	6.9	6.7	0.5	0.8
Cladophora dalmatica Kützing	-	-	-	-	-	-	-	-
Cladophora laetevirens (Dillwyn) Kützing	-	-	-	-	-	-	-	-
Cladophora vagabunda (Linnaeus) Hoek				-	-	-	-	-
***Cladophoropsis membranacea* (Hofman Bang ex C.Agardh) Børgesen**	0	0	0	0	0	0	0	0
Corallinaceae	23.9	7.4	13.7	11	13	5.2	22.8	2.9
***Cystoseira compressa subsp. pustulata* (Ercegovic) Verlaque**	0	0	0	0	0	0	0	0
***Dasya* spp.**	0	0	0	0	0	0	0	0
Dasya ocellata (Grateloup) Harvey	-	-	-	-	-	-	-	-
***Dendropoma lebeche* Templado, Richter & Calvo, 2016**	5.3	2	1.9	0.2	2.5	2.4	6.9	0.3
***Echinolittorina punctata* (Gmelin, 1791)**	0.1	0.3	0.2	0.3	0	0	0.1	0.2
Ectocarpaceae	0	0	0	0	0	0	0.1	0.2
Ectocarpus fasciculatus Harvey	-	-	-	-	-	-	-	-
Feldmannia irregularis (Kützing) G.Hamel		-	-	-	-	-	-	-
Feldmannia mitchelliae (Harvey) H.-S.Kim	-	-	-	-	-	-	-	-
Gelidiales	0	0	0.6	1	0.2	0.2	0.2	0.3
Gelidiella lubrica cf.	-	-	-	-	-	-	-	-
Gelidium pusillum (Stackhouse) Le Jolis	-	-	-	-	-	-	-	-
***Herposiphonia secunda* (C.Agardh) Ambronn**	0	0	0	0	0	0	0	0
***Jania* spp.**	1.7	2.8	14.1	7.2	21	4.5	7	5
***Laurencia* spp.**	0	0	0.1	0.2	1.3	0.6	0	0
Laurencia pyramidalis Bory de Saint-Vincent ex Kützing	-	-	-	-	-	-	-	-
***Lophosiphonia* s.l.spp.**	0	0	0	0	0	0	0.3	0
Lophosiphonia cristata Falkenberg		-	-	-	-	-	-	-
Polysiphonia scopulorum Harvey	-	-	-	-	-	-	-	-
***Melarhaphe neritoides* (Linnaeus, 1758)**	0.1	0.1	0	0	0	0	0.2	0.3
Mytilidae	0.1	0.1	0	0	0	0	0.2	0.2

***Neosiphonia sertularioides* (Grateloup) K.W.Nam & P.J.Kang**	1.3	2.5	0	0	0	0	0.8	0.8
Oscillatoriaceae	0	0	3.1	5.3	0	0	0	0
Lyngbya confervoides C.Agardh ex Gomont	-	-	-	-	-	-	-	-
***Padina pavonica* (Linnaeus) Thivy**	0	0	0	0	0	0	0	0
***Palisada* spp.**	7.1	3.4	7.6	2.5	4.7	2.8	6.3	2.3
***Patella* spp.**	0.3	0.3	0.4	0.2	0.3	0	0.6	0
***Phorcus turbinatus* (Born, 1778)**	0.6	0.9	0	0	0	0	0.2	0.3
Polyplacophora	0.2	0.2	0.2	0.2	0.5	0.4	0.6	0.2
***Polysiphonia opaca* (C.Agardh) Moris & De Notaris**	0.6	0.7	1.9	1.1	0.8	1.2	0.7	0.4
***Pseudochlorodesmis furcellata* (Zanardini) Børgesen**	0	0	0	0	0	0	0	0
***Ralfsia verrucosa* (Areschoug) Areschoug**	0	0	0	0	0	0	0	0
Red thin turf	0	0	0	0	0	0	0	0
Antithamnionella elegans (Berthold) J.H.Price & D.M.John	-	-	-	-	-	-	-	-
Taenioma nanum (Kützing) Papenfuss	-	-	-	-	-	-	-	-
Rivulariaceae	7.8	4.5	7.5	13	4.8	4.4	5.8	3.9
***Scytosiphon lomentaria* (Lyngbye) Link**	0	0	0	0	0	0	0.6	0.6
***Sphacelaria* spp.**	0	0	0	0	0.3	0.5	0	0
Sphacelaria cirrosa (Roth) C.Agardh	-	-	-	-	-	-	-	-
Sphacelaria tribuloides Meneghini	-	-	-	-	-	-	-	-
***Spyridia filamentosa* (Wulfen) Harvey**	0	0	0.6	1	1	1	0	0
***Ulva* spp.**	17.2	12.3	2.6	4.5	0.6	1	19.1	7.2
Ulva compressa Linnaeus	-	-	-	-	-	-	-	-
Ulva polyclada Kraft	-	-	-	-	-	-	-	-
***Vermetus* spp.**	0.5	0.8	0	0	0.1	0.2	0.9	0.7

SEASON	Spring		Summer		Autumn		Winter	
LOCATION	Tabarca		Tabarca		Tabarca		Tabarca	
TAXA	%	σ	%	σ	%	σ	%	σ
***Anadyomene stellata* (Wulfen) C.Agardh**	0	0	0	0	0	0	0.8	1.2
Asparagopsis sp - tetrasporophyte	0	0	0	0	0	0	2.9	2.5
***Ceramium* s.l.spp.**	0.4	0.7	0.4	0.7	0	0	3.1	1
Ceramium ciliatum (J.Ellis) Ducluzeau	-	-	-	-	-	-	-	-
Cerithiidae	0	0	0	0	0	0	0	0
***Chaetomorpha linum* (O.F.Müller) Kützing**	0	0	0	0	0	0	0	0
***Chondria* sp.**	0	0	0	0	0	0	0	0
***Chondria capillaris* (Hudson) M.J.Wynne**	0	0	0	0	0	0	0.2	0.2
***Chthamalus* spp.**	0	0	0.4	0.7	0	0	1	1.8
***Cladophora* spp.**	2.5	4.4	0.9	1.4	0	0	2.3	1.5
Cladophora vagabunda	-	-	-	-	-	-	-	-
Cladophora dalmatica	-	-	-	-	-	-	-	-
Cladophora laetevirens	-	-	-	-	-	-	-	-
***Cladophoropsis membranacea* (Hofman Bang ex C.Agardh) Børgesen**	0	0	0.4	0.7	0.4	0.7	0	0
Corallinaceae unidentified	16.5	19.6	24.2	3.6	26	11	26.7	4.4
***Cystoseira compressa subsp. pustulata* (Ercegovic) Verlaque**	0	0	0	0	0	0	0.1	0.1

Dasya **spp.**	0.4	0.7	0	0	0	0	1.4	2.3
Dasya ocellata (Grateloup) Harvey	-	-	-	-	-	-	-	-
Dendropoma lebeche **Templado, Richter & Calvo, 2016**	1.2	1.2	0.8	1.4	1.7	0.7	12.4	4.7
Echinolittorina punctata **(Gmelin, 1791)**	0	0	0	0	0	0	0	0
Ectocarpaceae	0	0	0	0	0	0	2.6	4.5
Ectocarpus fasciculatus Harvey	-	-	-	-	-	-	-	-
Feldmannia irregularis (Kützing) G.Hamel	-	-	-	-	-	-	-	-
Feldmannia mitchelliae (Harvey) H.-S.Kim	-	-	-	-	-	-	-	-
Gelidiales	0	0	0.9	0.7	2.5	4.4	1.8	1.6
Gelidiella lubrica cf.	-	-	-	-	-	-	-	-
Gelidium pusillum (Stackhouse) Le Jolis	-	-	-	-	-	-	-	-
Herposiphonia secunda **(C.Agardh) Ambronn**	0	0	0	0	0	0	2	1.9
Jania **spp.**	0	0	0	0	0.4	0.7	2.1	2.1
Laurencia **spp.**	0.4	0.7	0.8	0.7	0.4	0.8	1.5	0.3
Laurencia pyramidalis Bory de Saint-Vincent ex Kützing	-	-	-	-	-	-	-	-
Lophosiphonia **s.l.spp.**	0	0	0.8	0.7	0	0	0.8	0.6
Lophosiphonia cristata Falkenberg	-	-	-	-	-	-	-	-
Polysiphonia scopulorum Harvey	-	-	-	-	-	-	-	-
Melarhaphe neritoides **(Linnaeus, 1758)**	0	0	0	0	0	0	0	0
Mytilidae	0	0	0	0	0	0	0	0
Neosiphonia sertularioides **(Grateloup) K.W.Nam & P.J.Kang**	0	0	0.4	0.7	0	0	1.8	1.7
Oscillatoriaceae	0	0	0	0	0	0	0.1	0.2
Lyngbya confervoides C.Agardh ex Gomont	-	-	-	-	-	-	-	-
Padina pavonica **(Linnaeus) Thivy**	0	0	0	0	0	0	0.1	0.1
Palisada **spp.**	0	0	0	0	0	0	2.1	0.5
Patella **spp.**	1.8	0.7	0.4	0.7	1.7	1.4	4.3	2.5
Phorcus turbinatus **(Born, 1778)**	0	0	0	0	0	0	0	0
Polyplacophora	0	0	0.9	0.7	0.4	0.8	0	0
Polysiphonia opaca **(C.Agardh) Moris & De Notaris**	0	0	0	0	0	0	0.9	1.5
Pseudochlorodesmis furcellata **(Zanardini) Børgesen**	0	0	0	0	0	0	0.7	1.2
Ralfsia verrucosa **(Areschoug) Areschoug**	0	0	0	0	0	0	0.6	0.8
Red thin turf	0	0	0	0	0	0	0.1	0.1
Antithamnionella elegans (Berthold) J.H.Price & D.M.John	-	-	-	-	-	-	-	-
Taenioma nanum (Kützing) Papenfuss	-	-	-	-	-	-	-	-
Rivulariaceae	5.6	8.1	28.3	12	4.2	2.9	6.3	1.8
Scytosiphon lomentaria **(Lyngbye) Link**	0	0	0	0	0	0	1	1.8
Sphacelaria **spp.**	0	0	0	0	0	0	0.6	1.1
Sphacelaria cirrosa (Roth) C.Agardh	-	-	-	-	-	-	-	-
Sphacelaria tribuloides Meneghini	-	-	-	-	-	-	-	-
Spyridia filamentosa **(Wulfen) Harvey**	0	0	0	0	0	0	0	0
Ulva **spp.**	2.5	4.3	0	0	0	0	2.1	3.6
Ulva compressa Linnaeus	-	-	-	-	-	-	-	-
Ulva polyclada Kraft	-	-	-	-	-	-	-	-
Vermetus **spp.**	0	0	0	0	0	0	0	0

Infralittoral zone

SEASON	**Spring**		**Summer**		**Autumn**		**Winter**	
LOCATION	**Huertas**		**Huertas**		**Huertas**		**Huertas**	
TAXA	%	σ	%	σ	%	σ	%	σ
***Acanthonyx lunulatus* cf.**	0	0	0	0	0	0	0	0
***Acetabularia acetabulum* (Linnaeus) P.C.Silva**	0	0	0	0	0	0	0	0
***Acrothamnion preissii* (Sonder) E.M.Wollaston**	0	0	0	0	0	0	0	0
***Aiptasia* sp.**	0	0	0	0	0	0	0.2	0.1
***Alsidium corallinum* C.Agardh**	0	0	0	0	0.2	0.3	0.2	0.3
***Amphiroa rigida* J.V.Lamouroux**	0.1	0.1	0	0	0	0	0.1	0
***Asparagopsis* sp - tetrasporophyte**	0	0	0	0	0	0	0	0
Blenniidae	0	0	0	0	0	0	0	0
***Calcinus tubularis* (Linnaeus, 1767)**	0.2	0.1	0	0.1	0	0	0.1	0
***Caulerpa cylindracea* Sonder**	0.2	0.2	0.1	0.2	0.2	0.1	0.1	0.2
***Caulerpa prolifera* (Forsskål) J.V.Lamouroux**	0	0	0	0	0	0	0	0
***Ceramium* s.l.spp.**	0.1	0.1	0.1	0.2	0.1	0.1	0	0
Ceramium codii (H.Richards) Mazoyer	-	-	-	-	-	-	-	-
Ceramium aff. diaphanum	-	-	-	-	-	-	-	-
Ceramium ciliatum (J.Ellis) Ducluzeau	-	-	-	-	-	-	-	-
Ceramium circinatum (Kützing) J.Agardh	-	-	-	-	-	-	-	-
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor	-	-	-	-	-	-	-	-
Cerithiidae	0	0	0	0	0	0	0	0.1
***Chaetomorpha pachynema* (Montagne) Kützing**	0	0	0	0	0	0	0	0
***Chondria* spp.**	0	0	0	0	0	0	0	0.1
Chondria capillaris (Hudson) M.J.Wynne	-	-	-	-	-	-	-	-
Chondria dasyphylla (Woodward) C.Agardh	-	-	-	-	-	-	-	-
***Chthamalus* spp.**	0	0	0	0	0	0	0	0
***Cladophora* spp.**	0.9	0.9	1.9	1.2	0.2	0.1	0.7	0.2
Cladophora dalmatica Kützing	-	-	-	-	-	-	-	-
Cladophora laetevirens (Dillwyn) Kützing	-	-	-	-	-	-	-	-
Cladophora lehmanniana (Lindenberg) Kützing	-	-	-	-	-	-	-	-
Cladophora nigrescens cf.	-	-	-	-	-	-	-	-
Cladophora prolifera (Roth) Kützing	-	-	-	-	-	-	-	-
Cladophora vagabunda (Linnaeus) Hoek	-	-	-	-	-	-	-	-
***Cladophoropsis membranacea* (Hofman Bang ex C.Agardh) Børgesen**	0	0	0	0	0	0	0	0
***Cladosiphon lubricus* (Sauvageau) Kylin**	0	0.1	0	0	0	0	0	0
***Cladostephus spongiosum* (Hudson) C.Agardh**	0	0	0	0	0	0	0	0
***Cliona* sp.**	0	0	0	0	0	0	0	0
***Colpomenia* sp.**	0	0	0	0	0	0	0	0
***Columbella rustica* (Linnaeus, 1758)**	0	0.1	0	0	0	0.1	0.1	0.1
***Conus* sp.**	0	0	0	0	0	0	0	0
Corallinaceae unidentified	3.6	1.9	0.6	0.2	3.2	1.4	6.1	2.2
***Cystoseira algeriensis* Feldmann**	0.1	0.1	0	0	0	0	0.1	0.1
***Cystoseira amentacea* (C.Agardh) Bory de Saint-Vincent**	0	0	0	0	0	0	0.1	0.1
***Cystoseira compressa subsp. pustulata* (Ercegovic) Verlaque**	9.2	5.2	0	0.1	0	0	2.6	0.9

***Dasycladus vermicularis* (Scopoli) Krasser**	0.2	0.1	0	0	0.1	0	0.2	0.1
***Dasya* spp.**	0	0	0	0	0	0	0	0
Dasya hutchinsiae Harvey	-	-	-	-	-	-	-	-
Dasya ocellata (Grateloup) Harvey	-	-	-	-	-	-	-	-
Dasya rigidula (Kützing) Ardissone	-	-	-	-	-	-	-	-
***Dendropoma lebeche* Templado, Richter & Calvo, 2016**	0.1	0.3	0	0	0	0	0.2	0.3
***Dictyota* spp.**	20.7	7.3	0.4	0.4	10.5	6.6	19	1.5
Dictyota fasciola (Roth) J.V.Lamouroux	-	-	-	-	-	-	-	-
Dictyota mediterranea (Schiffner) G.Furnari	-	-	-	-	-	-	-	-
Dictyota spiralis Montagne	-	-	-	-	-	-	-	-
***Echinolittorina punctata* (Gmelin, 1791)**	0	0	0	0	0	0	0	0
Ectocarpaceae	0	0	0	0	0	0	1.1	1.5
Acinetospora crinita (Carmichael) Sauvageau	-	-	-	-	-	-	-	-
Ectocarpus fasciculatus cf.	-	-	-	-	-	-	-	-
Feldmannia irregularis (Kützing) G.Hamel	-	-	-	-	-	-	-	-
Feldmannia mitchelliae cf.	-	-	-	-	-	-	-	-
Feldmannia paradoxa (Montagne) G.Hamel	-	-	-	-	-	-	-	-
***Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders**	0	0	0	0	0	0	0	0
***Elysia timida* (Risso, 1818)**	0	0	0	0	0	0	0	0
***Eriphia verrucosa* (Forskål, 1775)**	0	0	0	0	0	0	0	0
***Gastroclonium clavatum* (Roth) Ardissone**	0	0	0	0	0	0	0	0
Gelidiales	0	0	0	0	0	0	0	0
Gelidiella lubrica cf.	-	-	-	-	-	-	-	-
Gelidium pusillum (Stackhouse) Le Jolis	-	-	-	-	-	-	-	-
***Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux**	0	0	0	0	0	0	0	0
***Halopteris scoparia* (Linnaeus) Sauvageau**	1.7	0.7	0	0.1	0	0	1.4	1.1
***Herposiphonia secunda* (C.Agardh) Ambronn**	0.1	0.2	0	0	0	0	0	0
***Hildenbrandia* sp.**	0	0	0	0	0	0	0	0
***Hypnea musciformis* (Wulfen) J.V.Lamouroux**	0	0	0	0	0	0	0	0
***Jania* spp.**	3.9	3.2	33.1	19.8	35.9	7.6	20	12.8
***Laurencia pyramidalis* Bory ex Kützing**	0	0	0	0	0	0	0	0
***Laurencia* sp.**	0.1	0.3	0.1	0	0	0.1	0	0
***Liagora* sp.**	0	0	0	0	0	0	0	0
***Liagora viscida* (Forsskål) C.Agardh**	0	0	0	0	0	0	0	0
***Lophosiphonia* s.l.spp.**	0.1	0.3	0.2	0.3	0	0.1	0.1	0.1
Lophosiphonia cristata Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia obscura (C.Agardh) Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia reptabunda (Suhr) Kylin	-	-	-	-	-	-	-	-
Polysiphonia scopulorum Harvey	-	-	-	-	-	-	-	-
***Myriactula* sp.**	0	0	0	0	0	0	0	0
Mytilidae	0	0	0	0	0	0	0	0
***Neosiphonia ferulacea* (Suhr ex J.Agardh) S.M.Guimarães & M.T.Fujii**	0	0	0	0	0	0	0	0
***Neosiphonia sertularioides* (Grateloup) K.W.Nam & P.J.Kang**	0	0	0	0	0	0	0	0
Oscillatoriaceae	0.2	0.3	0	0	0	0	0.8	0.9

Blennothrix lyngbyacea (Kützing ex Gomont) Anagnostidis & Komárek	-	-	-	-	-	-	-	-
Lyngbya spp.	-	-	-	-	-	-	-	-
Pachygrapsus marmoratus (Fabricius, 1787)	0	0	0	0	0	0	0	0
Padina pavonica (Linnaeus) Thivy	45.2	8	19.2	12.9	22.9	1.9	31	10.1
Palisada spp.	1.7	0.8	0.1	0.1	0.5	0.5	1.7	0.9
Palisada tenerrima (Cremades) Serio, Cormaci, G.Furnari & Boisset	-	-	-	-	-	-	-	-
Patella sp.	0	0	0	0	0	0	0.1	0.1
Phaeophila dendroides (P.L.Crouan & H.M.Crouan) Batters	0	0	0	0	0	0	0	0
Polysiphonia opaca (C.Agardh) Moris & De Notaris	0	0	0	0	0	0	0.1	0.1
Pseudochlorodesmis furcellata (Zanardini) Børgesen	0	0	0	0	0	0	0	0
Red thin turf	0	0	0	0	0	0	0	0.1
Acrochaetium sp.	-	-	-	-	-	-	-	-
Antithamnion cruciatum (C.Agardh) Nägeli	-	-	-	-	-	-	-	-
Erythrotrichia carnea (Dillwyn) J.Agardh	-	-	-	-	-	-	-	-
Spermothamnion spp.	-	-	-	-	-	-	-	-
Rivulariaceae	0.1	0.1	0.1	0.2	0.1	0.1	0	0
Sabella sp.	0	0	0	0	0	0	0	0
Scytosiphon lomentaria (Lyngbye) Link	0	0	0	0	0	0	0.1	0.1
Siphonocladus pusillus (C.Agardh ex Kützing) Hauck	0	0	0	0	0	0	0	0
Sphacelaria spp.	0.3	0.3	0.1	0.1	0.1	0.1	0.2	0.3
Sphacelaria cirrosa (Roth) C.Agardh	-	-	-	-	-	-	-	-
Sphacelaria rigidula Kützing	-	-	-	-	-	-	-	-
Sphacelaria tribuloides Meneghini	-	-	-	-	-	-	-	-
Spyridia filamentosa (Wulfen) Harvey	0.4	0.6	0.7	0.8	0	0	0.1	0
Stramonita haemastoma (Linnaeus, 1767)	0	0	0	0	0	0	0	0
Symploca sp.	0	0	0	0	0	0	0	0
Ulva spp.	0.3	0.5	0	0	0	0	0.6	0.9
Ulva compressa Linnaeus	-	-	-	-	-	-	-	-
Ulva polyclada Kraft	-	-	-	-	-	-	-	-
Ulva prolifera cf.	-	-	-	-	-	-	-	-
Valonia utricularis (Roth) C.Agardh	0	0	0	0	0	0	0	0
Vermetus spp.	2.5	1	0.4	0.1	1.6	1.1	2.2	0.5

SEASON	Spring		Summer		Autumn		Winter	
LOCATION	**Tabarca**		**Tabarca**		**Tabarca**		**Tabarca**	
TAXA	%	σ	%	σ	%	σ	%	σ
Acanthonyx lunulatus cf.	0	0	0	0	0	0	0	0
Acetabularia acetabulum (Linnaeus) P.C.Silva	1.3	1	0	0	0	0	0	0
Acrothamnion preissii (Sonder) E.M.Wollaston	0	0	0	0	0	0	0	0
Aiptasia sp.	0	0.1	0	0	0	0	0	0
Alsidium corallinum C.Agardh	0	0	0	0	0	0	0	0
Amphiroa rigida J.V.Lamouroux	0	0	0	0	0	0.1	0	0
Asparagopsis sp - tetrasporophyte	0	0	0	0	0	0	0.2	0.2
Blenniidae	0	0	0	0	0	0.1	0	0

***Calcinus tubularis* (Linnaeus, 1767)**	0	0	0	0	0	0	0	0
***Caulerpa cylindracea* Sonder**	1	0.9	0	0.1	1	0.5	0.5	0.2
***Caulerpa prolifera* (Forsskål) J.V.Lamouroux**	0	0	0	0	0	0	0	0
***Ceramium* s.l.spp.**	0.2	0.4	0	0	0.1	0.1	0.2	0.2
Ceramium codii (H.Richards) Mazoyer	-	-	-	-	-	-	-	-
Ceramium aff. diaphanum	-	-	-	-	-	-	-	-
Ceramium ciliatum (J.Ellis) Ducluzeau	-	-	-	-	-	-	-	-
Ceramium circinatum (Kützing) J.Agardh	-	-	-	-	-	-	-	-
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor	-	-	-	-	-	-	-	-
Cerithiidae	0	0	0	0	0	0	0	0
***Chaetomorpha pachynema* (Montagne) Kützing**	0	0	0	0	0	0	0.1	0.1
***Chondria* spp.**	0.4	0.9	0	0	0	0	0	0.1
Chondria capillaris (Hudson) M.J.Wynne	-	-	-	-	-	-	-	-
Chondria dasyphylla (Woodward) C.Agardh	-	-	-	-	-	-	-	-
***Chthamalus* spp.**	0	0	0	0	0	0	0	0
***Cladophora* spp.**	0	0	0.2	0.3	0.1	0.1	0	0
Cladophora dalmatica Kützing	-	-	-	-	-	-	-	-
Cladophora laetevirens (Dillwyn) Kützing	-	-	-	-	-	-	-	-
Cladophora lehmanniana (Lindenberg) Kützing	-	-	-	-	-	-	-	-
Cladophora nigrescens cf.	-	-	-	-	-	-	-	-
Cladophora prolifera (Roth) Kützing	-	-	-	-	-	-	-	-
Cladophora vagabunda (Linnaeus) Hoek	-	-	-	-	-	-	-	-
***Cladophoropsis membranacea* (Hofman Bang ex C.Agardh) Børgesen**	0	0	0	0	0.2	0.3	0	0.1
***Cladosiphon lubricus* (Sauvageau) Kylin**	0	0	0	0	0	0	0	0
***Cladostephus spongiosum* (Hudson) C.Agardh**	0	0.1	0	0	0	0	0	0
***Cliona* sp.**	0	0	0	0	0	0	0	0
***Colpomenia* sp.**	0	0	0	0	0	0	0	0
***Columbella rustica* (Linnaeus, 1758)**	0	0	0	0	0	0	0	0
***Conus* sp.**	0	0	0	0	0	0	0	0
Corallinaceae unidentified	2.7	1.9	1.5	1.2	6.2	3.8	3	1
***Cystoseira algeriensis* Feldmann**	0	0	0	0	0	0	0	0
***Cystoseira amentacea* (C.Agardh) Bory de Saint-Vincent**	0.1	0.3	0	0	0	0	0.2	0.4
***Cystoseira compressa subsp. pustulata* (Ercegovic) Verlaque**	12.5	5.6	0.1	0.1	0	0	2.8	3.5
***Dasycladus vermicularis* (Scopoli) Krasser**	3	1.9	0.3	0.1	3.1	1.5	1.9	0.8
***Dasya* spp.**	0	0	0	0	0	0	0.1	0.1
Dasya hutchinsiae Harvey	-	-	-	-	-	-	-	-
Dasya ocellata (Grateloup) Harvey	-	-	-	-	-	-	-	-
Dasya rigidula (Kützing) Ardissone	-	-	-	-	-	-	-	-
***Dendropoma lebeche* Templado, Richter & Calvo 2016**	0.2	0.3	0	0.1	0.4	0.3	0.6	0.1
***Dictyota* spp.**	23.1	9.6	0.1	0.2	7.1	4	20	1.6
Dictyota fasciola (Roth) J.V.Lamouroux	-	-	-	-	-	-	-	-
Dictyota mediterranea (Schiffner) G.Furnari	-	-	-	-	-	-	-	-
Dictyota spiralis Montagne	-	-	-	-	-	-	-	-

***Echinolittorina punctata* (Gmelin, 1791)**	0	0	0	0	0	0	0	0
Ectocarpaceae	0	0	0	0	0	0	0.3	0.5
Acinetospora crinita (Carmichael) Sauvageau	-	-	-	-	-	-	-	-
Ectocarpus fasciculatus cf.	-	-	-	-	-	-	-	-
Feldmannia irregularis (Kützing) G.Hamel	-	-	-	-	-	-	-	-
Feldmannia mitchelliae cf.	-	-	-	-	-	-	-	-
Feldmannia paradoxa (Montagne) G.Hamel	-	-	-	-	-	-	-	-
***Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders**	0	0	0	0	0.1	0.1	0	0
***Elysia timida* (Risso, 1818)**	0	0	0	0	0	0	0	0
***Eriphia verrucosa* (Forskål, 1775)**	0	0	0	0	0	0	0	0
***Gastroclonium clavatum* (Roth) Ardissone**	0	0	0	0	0	0	0	0
Gelidiales	0.4	0.7	0	0	0.3	0.3	0	0
Gelidiella lubrica cf.	-	-	-	-	-	-	-	-
Gelidium pusillum (Stackhouse) Le Jolis	-	-	-	-	-	-	-	-
***Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux**	0	0	0	0	0	0	0	0
***Halopteris scoparia* (Linnaeus) Sauvageau**	22.6	5.5	10.7	17.7	0.1	0.1	8.8	6.1
***Herposiphonia secunda* (C.Agardh) Ambronn**	0	0	0.1	0.1	0.5	0	0.5	0.4
***Hildenbrandia* sp.**	0	0	0	0	0	0	0	0
***Hypnea musciformis* (Wulfen) J.V.Lamouroux**	0	0	0	0	0	0	0	0
***Jania* spp.**	13.2	6.6	62	18.7	59.6	5.3	58	18.6
***Laurencia pyramidalis* Bory ex Kützing**	3.3	5.2	0	0	0	0	0.2	0.1
***Laurencia* sp.**	0.5	0.9	0	0.1	0.1	0.1	0.3	0
***Liagora* sp.**	0.1	0.3	0	0	0	0	0	0
***Liagora viscida* (Forsskål) C.Agardh**	0	0	0	0	0	0	0	0
***Lophosiphonia* s.l.spp.**	0	0	0	0	0	0	0	0.1
Lophosiphonia cristata Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia obscura (C.Agardh) Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia reptabunda (Suhr) Kylin	-	-	-	-	-	-	-	-
Polysiphonia scopulorum Harvey	-	-	-	-	-	-	-	-
***Myriactula* sp.**	0	0	0	0	0	0	0	0
Mytilidae	0	0	0	0	0	0	0	0
Neosiphonia ferulacea (Suhr ex J.Agardh) S.M.Guimarães & M.T.Fujii	0	0	0	0	0	0	0	0
***Neosiphonia sertularioides* (Grateloup) K.W.Nam & P.J.Kang**	0	0	0	0	0	0	0	0.1
Oscillatoriaceae	0	0	0	0	0.1	0.2	0	0
Blennothrix lyngbyacea (Kützing ex Gomont) Anagnostidis & Komárek	-	-	-	-	-	-	-	-
Lyngbya spp.	-	-	-	-	-	-	-	-
***Pachygrapsus marmoratus* (Fabricius, 1787)**	0	0	0	0	0	0	0	0
***Padina pavonica* (Linnaeus) Thivy**	26.5	10	18.3	6.8	5	3.5	12	2.8
***Palisada* spp.**	0	0	0	0	0	0	0	0
Palisada tenerrima (Cremades) Serio, Cormaci, G.Furnari & Boisset	-	-	-	-	-	-	-	-
***Patella* sp.**	0	0	0	0	0	0	0	0

***Phaeophila dendroides* (P.L.Crouan & H.M.Crouan) Batters**	0	0	0	0	0	0	0	0
***Polysiphonia opaca* (C.Agardh) Moris & De Notaris**	0	0	0	0	0	0.1	0	0
***Pseudochlorodesmis furcellata* (Zanardini) Børgesen**	0	0	0	0	0	0	0	0
Red thin turf	0	0	0	0	0	0	0	0
Acrochaetium sp.	-	-	-	-	-	-	-	-
Antithamnion cruciatum (C.Agardh) Nägeli	-	-	-	-	-	-	-	-
Erythrotrichia carnea (Dillwyn) J.Agardh	-	-	-	-	-	-	-	-
Spermothamnion spp.	-	-	-	-	-	-	-	-
Rivulariaceae	0.2	0.4	0	0	0.1	0.1	0.2	0.2
***Sabella* sp.**	0	0	0	0	0	0	0	0
***Scytosiphon lomentaria* (Lyngbye) Link**	0	0	0	0	0	0	0	0.1
***Siphonocladus pusillus* (C.Agardh ex Kützing) Hauck**	0	0	0	0	0	0	0	0
***Sphacelaria* spp.**	0.2	0.2	0.1	0.1	0	0	0.4	0.6
Sphacelaria cirrosa (Roth) C.Agardh	-	-	-	-	-	-	-	-
Sphacelaria rigidula Kützing	-	-	-	-	-	-	-	-
Sphacelaria tribuloides Meneghini	-	-	-	-	-	-	-	-
***Spyridia filamentosa* (Wulfen) Harvey**	0.3	0.5	0.1	0.1	0	0	2.2	0.1
***Stramonita haemastoma* (Linnaeus, 1767)**	0	0	0	0	0	0	0	0.1
***Symploca* sp.**	3.2	3.8	0	0.1	0	0	0	0.1
***Ulva* spp.**	0	0	0	0	0	0	0	0
Ulva compressa Linnaeus	-	-	-	-	-	-	-	-
Ulva polyclada Kraft	-	-	-	-	-	-	-	-
Ulva prolifera cf.	-	-	-	-	-	-	-	-
***Valonia utricularis* (Roth) C.Agardh**	0	0	0	0	0	0	0	0
***Vermetus* spp.**	0	0.1	0	0	0	0	0.2	0.3

Outer margin

SEASON	**Spring**		**Summer**		**Autumn**		**Winter**	
LOCATION	**Huertas**		**Huertas**		**Huertas**		**Huertas**	
TAXA	%	σ	%	σ	%	σ	%	σ
***Acetabularia acetabulum* (Linnaeus) P.C.Silva**	0	0	0	0	0	0	0	0
***Amphiroa rigida* J.V.Lamouroux**	0.3	0.5	0	0	0	0	0.3	0.5
***Anadyomene stellata* (Wulfen) C.Agardh**	0	0	0	0	0	0	0	0
Asparagopsis sp - tetrasporophyte	0	0	0	0	0	0	0	0
***Calcinus tubularis* (Linnaeus, 1767)**	0.3	0.5	0	0	0.3	0.5	0	0
***Caulerpa cylindracea* Sonder**	0.8	0.9	0.3	0.5	0.6	0.5	0.3	0.5
***Ceramium* s.l.spp.**	0.6	0.9	0	0	0	0	0.3	0.5
Ceramium codii (H.Richards) Mazoyer	-	-	-	-	-	-	-	-
Ceramium aff. diaphanum	-	-	-	-	-	-	-	-
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor	-	-	-	-	-	-	-	-
***Chaetomorpha pachynema* (Montagne) Kützing**	0	0	0	0	0	0	0.3	0.5
***Chondracanthus acicularis* (Roth) Fredericq**	0.1	0.2	0	0	0	0	0	0

Chondria boryana **(De Notaris ex J.Agardh) De Toni**	0.1	0.2	1.7	2.9	0	0	0.3	0.5
Chondria **sp.**	0.6	0.5	0	0	0	0	0	0
Cladophora **spp.**	1.7	2.9	0.6	0.5	0	0	0.3	0.5
Cladophora dalmatica Kützing	-	-	-	-	-	-	-	-
Cladophora laetevirens (Dillwyn) Kützing	-	-	-	-	-	-	-	-
Cladophora lehmanniana (Lindenberg) Kützing	-	-	-	-	-	-	-	-
Cladosiphon lubricus **(Sauvageau) Kylin**	0	0	0	0	0	0	0	0
Cladostephus spongiosum **(Hudson) C.Agardh**	0.1	0.2	1.7	2.9	0	0	0	0
Colpomenia **sp.**	0.1	0.2	0	0	0	0	0	0
Corallinaceae unidentified	14.2	4.2	7.5	5.8	11.1	5.9	17.8	12
Cystoseira algeriensis **Feldmann**	3.3	2.9	0	0	0	0	5.8	6.3
Cystoseira amentacea **(C.Agardh) Bory de Saint-Vincent**	0	0	0	0	0	0	2.2	2.4
Cystoseira compressa subsp. pustulata **(Ercegovic) Verlaque**	18.8	7.8	0	0	0.3	0.5	6.7	7.6
Dasycladus vermicularis **(Scopoli) Krasser**	0	0	0	0	0	0	0	0
Dasya **spp.**	0	0	0	0	0	0	0	0
Dasya hutchinsiae Harvey	-	-	-	-	-	-	-	-
Dasya ocellata (Grateloup) Harvey	-	-	-	-	-	-	-	-
Dendropoma lebeche **Templado, Richter & Calvo, 2016**	5.4	4.6	0	0	5.8	10.1	6.9	3.4
Dictyota **spp.**	4.2	1.4	0.3	0.5	3.6	2.4	10.3	3.8
Dictyota fasciola (Roth) J.V.Lamouroux	-	-	-	-	-	-	-	-
Dictyota spiralis Montagne	-	-	-	-	-	-	-	-
Ectocarpaceae	0	0	0	0	0	0	13.3	14
Acinetospora crinita (Carmichael) Sauvageau	-	-	-	-	-	-	-	-
Feldmannia irregularis (Kützing) G.Hamel	-	-	-	-	-	-	-	-
Feldmannia lebelii (J.E. Areschoug ex P.L.Crouan & H.M.Crouan) G.Hamel	-	-	-	-	-	-	-	-
Ellisolandia elongata **(J.Ellis & Solander) K.R.Hind & G.W.Saunders**	6.4	6.3	0.6	0.5	0	0	8.6	6.7
Gastroclonium clavatum **(Roth) Ardissone**	0.4	0.4	0	0	0	0	2.2	2.4
Gelidiales	0	0	0	0	0	0	0	0
Gelidiella lubrica cf.	-	-	-	-	-	-	-	-
Gelidium pusillum (Stackhouse) Le Jolis	-	-	-	-	-	-	-	-
Halimeda tuna **(J.Ellis & Solander) J.V.Lamouroux**	0	0	0	0	0	0	0	0
Halopteris scoparia **(Linnaeus) Sauvageau**	0	0	0	0	0	0	0	0
Herposiphonia secunda **(C.Agardh) Ambronn**	0.3	0.5	0	0	0.3	0.5	0	0
Hildenbrandia **sp.**	0	0	0	0	0.3	0.5	0.3	0.5
Hypnea musciformis **(Wulfen) J.V.Lamouroux**	1.7	2.9	7.5	4.3	5.8	6.3	0	0
Jania **spp.**	3.6	5.5	47	19.7	40.6	4.6	23.1	8.1
Laurencia obtusa **(Hudson) J.V.Lamouroux**	0.1	0.3	0	0	0	0	0	0
Laurencia pyramidalis **Bory ex Kützing**	1.6	2.1	0	0	0	0	0	0
Laurencia **sp.**	2	3.4	0	0	1.9	2.7	2.5	2.9
Liagora **sp.**	0	0	0	0	0	0	0	0
Lophosiphonia **s.l.spp.**	0	0	0	0	0	0	0	0
Lophosiphonia cristata Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia obscura (C.Agardh) Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia reptabunda (Suhr) Kylin	-	-	-	-	-	-	-	-
Polysiphonia scopulorum Harvey	-	-	-	-	-	-	-	-

Myriactula **sp.**	0	0	0	0	0	0	0	0
Neosiphonia sertularioides **(Grateloup) K.W.Nam & P.J.Kang**	0	0	0	0	0.3	0.5	0.3	0.5
Padina pavonica **(Linnaeus) Thivy**	31.7	2.2	11	4.6	6.1	0.5	14.4	8.3
Palisada **spp.**	7.5	4.3	5	0	0	0	5	0
Palisada tenerrima (Cremades) Serio, Cormaci, G.Furnari & Boisset	-	-	-	-	-	-	-	-
Phaeophila dendroides **(P.L.Crouan & H.M.Crouan) Batters**	0	0	0	0	0	0	0	0
Polysiphonia opaca **(C.Agardh) Moris & De Notaris**	0.4	0.4	0.3	0.5	0	0	0.3	0.5
Polysiphonia **spp.**	0	0	0	0	0	0	0	0
Pseudochlorodesmis furcellata **(Zanardini) Børgesen**	0	0	0	0	0	0	0	0
Red thin turf	0	0	0	0	0	0	0	0
Acrochaetium sp.	-	-	-	-	-	-	-	-
Antithamnion cruciatum (C.Agardh) Nägeli	-	-	-	-	-	-	-	-
Erythrotrichia carnea (Dillwyn) J.Agardh	-	-	-	-	-	-	-	-
Spermothamnion spp.	-	-	-	-	-	-	-	-
Rhodophyllis divaricata **(Stackhouse) Papenfuss**	0	0	0	0	0	0	0	0
Rivulariaceae	0	0	0	0	0	0	0	0
Scytosiphon lomentaria **(Lyngbye) Link**	0	0	0	0	0	0	0.3	0.5
Siphonocladus pusillus **(C.Agardh ex Kützing) Hauck**	0	0	0	0	0	0	0	0
Sphacelaria **spp.**	0.2	0.3	0	0	1.1	1.4	0.3	0.5
Sphacelaria cirrosa (Roth) C.Agardh	-	-	-	-	-	-	-	-
Sphacelaria rigidula Kützing	-	-	-	-	-	-	-	-
Sphacelaria tribuloides Meneghini	-	-	-	-	-	-	-	-
Spyridia filamentosa **(Wulfen) Harvey**	1.7	2.9	3.3	2.9	0	0	0.3	0.5
Stramonita haemastoma **(Linnaeus, 1767)**	0	0	0.3	0.5	0	0	0	0
Symploca **sp.**	0	0	0	0	0	0	0	0
Ulva **spp.**	0	0	0	0	0	0	1.7	2.9
Ulva compressa Linnaeus	-	-	-	-	-	-	-	-
Ulva polyclada Kraft	-	-	-	-	-	-	-	-
Vermetus **spp.**	1.7	2.9	0.8	0	6.9	2.7	2.5	2.9

SEASON	**Spring**		**Summer**		**Autumn**		**Winter**	
LOCATION	**Tabarca**		**Tabarca**		**Tabarca**		**Tabarca**	
TAXA	%	σ	%	σ	%	σ	%	σ
Acetabularia acetabulum **(Linnaeus) P.C.Silva**	0.6	0.4	0	0	0	0	0	0
Amphiroa rigida **J.V.Lamouroux**	0.4	0.5	0	0	0.6	1	0.3	0.5
Anadyomene stellata **(Wulfen) C.Agardh**	0	0	0	0	0.3	0.5	0	0
Asparagopsis sp - tetrasporophyte	0	0	0	0	0.1	0	0.1	0
Calcinus tubularis **(Linnaeus, 1767)**	0	0	0	0	0	0	0	0
Caulerpa cylindracea **Sonder**	0.9	0.7	0	0	1.1	0.5	1.1	1
Ceramium **s.l.spp.**	0.5	0.9	0	0	0	0	0.9	1
Ceramium codii (H.Richards) Mazoyer	-	-	-	-	-	-	-	-
Ceramium aff. diaphanum	-	-	-	-	-	-	-	-
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor	-	-	-	-	-	-	-	-
Chaetomorpha pachynema **(Montagne) Kützing**	0	0	0	0	0	0	0	0
Chondracanthus acicularis **(Roth) Fredericq**	0	0	0	0	0	0	0.3	0.5

Chondria boryana (De Notaris ex J.Agardh) De Toni	0	0	0	0	0	0	0	0
Chondria sp.	0	0	0	0	0	0	0	0
Cladophora spp.	0.2	0.4	0	0	0	0	0	0
Cladophora dalmatica Kützing	-	-	-	-	-	-	-	-
Cladophora laetevirens (Dillwyn) Kützing	-	-	-	-	-	-	-	-
Cladophora lehmanniana (Lindenberg) Kützing	-	-	-	-	-	-	-	-
Cladosiphon lubricus (Sauvageau) Kylin	0	0	0	0	0	0	0	0
Cladostephus spongiosum (Hudson) C.Agardh	2.5	2.9	1.9	2.7	0	0	2	2.7
Colpomenia sp.	0	0	0	0	0	0	0	0
Corallinaceae unidentified	19.2	8.2	5.8	0	14.7	6.7	13.9	7.7
Cystoseira algeriensis Feldmann	0	0	0	0	0	0	0	0
Cystoseira amentacea (C.Agardh) Bory de Saint-Vincent	0	0	0	0	0	0	0	0
Cystoseira compressa subsp. pustulata (Ercegovic) Verlaque	27.7	7.8	0	0	0	0	3.9	5.4
Dasycladus vermicularis (Scopoli) Krasser	0	0	0	0	0	0	0.3	0.5
Dasya spp.	0	0.1	0	0	0	0	0.3	0.5
Dasya hutchinsiae Harvey	-	-	-	-	-	-	-	-
Dasya ocellata (Grateloup) Harvey	-	-	-	-	-	-	-	-
Dendropoma lebeche Templado, Richter & Calvo, 2016	2.9	5.3	0.8	0.8	2	3.4	1.7	2.9
Dictyota spp.	25.8	6.8	0	0	7.2	6.9	18.3	3.8
Dictyota fasciola (Roth) J.V.Lamouroux	-	-	-	-	-	-	-	-
Dictyota spiralis Montagne	-	-	-	-	-	-	-	-
Ectocarpaceae	0	0	0	0	0	0	0.3	0.5
Acinetospora crinita (Carmichael) Sauvageau	-	-	-	-	-	-	-	-
Feldmannia irregularis (Kützing) G.Hamel	-	-	-	-	-	-	-	-
Feldmannia lebelii (J.E. Areschoug ex P.L.Crouan & H.M.Crouan) G.Hamel	-	-	-	-	-	-	-	-
Ellisolandia elongata (J.Ellis & Solander) K.R.Hind & G.W.Saunders	1.3	0.5	0	0	2.2	3.2	2.5	3
Gastroclonium clavatum (Roth) Ardissone	0	0	0	0	0	0	1.7	2.9
Gelidiales	0	0	0	0	0	0	0	0
Gelidiella lubrica cf.	-	-	-	-	-	-	-	-
Gelidium pusillum (Stackhouse) Le Jolis	-	-	-	-	-	-	-	-
Halimeda tuna (J.Ellis & Solander) J.V.Lamouroux	0	0	0	0	0	0	0	0
Halopteris scoparia (Linnaeus) Sauvageau	0	0	0	0	0	0	0.3	0.5
Herposiphonia secunda (C.Agardh) Ambronn	0.2	0.4	0.3	0.5	0.8	0	0.8	0.8
Hildenbrandia sp.	0	0	0	0	0	0	0	0
Hypnea musciformis (Wulfen) J.V.Lamouroux	1.1	1	0	0	0	0	1.7	2.9
Jania spp.	15.2	12	76	4.8	59.7	4.8	59.7	13
Laurencia obtusa (Hudson) J.V.Lamouroux	0	0	0	0	0	0	0	0
Laurencia pyramidalis Bory ex Kützing	8.1	9.9	0	0	0	0	2	2.7
Laurencia sp.	0	0	0	0	0	0	0.8	0
Liagora sp.	1.3	2.5	0	0	0	0	0	0
Lophosiphonia s.l.spp.	0	0	0	0	0	0	0.3	0.5
Lophosiphonia cristata Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia obscura (C.Agardh) Falkenberg	-	-	-	-	-	-	-	-
Lophosiphonia reptabunda (Suhr) Kylin	-	-	-	-	-	-	-	-
Polysiphonia scopulorum Harvey	-	-	-	-	-	-	-	-

***Myriactula* sp.**	0	0	0	0	0	0	0	0
***Neosiphonia sertularioides* (Grateloup) K.W.Nam & P.J.Kang**	0	0	0	0	0.3	0.5	0.3	0.5
***Padina pavonica* (Linnaeus) Thivy**	17.1	6.8	13	11.8	5.6	4.2	11.7	4.4
***Palisada* spp.**	0	0	0	0	0	0	0	0
Palisada tenerrima (Cremades) Serio, Cormaci, G.Furnari & Boisset	-	-	-	-	-	-	-	-
***Phaeophila dendroides* (P.L.Crouan & H.M.Crouan) Batters**	0	0	0	0	0	0	0	0
***Polysiphonia opaca* (C.Agardh) Moris & De Notaris**	0	0	0	0	0	0	0	0
***Polysiphonia* spp.**	0	0	0	0	0	0	0	0
***Pseudochlorodesmis furcellata* (Zanardini) Børgesen**	0	0	0	0	0	0	0	0
Red thin turf	0.2	0.4	0	0	0	0	0	0
Acrochaetium sp.	-	-	-	-	-	-	-	-
Antithamnion cruciatum (C.Agardh) Nägeli	-	-	-	-	-	-	-	-
Erythrotrichia carnea (Dillwyn) J.Agardh	-	-	-	-	-	-	-	-
Spermothamnion spp.	-	-	-	-	-	-	-	-
Rhodophyllis divaricata	0	0	0	0	0	0	0	0
Rivulariaceae	0.2	0.4	0	0	0	0	0	0
***Scytosiphon lomentaria* (Lyngbye) Link**	0	0	0	0	0	0	0	0
***Siphonocladus pusillus* (C.Agardh ex Kützing) Hauck**	0	0	0	0	0	0	0	0
***Sphacelaria* spp.**	0.7	0.8	0.3	0.5	0	0	0.8	1.4
Sphacelaria cirrosa (Roth) C.Agardh	-	-	-	-	-	-	-	-
Sphacelaria rigidula Kützing	-	-	-	-	-	-	-	-
Sphacelaria tribuloides Meneghini	-	-	-	-	-	-	-	-
***Spyridia filamentosa* (Wulfen) Harvey**	1.7	2.3	0	0	0.6	0.5	8.9	2.7
***Stramonita haemastoma* (Linnaeus, 1767)**	0	0	0	0	0	0	0.3	0.5
***Symploca* sp.**	0	0	0.3	0.5	0	0	0	0
***Ulva* spp.**	0	0	0	0	0	0	0	0
Ulva compressa Linnaeus	-	-	-	-	-	-	-	-
Ulva polyclada Kraft	-	-	-	-	-	-	-	-
***Vermetus* spp.**	0	0	0.3	0.5	0	0	0.6	0.5

Table S2. A. Results of distance-based permutational two-way PERMANOVA comparing α-diversity using *zone* and *season* as fixed factors. B. Results of pairwise analyses. Se, *season*; Z, *zone*; df, degrees of freedom; SS, sums of squares; MS, mean squares; Pseudo-F, pseudo-*F* ratio; t, pseudo-*t* statistic; P(perm), permutation *P*-value

A

PERMANOVA table of results						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Se	3	104.46	34.821	45.68	0.001	999
Z	2	43.369	21.685	28.447	0.001	998
Se x Z	6	20.238	3.373	4.425	0.002	998
Res	959	731.02	0.76228			
Total	970	970				

B

Pairwise analysis within levels of factor *zone*	**Midlittoral**		**Infralittoral**		**Outer margin**	
Groups	t	P(perm)	t	P(perm)	t	P(perm)
Spring, Summer	2.881	0.004	11.194	0.001	6.635	0.001
Spring, Autumn	2.898	0.003	8.819	0.001	5.193	0.001
Spring, Winter	0.958	0.322	1.620	0.122	0.042	0.965
Summer, Autumn	0.022	0.987	2.958	0.006	1.963	0.053
Summer, Winter	1.879	0.050	10.030	0.001	6.048	0.001
Autumn, Winter	1.880	0.071	7.497	0.001	4.550	0.001

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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. Estudiamos 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 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

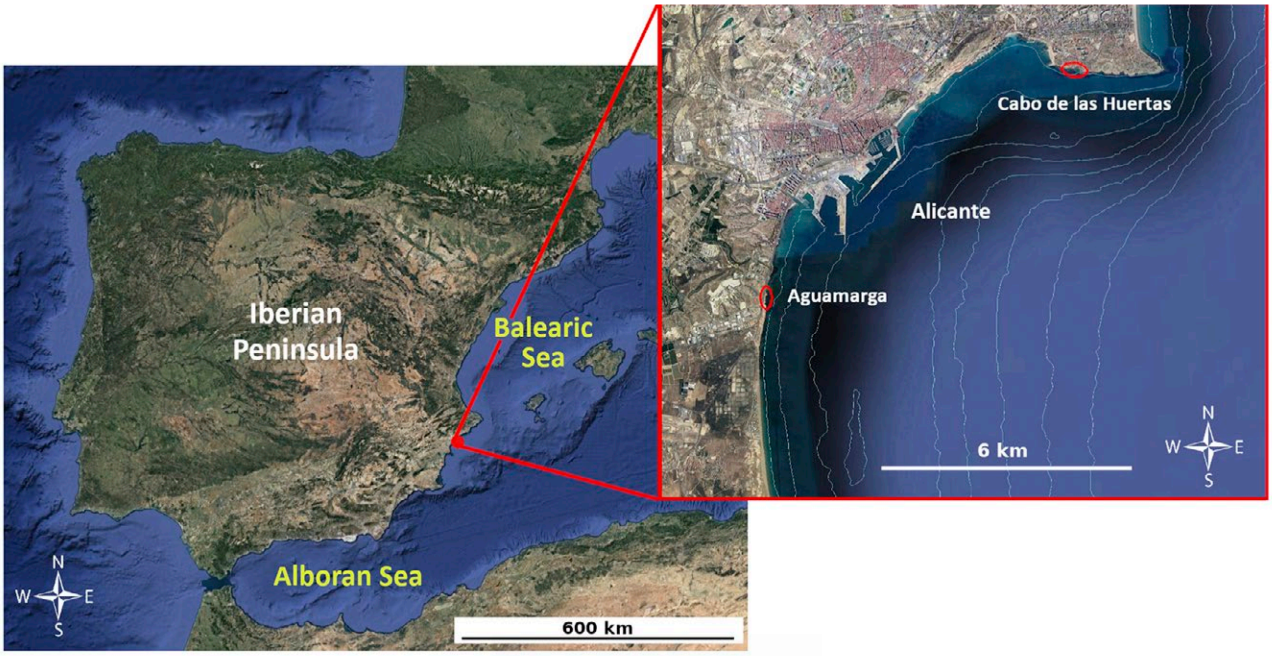

Fig. 1. – Study area showing the sampling locations: Cabo de las Huertas (the non-degraded location) and Aguamarga (the anthropogenic-degraded location). Isobath interval is equal to five metres. Modified from Google Earth.

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°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, 2000/06/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 µm and frozen. The analysis was carried out using an Automated Wet Chemistry Analyser (Skalar Analytical B.V., Breda, the Netherlands).

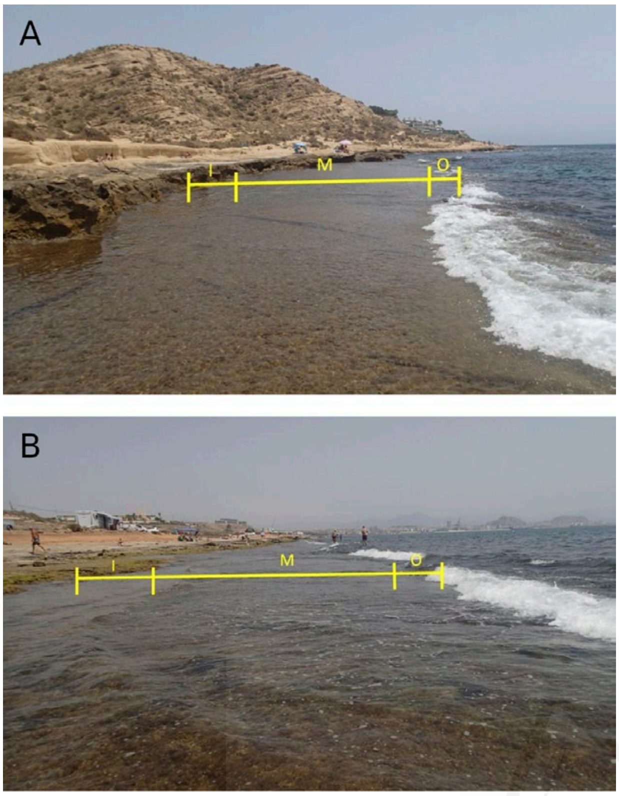

Fig. 2. – Zones surveyed at the non-degraded location (A) and the degraded location (B). Inner zone (I), mid-platform zone (M), outer platform zone (O).

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 overstory-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-*

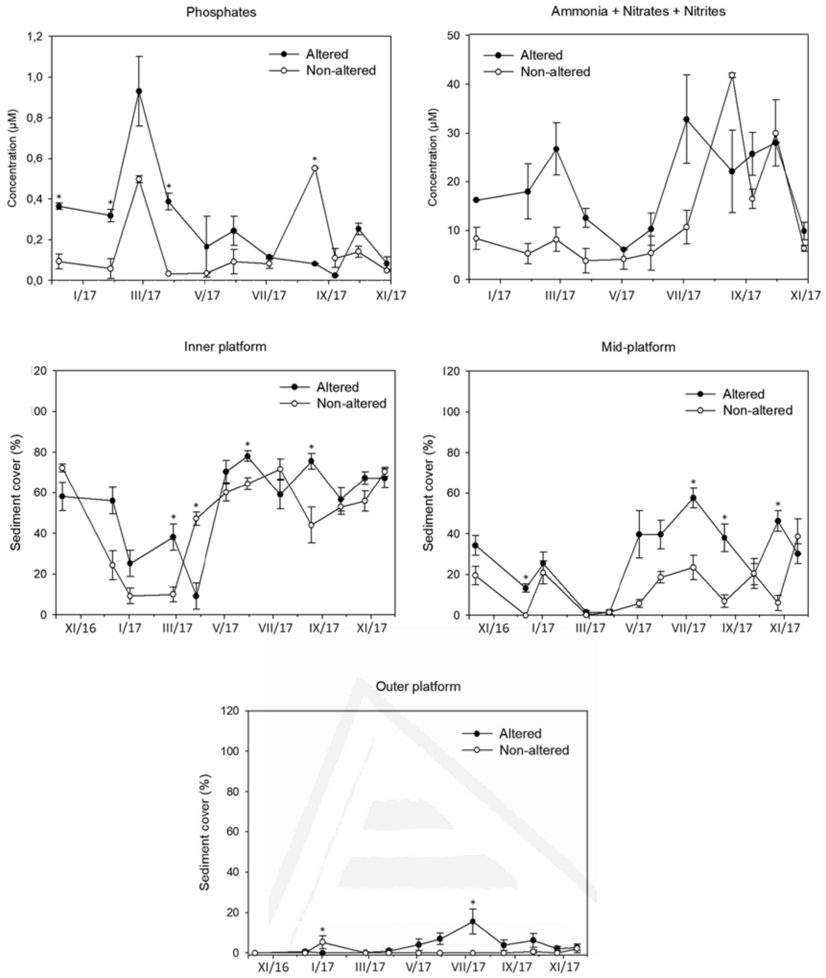

Fig. 3. – Values of nutrient concentration and sediment cover for each location (degraded and non-degraded). Vertical bars: standard error. Asterisks indicate significant differences between locations (α=0.05).

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 'Lo×Zo×Da' 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
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	7220.00	5.654	0.001	998
Zo×Si(Lo)	8	13363.00	1670.4	26.975	0.001	999
Da×Si(Lo)	44	73715.00	1675.3	27.055	0.001	998
Lo×Zo×Da	22	1,23E+09	5570.4	43.622	0.001	998
Zo×Da×Si(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 '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
26/03/2017	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

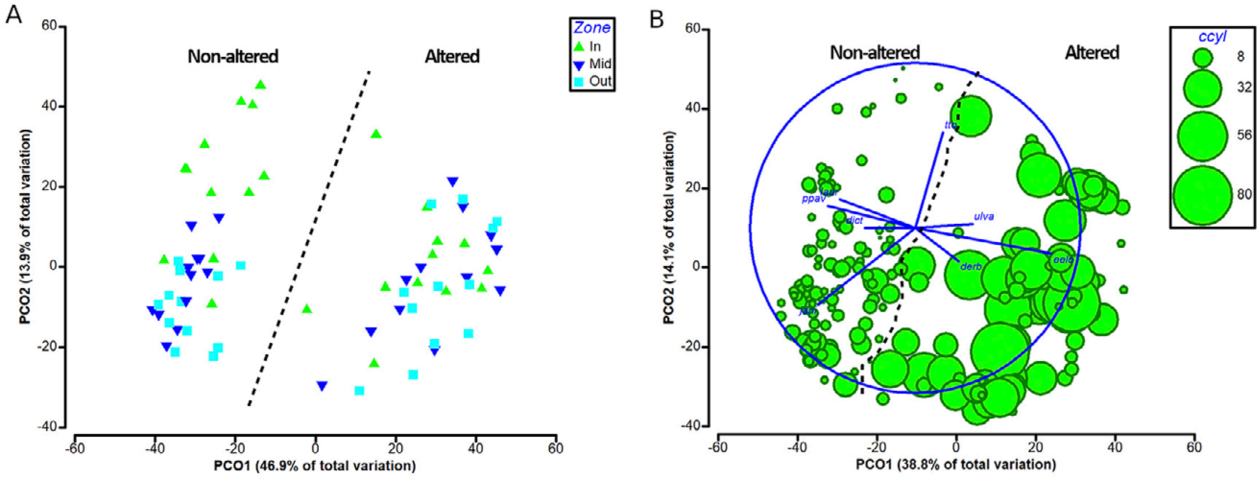

Fig. 4. – Principal coordinates ordination (PCO) of all inventories based on a Bray-Curtis similarity matrix of square-root transformed percent cover values of each taxa. Non-degraded location samples are separated from the degraded ones by a dotted line. A, PCO resulting from pooling replicates and 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 ‘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	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
Lo×Zo	2	13204	6602.1	5.3732	0.033	998
Lo×Da	11	89549	8140.8	16.274	0.001	999
Zo×Da	22	44416	2018.9	3.9575	0.001	999
Zo×Si(Lo)	8	9829.7	1228.7	6.0943	0.001	996
Da×Si(Lo)	44	22011	500.24	2.4812	0.001	998
Lo×Zo×Da	22	18902	859.19	1.6842	0.051	998
Zo×Da×Si(Lo)	88	44893	510.15	2.5303	0.001	999
Residual	432	87098	201.62			

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	0.401	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

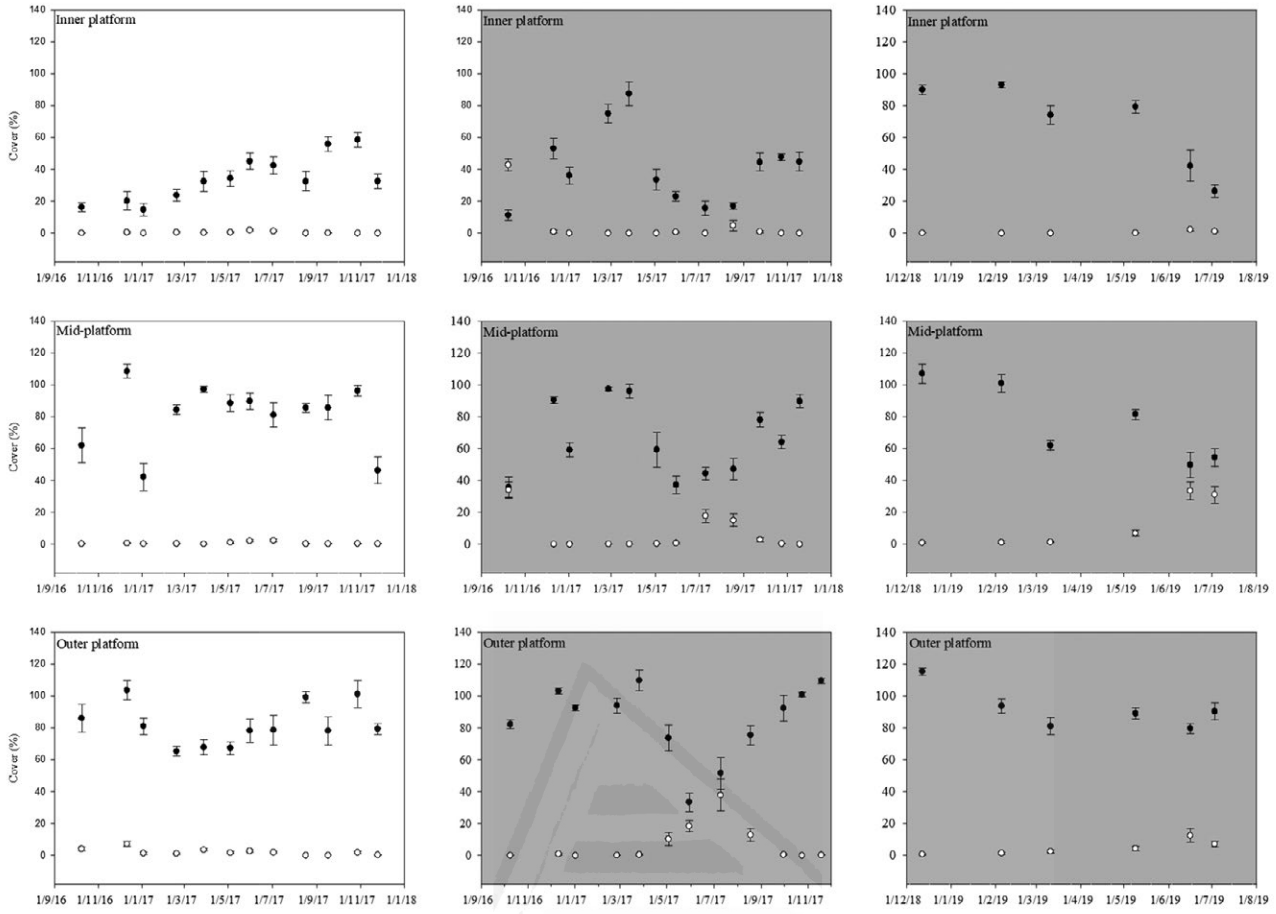

Fig. 5. – Temporal dynamics in the cover of overstory (black dots) and *C. cylindracea* (white dots) under non-degraded (white background) and degraded (grey background) conditions in the zones distributed along the shallow vermetid platforms. Data from a current survey being carried out at the degraded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

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	0.661	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

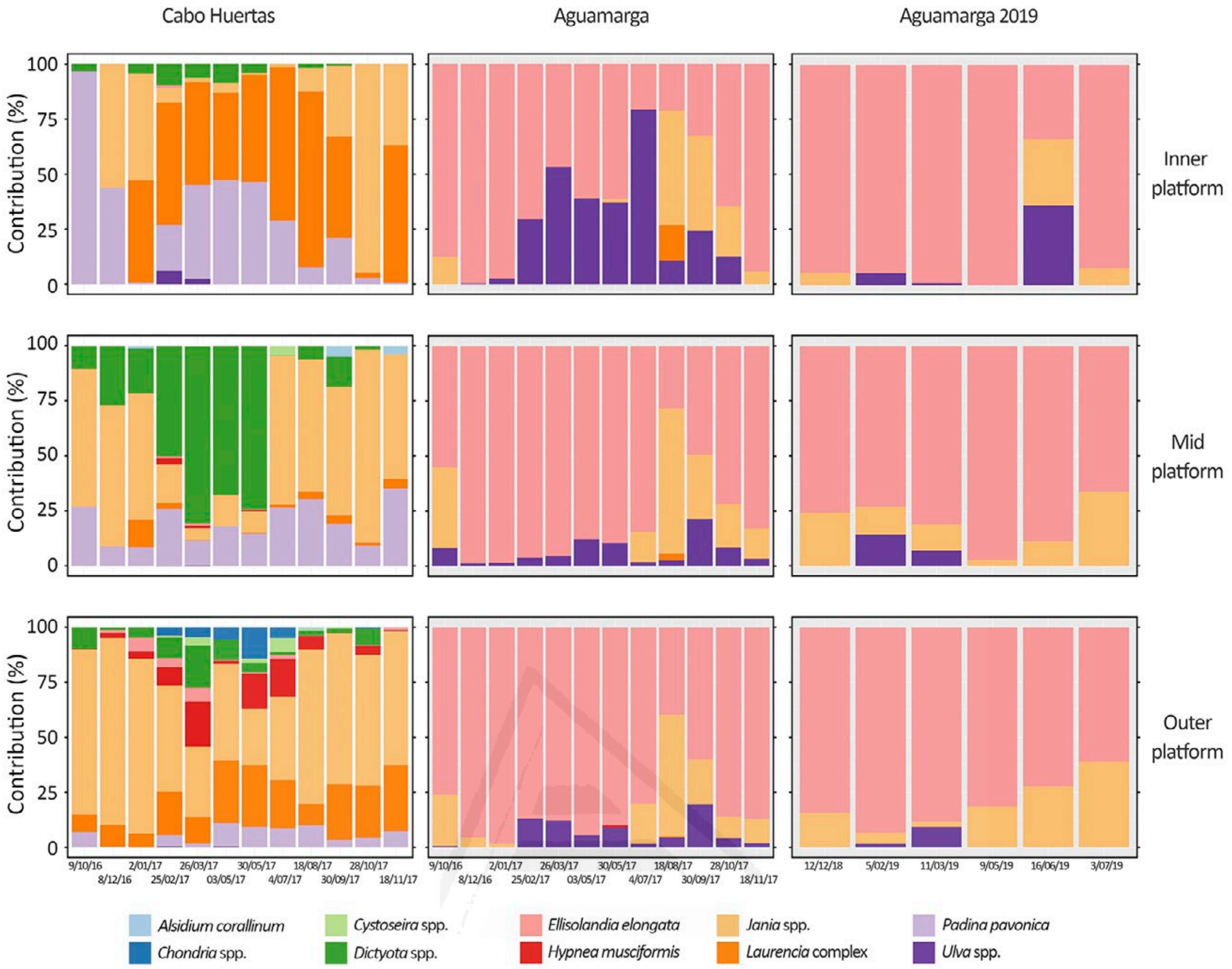

Fig. 6. – Stacked plots showing the proportion of each algae contributing to the total overstory cover in each survey. The graphics are arranged as in Figure 5.

(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 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 Dethier 1994) is higher than that of the inner ones (Terradas-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 souteastern 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 ‘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×Zo×Da’ for pairs of levels of the factor ‘Location’ (Monte Carlo p-values).

Supplementary data

Table S1.- A. Summary of 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.* p-values are in bold when they are significant (α = 0.05). B. Pair-wise tests for term 'LoxDa' for pairs of levels of factor 'Location'. p(MC)= Monte Carlo p-value.

A.

Phosphates

Source of variation	df	SS	MS	Pseudo-F	p(perm)	Permutations
Lo	1	0.14091	0.14091	21.641	**0.001**	996
Da	10	1333,00	0.1333	20.472	**0.001**	998
LoxDa	10	0.60351	0.060351	92.686	**0.001**	998
Res	22	0.14325	0.0065114			
Total	43	2,22E+04				

Nitrogen

Source of variation	df	SS	MS	Pseudo-F	p(perm)	Permutations
Lo	1	412.22	412.22	12.9	**0.002**	995
Da	10	3288.3	328.83	10.291	**0.001**	998
LoxDa	10	1223.7	122.37	38.294	**0.001**	999
Res	22	702.99	3,20E+04			
Total	43	5627.2				

B.

Pairwise test for term 'LocationXDate' for pairs of levels of factor 'Location'

Date	**Phosphates** p(MC)	**Nitrogen** p(MC)
08/12/2016	**0.035**	0.071
28/01/2017	**0.054**	0.176
25/02/2017	0.127	0.091
26/03/2017	**0.009**	0.114
03/05/2017	0.484	0.457
30/05/2017	0.253	0.428
04/07/2017	0.229	0.14
18/08/2017	**0.001**	0.143
07/09/2017	0.251	0.191
30/09/2017	0.098	0.819
28/10/2017	0.372	0.196

Table S2.- A. Summary of four-factor PERMANOVA univariate test (with *location*, *zone*, *date* and *site* nested in *location*) comparing sediment cover between samples. Lo, *location*; Da, *date*. p-values are in bold when they are significant (α = 0.05). B. Pair-wise tests for term 'LoxZoXDa' for pairs of levels of factor 'Location'. p(MC)= Monte Carlo p-value.

A.

Source of variation	df	SS	MS	Pseudo-F	p(perm)	Permutations
Lo	1	1,12E+04	1,12E+04	19.266	**0.096**	10*
Zo	2	2,71E+08	1,35E+09	214.35	**0.001**	997
Da	11	62217,00	5656.1	14.089	**0.001**	998
Si(Lo)	4	2325.4	581.35	49.497	**0.001**	998
LoxZo	2	4446.2	2223.1	35.207	0.087	999
LoxDa	11	1,50E+04	1367.1	34.053	**0.004**	998
ZoxDa	22	4,17E+04	1896.5	70.203	**0.001**	999
ZoxSi(Lo)	8	5051.5	631.43	53.762	**0.001**	999
DaxSi(Lo)	44	17664,00	401.45	3.418	**0.001**	996
LoxZoxDa	22	2,10E+04	955.52	3.537	**0.001**	996
ZoxDaxSi(Lo)	88	2,38E+04	270.15	23.001	**0.001**	998
Residual	432	5,07E+04	117.45			

(*) Monte Carlo p-value=0.025

B.

PAIR-WISE TESTS for term 'LoxZoxDa' for pairs of levels of factor 'Location'

Date	p(MC) Inner zone	p(MC) Mid-zone	p(MC) Outer zone
09/10/2016	0.076	0.138	-
08/12/2016	0.108	**0.001**	0.385
02/01/2017	0.08	0.777	**0.001**
25/02/2017	**0.04**	0.426	0.382
26/03/2017	**0.005**	-	0.394
03/05/2017	0.306	0.203	0.23
30/05/2017	0.034	0.203	0.197
04/07/2017	0.393	**0.041**	**0.002**
18/08/2017	**0.044**	**0.05**	0.126
30/09/2017	0.72	0.979	0.214
28/10/2017	0.236	**0.007**	0.17
18/11/2017	0.672	0.631	0.845

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Early succession patterns in a Mediterranean vermetid reef

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ABSTRACT

Vermetid reefs are distinctive bioconstructions of the Mediterranean and other warm temperate and subtropical seas. In the Iberian Peninsula the vermetid endemism *Dendropoma lebeche* Templado et al., 2016 and the coralline alga *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason are the main biogenic engineers of this natural heritage. However, very few empirical studies deal with their early patterns of succession. We installed two sets of colonization plates in spring (May) and autumn (November) along a healthy vermetid reef on the island Nueva Tabarca (Alicante, SE Iberian Peninsula), to study the early succession patterns of assemblages. Taxonomic composition and the Shannon diversity index were considered over a 1–2 year period. The seasonal month of installation had a detectable effect on taxonomic composition during the first nine months of immersion, also conditioning the diversity pattern. The succession proceeded faster for the May installation set, where both engineering species showed higher cover values from the beginning. Even though there was hardly any three-dimensional accretion on the plates during this study, those that remained well over a year reached *Dendropoma* densities close to those reported for healthy Mediterranean vermetid reefs. The use of colonization plates as recruitment enhancers could be a potential tool for restoration procedures, because of the minor impact of their installation and the relatively short time required to achieve high vermetid densities.

1. Introduction

The Mediterranean Sea is considered as one of the world biodiversity hotspots, with approximately 17,000 marine species listed (Coll et al., 2010; Lejeusne et al., 2010). This richness is related to its Tertiary history and the climatic fluctuations it underwent through the Quaternary (Bianchi et al., 2012). Moreover, its high environmental variability along with distinct oceanographic conditions from the neighbouring Atlantic vicinity (Zabala and Ballesteros, 1989) make the Mediterranean a refuge for many species with a variety of biogeographical affinities (Bianchi and Morri, 2000; Bianchi et al., 2012). This promotes speciation of many clades, showing high levels of endemism (Boudouresque, 2004; Templado, 2014).

This high species diversity has its counterpart at community level. Many assemblages thriving in this sea have unique features linked to these eclectic and rather particular environmental conditions. This is especially true for marine bioconstructions, in which the Mediterranean is particularly rich (Laborel, 1987; Ingrosso et al., 2018).

One of these bioconstructions is the vermetid reef, built mainly by encrusting coralline algae and vermetid gastropods. On a global scale, vermetid reefs are distinctive of very shallow rocky shores in subtropical and warm-temperate seas (Safriel, 1975; Laborel and Kempf, 1965; Milazzo et al., 2016). In the Mediterranean, they are well developed in warm regions, especially on sandstone abrasion platforms (Antonioli et al., 1999; Badreddine et al., 2019). Recently, it has been found that the main Mediterranean vermetid builder *Dendropoma petraeum* (Monterosato, 1892) is a complex of different endemic species with no overlapping ranges (Templado et al., 2016). Among coralline algae, the main Mediterranean species contributing to such bioconstructions is *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason. However, some other coralline species from the genus *Lithophyllum* Philippi could be important in some geographic or ecological conditions (Mannino, 1992; Bressan et al., 2003; pers. obs).

These reefs exert an important role as engineered habitat (Milazzo et al., 2016) providing not only shelter for many species (Chemello, 2009; Donnarumma et al., 2018a) but also contributing to the genesis of the platform itself (Safriel, 1975; Laborel and Laborel-Deguen, 1996). They are very sensitive to water degradation, being indicators of good ecological status in Mediterranean waters (Ramos-Esplà et al., 2008; Asnaghi et al., 2009; Badreddine et al., 2019).

All these reasons make it worthwhile to develop legal policies to protect this natural heritage. The vermetid reef is included in Annex I of the European Habitats Directive under 'reefs' (code 1170), while the main builder species (coralline algae and vermetids) are included in the

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annexes of the Berne Convention and in Annex II of the Barcelona Convention (SPAMI Protocol). In Spain, the National Catalogue of Threatened Species suggests protection of these reefs at the national level, and the vermetid reef itself is listed as a vulnerable habitat in the IUCN Red List (Gubbay et al., 2016).

Despite their ecological importance, the distribution of vermetid reefs in the Mediterranean Sea is little known (Milazzo et al., 2016). Some recent studies deal with the morphological structure of the reef in detail (Balistreri et al., 2015; Donnarumma et al., 2018b), whereas others have focused on factors that could affect its survival, such as anthropogenic activities, trampling, bioinvasions and sea acidification (Milazzo et al., 2009; Galil, 2013; Milazzo et al., 2014; Fine et al., 2016; Badreddine et al., 2019). However, there are very few empirical studies concerning the resilience of vermetid reefs against disturbances. It has been suggested that strong storms limit the growth and aging of these reefs to 600–700 years (Antonioli et al., 1999; Silenzi et al., 2004). The dispersal capability of the *D. petraeum* complex is also rather limited. Two species from this complex, *Dendropoma lebeche* Templado et al., 2016 from the western Mediterranean and *Dendropoma cristatum* (Biondi, 1859) from the central Mediterranean (Templado et al., 2016) show a similar dispersal pattern. The larva is lecitotrophic without a pelagic phase. Once hatching occurs, the juveniles spend only a few hours crawling until recruitment takes place. Moreover, recruitment seems to be limited to warm months, being reported from March to October in *D. lebeche* (Calvo et al., 1998) and from June to September in *D. cristatum* (Franzitta et al., 2016).

As for the main coralline-algal guild, fertile conceptacles in *N. brassica-florida* are also more abundant in warmer months (Bressan et al., 2003). Coralline algae could foster the recruitment of vermetids, as reported for Atlantic vermetid reefs (Spotorno-Oliveira et al., 2015). Facilitation processes linked to the microbial biofilm have also been demonstrated for *D. cristatum* recruitment, although inhibitory effects of some bacterial components are also reported (La Marca et al., 2018 and references therein). In contrast, the main erect algae from shallow Mediterranean platforms could impair the survival of the vermetid reefs, especially when algal abundance has been promoted by anthropogenic activity (Galil, 2013). Additionally, the strong seasonality of macroalgal species thriving on vermetid reefs (Einav et al., 1998; Terradas-Fernández et al., 2018) could affect reef recovery after an effective disturbance, depending on the time of the year it occurs.

All in all, there is a lack of empirical evidence to know how Mediterranean vermetid reefs (and most other Mediterranean bioconstructions) recover after an effective disturbance. The use of colonizing plates is a good surrogate to evaluate such recovery (Antoniadou et al., 2010), considering that the surface area of many clearings formed in the littoral fringe by disturbances is comparable to the size of such plates (Benedetti-Cecchi and Cinelli, 1993). In our study, we therefore address the early pattern of succession of a vermetid community through the installation of artificial plates in a vermetid reef. The effect of installation date on the succession pattern was assessed by comparing two seasonally contrasting months (May and November) and differing plate immersion periods, for more than a year. Considering the above factors, further understanding of the recovery rates in Mediterranean vermetid reefs could also provide better criteria for improving existing and potential restoration procedures.

2. Materials and methods

2.1. Study area

The study was carried out in the marine reserve of Isla de Nueva Tabarca (Alicante, SE Iberian Peninsula). The shore of the island comprises two main kinds of geological substrates (Martínez-Martínez et al., 2017). The westernmost side is dominated by calcarenitic and limestone rocks, while the central and eastern parts are dominated by Triassic fine-grained metagabbro. Vermetid reefs are found on both substrates, but the reef constitution differs. In calcarenitic limestones the reef generates an outer rim bordering a central platform (Terradas-Fernández et al., 2018; Ingrosso et al., 2018). However, in the metagabbro rocks where the study was undertaken, the vermetid reef occurs in the form of interspersed patches of pillow-like concretions on rocky platforms (Fig. A.1). The experiment was set up in an area ca. 100 m in width, facing north along the coast at 38°09′59.13″ N; 0°28′27.68″ W (Fig. A.2). The community on the platform floor from where the pillow-like vermetid concretions emerge is distinctive of very shallow light-saturated infralittoral bottoms, subject to strong seasonality (Einav and Israel, 2007; Terradas-Fernández et al., 2018). Thus, Dictyotaceae algae are the dominant guild during winter and springtime, whereas articulated corallines are more abundant during late summer and autumn months. No pollution sources or other evident signs of anthropogenic disturbances were detected in the area (Ramos-Esplà et al., 2008; pers. obs.).

2.2. Experimental set-up and processing

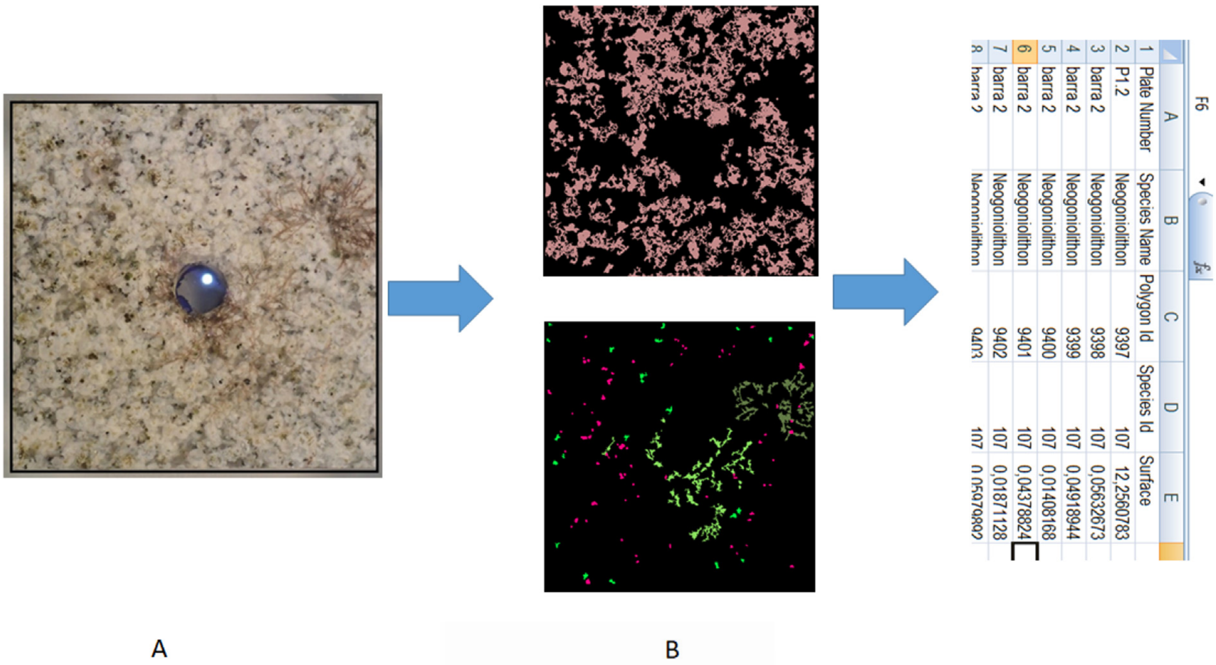
Two sets of fifteen granite square plates, 10 × 10 × 1.5 cm, cushioned by a foamy textile underlayer were randomly installed adjacent to the vermetid pillow formations but avoiding direct contact (to prevent damage), keeping a distance > 0.5 m between each sampling plate (Fig. A.3). By means of a drill, plates were attached to the platform floor with a stainless TRIPLEX parabolt 12 × 75 mm placed at their centre. Granite plates were used because of its durability in surf-exposed zones (over ten years, pers. obs). Besides this, the nature of the rocky substrate seems to have only minor effects on *Dendropoma* density (Donnarumma et al., 2018b; pers. obs).

The first set was installed in May 2015, and the second in November 2015. Since its installation, three random plates in each set were removed every three months during the first year. The remaining plates were removed in May 2017, so only one plate from the November set was left. Plates were preserved in 4% formaldehyde-seawater solution before analysis. All plates removed were photographed. Each taxon was identified and its percentage cover in relation to the plate area (100 cm^2) was quantified by means of a hierarchical segmentation-based software for cover classification images (http://www.seascapesoft.org) (Teixidó et al., 2011; Fig. 1). Simultaneously with image processing, plates were inspected under a stereomicroscope. Due to the near lack of vertical development of the taxa settled on the plates, quantification of the percentage area occupied by each taxon by means of photo-digitalization methods was expected to provide the most information about community complexity (Sant et al., 2017). Vermetid recruits were also counted. For taxonomic determination, small samples were removed from the plate when necessary. Most algae were identified to genus or species level, using different identification manuals (Giaccone, 1972; Irvine and Yvonne, 1994; Bressan et al., 2003; Cormaci et al., 2012; Cormaci et al., 2014). Some zoological groups and Cyanobacteria were identified to higher taxonomic levels.

Temperature data were obtained by CIMAR Research Station from a shallow vermetid platform close to Nueva Tabarca at 0.5 m depth, while photoperiod data were provided by the National Astronomical Observatory of Spain (http://www.fomento.gob.es) (Fig. 2).

2.3. Data analysis

To assess the successional pattern through the experimental *immersion period* along with the possible effects of the *installation month* (November vs. May) on the community colonizing the plates, a two-way permutational multivariate analysis of variance (PERMANOVA, Anderson et al., 2008) was performed on the Bray-Curtis dissimilarity matrix calculated on the untransformed data of percentage cover for each taxon. The analysed factors *immersion period* (T) and *installation month* (D) were treated as fixed factors. A PCO analysis of the Bray-Curtis matrix provided a graphical representation. A further



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	A	B	C	D	E
1	Plate Number	Species Name	Polygon Id	Species Id	Surface
2	P1.2	Neogoniolithon	9397	107	12,2560783
3	barra 2	Neogoniolithon	9398	107	0,05632673
4	barra 2	Neogoniolithon	9399	107	0,04918944
5	barra 2	Neogoniolithon	9400	107	0,01408168
6	barra 2	Neogoniolithon	9401	107	0,04378824
7	barra 2	Neogoniolithon	9402	107	0,01871128
8	barra 2	Neogoniolithon	9403	107	0,05979892

Fig. 1. Example of abundance estimation using Seascape software on a plate from the May 2016 deployment set removed in July 2016. Notice that almost all patches are located within the plate area, suggesting that recruitment must be the main colonization strategy. Dominant taxa are Rhodomelaceae (dark brown in A, green in B) and *N. brassica-florida* (pink in B above). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

discriminant canonical analysis of principal coordinates (CAP) was also done to show the effects of the *immersion period*.

Taxa responsible for differences among factors were identified by SIMPER analysis (Clarke and Gorley, 2006). The most important taxa were further evaluated by analysis of variance (ANOVA), using the same design but considering only the first year to keep it balanced. Shannon-Wiener diversity index (based on log2) was computed using taxa percentage cover and tested using the same ANOVA design.

The a posteriori SNK test was performed when significant effects were found. Data were transformed when necessary (Underwood, 1997) and heterogeneity of variances was evaluated by means of Cochran's test. All multivariate statistical analyses were performed using the PRIMER–E® v.6 + PERMANOVA package (Anderson et al., 2008), while univariate analysis was with R software version 3.2.2 (R Development Core Team, 2011). Cover values are shown as the mean and the standard error (mean ± SE), unless otherwise stated.

3. Results

3.1. Multivariate analysis

Both factors analysed, *immersion period* (*T*) and *installation month* (*D*), had significant individual and interactive effects on community composition. However, pairwise *post-hoc* comparisons showed that differences in *installation month* were only significant up to nine months of *immersion period*. For the latter, in most cases, only the first extraction set (3 months of immersion) differed significantly from the remaining older ones (Table 1).

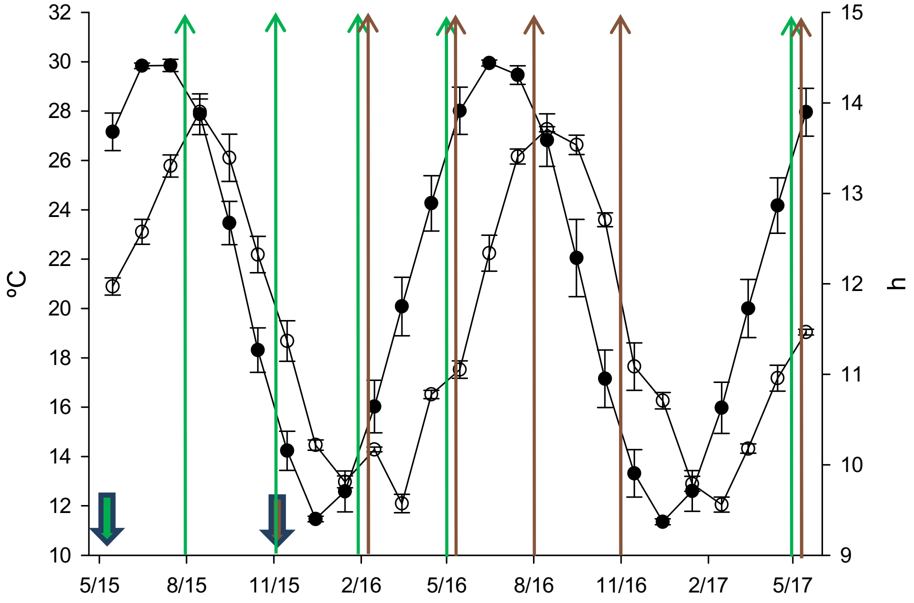

Fig. 2. Temperature (in degrees Celsius, black circles) and photoperiod (in hours, empty circles) values during the study period. Thick downward arrows indicate the *installation month* (green, May; brown, November), whereas thin upward arrows indicate when the plate sets were removed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Results of distance-based permutational two-way PERMANOVA using *immersion period* '*T*' and *installation month* '*D*' as fixed factors (A). Results of pairwise analyses from interaction 'TxD' for pairs of levels of factor '*D*' and '*T*' (B): df, degrees of freedom; SS, sums of squares; MS, mean squares; Pseudo-F, pseudo-F ratio; t, pseudo-t statistic; P(perm), permutation *P*-value; P (MC), Montecarlo *P*-value.

A

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
D	1	15,894	15,894	12.778	0.001	998
T	5	20,445	4089.1	32.876	0.001	999
D × *T*	3	12,943	4314.4	34.688	0.001	997
Res	18	22,388	1243.8			
Total	27	71,737				

B

Pairwise analyses

For pairs of levels of factor *D*	Within *T* levels	t	P (MC)
	3	0.109	0.018
	6	2.532	0.014
	9	0.096	0.006
	12	0.136	0.136
Pairwise analyses For pairs of levels of factor *T*	Within *D* levels	t	P (MC)
	3,6 (May)	1.698	0.081
	3,9 (May)	1.862	0.058
	3,12 (May)	1.620	0.116
	6,9 (May)	1.003	0.436
	6,12 (May)	1.134	0.306
	9,12 (May)	0.857	0.545
	3,6 (Nov)	1.883	0.069
	3,9 (Nov)	4.784	0.004
	3,12 (Nov)	3.616	0.006
	6,9 (Nov)	1.576	0.136
	6,12 (Nov)	1.743	0.08
	9,12 (Nov)	1.546	0.105

The PCO analysis (Fig. 3) showed that the first axis segregated the different samples to some extent. This was according to the *immersion period,* those with least time immersed being in a rightward position. However, that segregation was poorer for those plates installed in May. *Neogoniolithon brassica-florida*, the main alga with an engineering role, was also well correlated with the first axis.

Regarding *installation month*, May and November installed sets were relatively well segregated by the second axis. Most Cyanobacteria (*Rivularia* spp. and *Calothrix* spp.) were also well correlated with the second axis, due to their greater abundance on those plates installed in November.

The CAP plot (Fig. 3) showed a similar trend, differentiating better the samples according to their *immersion period*. Thus, longer immersion time was positively correlated with the first axis, in the same way as with the main species contributing to vermetid reef formation, *D. lebeche* and *N. brassica-florida*.

The SIMPER analysis (Table 2) also showed that engineer taxa (*N. brassica-florida and D. lebeche*) were more abundant in long immersion periods. However, the successional pattern between the two installation months was different. Thus, in the May installation set, *N. brassica florida* showed high cover values and contributed most to similarity from the very beginning. Other Corallinales (*Hydrolithon* spp.) and Rhodomelaceae contributed moderately to similarity and abundance during the first six months of immersion. Instead, for the November installation set, Cyanobacteria (mainly *Calothrix* spp. and *Rivularia* spp.) had high contributions from the very beginning. This resulted from the poor recruitment by other taxa during the first six months of immersion in the November installation set.

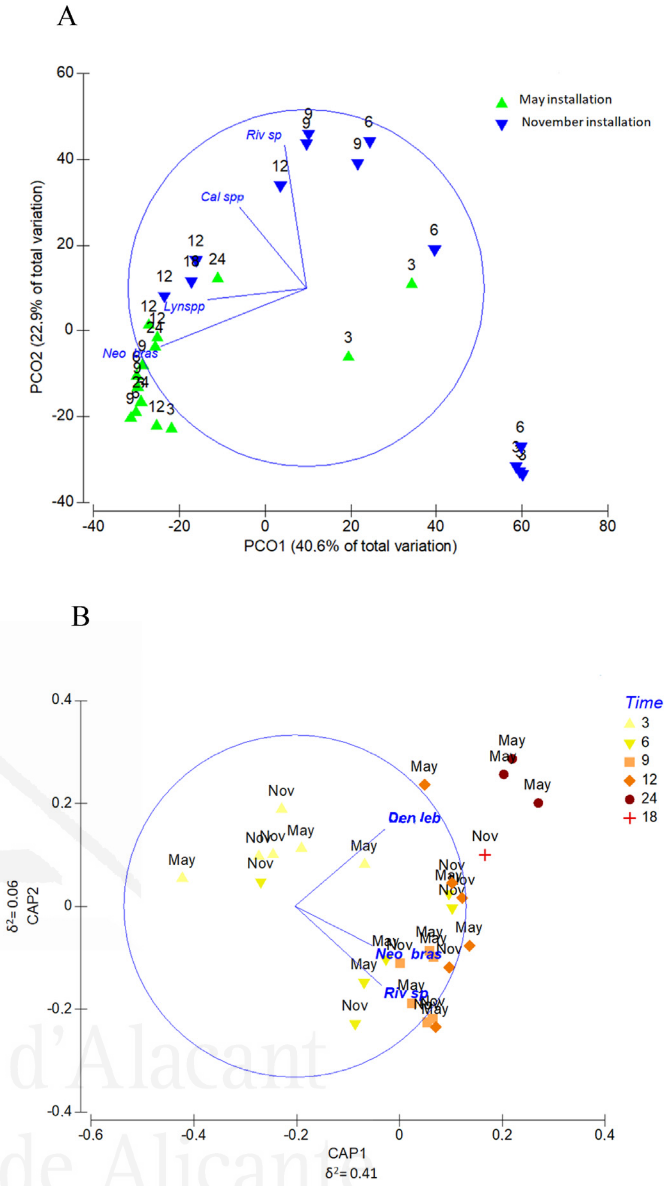

Fig. 3. A. Unconstrained PCO analysis of those taxa colonizing the plates. The numbers shown represent the *immersion period* (in months). B. Constrained CAP analysis comparing taxonomic composition of plates according to the *immersion period* (in months). Those taxa with a Pearson correlation with PCO axes over 0.5 are shown (*Cal* spp., *Calothrix* spp.; *Den leb, Dendropoma lebeche*; *Lyng* spp., *Lyngbya* spp.; *Neo bras, Neogoniolithon brassica-florida*; *Riv, Rivularia* spp*)*.

3.2. Main taxa cover trends

From most abundant taxa, *N. brassica-florida*, *Hydrolithon* spp. and Cyanobacteria showed significant differences between *installation month*, *immersion period*, and their interactive effects (Table 3, Fig. 4).

For *N. brassica-florida,* the May installation set showed an abrupt increase from the beginning, reaching values over 60% cover at 12 months (65 ± 14%). The 24-month plates showed a slight decrease (37 ± 9%). Conversely, the November set showed a lag with nil cover until the ninth month, when it started to increase up to over 20% at 12 and 18 months.

The pattern of *Hydrolithon* spp. was quite different, showing one peak in abundance during November, for May and November installation sets. The November peak for the May installed set occurred at 6 months (8 ± 3%), and at 12 months for the November installed, reaching lower values (1.9 ± 0.29%).

Table 2
Main taxa contributions to SIMPER similarity and average abundances for *installation month* and *immersion period*. Cut-off for low contributions: 98%. Contribution to similarity (left) and abundances (right) respectively, in percentage for each taxon.

May installation set					
Month of removal	August	November	February	May	May
Immersion period	3 months	6 months	9 months	12 months	24 months
Calothrix spp.	29.37/2.51	7.37/9.84	3.55/5.91	4.37/4.04	5.51/6.25
Chroococcales		1.71/2.98	1.79/4.05	1.93/4.83	4.09/6.31
Dendropoma lebeche	0.92/0.20			1.62/1.65	13.23/10.42
Hydrolithon spp.	18.73/0.35	5.08/7.52			
Lophosiphonia cristata	13.87/1.15	2.94/9.59	0.70/0.79		
Lyngbya sp.		2.67/2.56	1.10/1.05		1.16/1.49
Neogoniolithon brassica-florida	25.46/11.79	75.00/53.02	78.28/65.99	78.71/65.24	61.38/37.01
Phaeophila dendroides	6.08/0.38	3.57/8.06	5.5/5.41	2.41/2.64	1.27/1.46
Polysiphonia opaca			2.17/3.34		
Rivularia spp.	4.30/0.80		5.00/3.85	7.47/12.57	8.07/6.85
Vermetus triquetrus				2.10/2.56	4.09/6.00

November installation set					
Month of removal	February	May	August	November	May
Immersion period	3 months	6 months	9 months	12 months	18 months
Brachytrichia sp.					4.51/2.88
Calothrix spp.	31.03/0.08	27.44/2.61	16.47/10.41	28.28/17.73	20.48/13.01
Chroococcales		9.91/0.31	7.42/5.28		3,73/2.38
Dendropoma lebeche				1.63/1.34	6.15/3.93
Entophysalis sp.					2.16/1.38
Hydrolithon spp.				2.54/1.52	
Jania adhaerens	3.73/0.01				
Lophosiphonia cristata			2.2/0.93		
Lyngbya sp.	6.68/0.06		2.17/0.71	1.55/1.85	3.73/2.38
Neogoniolithon brassica-florida			1.15/0.69	31.01/23.03	38.99/24.88
Phaeophila dendroides	9.51/0.06		1.8/2.15	0.87/1.71	1.86/1.46
Polysiphonia opaca				2.14/3.97	4.19/2.67
Rivularia spp.	47.92/0.07	62.02/7.34	67.52/21.47	30,17/16.66	11.2/7.15
Vermetus triquetrus					1.56/1.00

Table 3
ANOVAs of the effects of *installation month* (*D*) and *immersion period* (*T*) on the percentage cover of the main taxa involved, for differences among treatments (also for the number of individuals or recruits in *D. lebeche*). C. test, Cochran test; Trans, transformation used; df, degrees of freedom; MS, mean squares; F, *F* test statistic; P, *P*-value.

Taxonomic group		Total cover		*N. brassica-florida*		*Hydrolithon* spp.		*D. lebeche %*	
Source of variation	df	MS	F	MS	F	MS	F	MS	F
D	1	80.487	35308***	11,136	62337***	1.778	15634**	0.196	0.674
T	3	55.575	24380***	1557.3	8717**	0.982	8645**	2.675	9205***
D ×*T*	3	9.740	4273*	786.2	4400*	2.146	18879**	0.026	0.088
Residual	16	2.280		178.6		0.114		0.291	
Trans		sqrt		none		log (x + 1)		none	
C. test		*P* = .03		*P* > .05		*P* > .05		P > .05	

Taxonomic group		*D. lebeche* ind		Cyanobacteria		Rhodomelaceae	
Source of variation	df	MS	F	MS	F	MS	F
D	1	15.04	0.052	433.88	4301*	3.563	7509*
T	3	1070.15	3.712*	1067.12	10578***	1.451	3.058
D × *T*	3	298.26	1.035	383.65	3803*	1.699	3580*
Residual	16	288.29		100.88		0.475	
Trans		none		none		log (x + 1)	
C. test		P > .05		P > .05		P > .05	

* P < .05.
** P < .01.
*** P < .001.

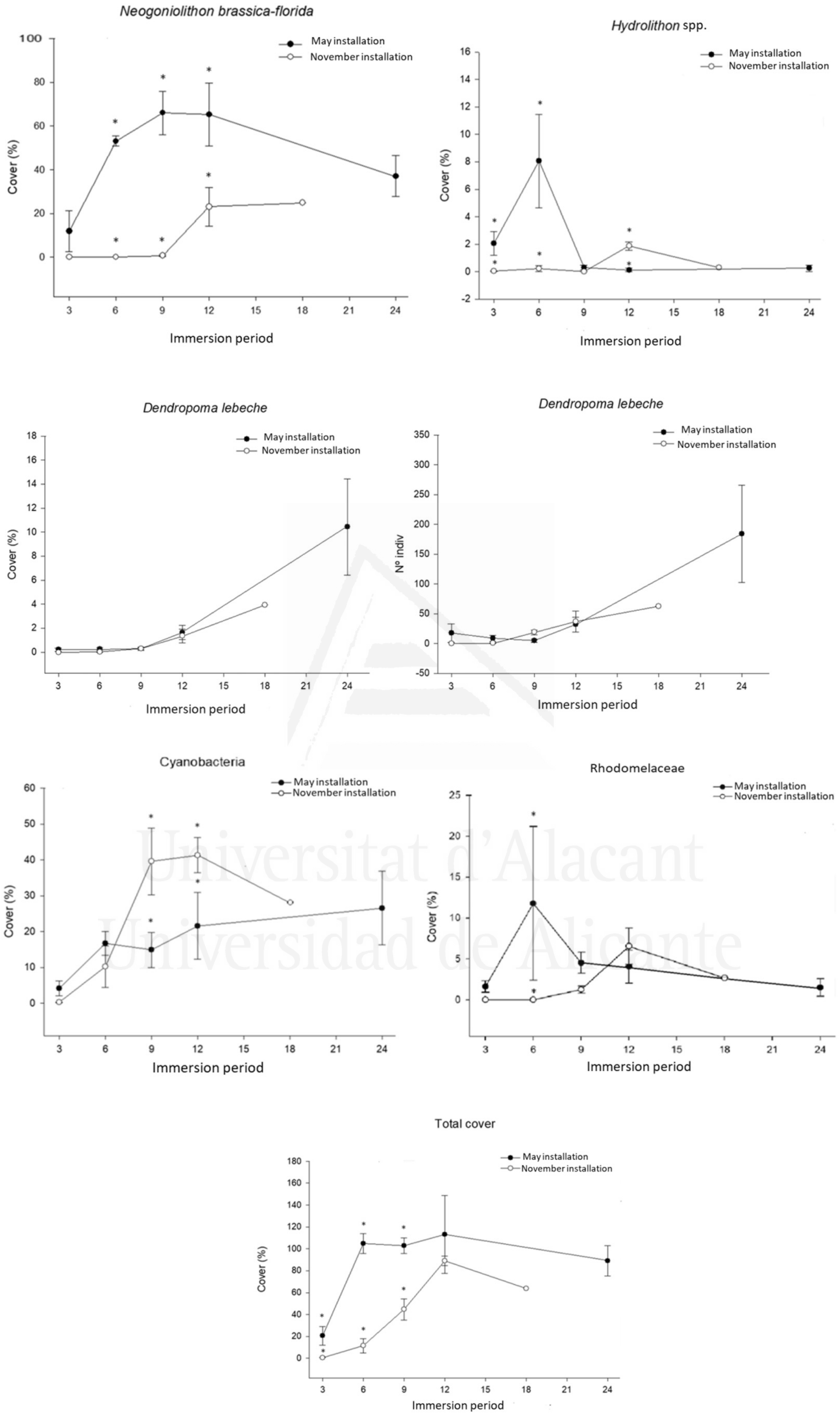

Fig. 4. Abundance of most characteristic taxa over the *immersion period* (months). Abundance is shown in percentage except for *D. lebeche*, where it is also shown in number of recruits. Asterisks indicate significant differences in SNK tests between the two installation sets. Only one plate remained in the last November set (18 months). All the results are shown as mean and standard error (mean ± SE).

Cyanobacteria showed an increase until the sixth month, irrespective of the *installation month*. Those plates installed in May showed a slighter increase until the end of the experiment (27 ± 10%), whereas November plates increased faster, reaching higher values (41 ± 5% at 12 months). The last plate from the November installation (18 months of immersion) showed a slight cover decrease (29%), close to the last extraction set in May.

The vermetid *D. lebeche* also showed significant differences according to the *immersion period*, but not in relation to the *installation month* (Table 3). The cover values were low but showed an exponential increasing trend, also when the number of recruits was considered instead of cover (Fig. 4). Despite this analogous pattern, there were slight differences between the two approaches. Thus, in the May installation, recruits were detected at three months (August, 17 ± 10 recruits), showing a small decreasing trend in number to the ninth month (February, 5 ± 2 recruits). That pattern was less appreciable in cover percentage due to their low cover values. Number of recruits and percentage cover resumed their increase from 12 months of immersion (May, 32 ± 12 recruits and 2 ± 0.6% cover) until the end of the experiment at 24 months (184 ± 81 recruits and 10 ± 4% cover). Conversely, in the November installation set recruits were practically not detected until the ninth month with cover values near nil (August, 19 ± 4 recruits and 0.28 ± 0.1% cover). Then, there was a steady increase until the end of the experiment (63 recruits and 4% cover in the last plate).

Rhodomelaceae (mainly *Lophosiphonia* spp. and *Polysiphonia* spp.) showed significant differences according to *installation month* and its interaction with *immersion period* (Table 3). There was a higher abundance during November for both May (12 ± 9%) and November (7 ± 2%) installation sets at 6 and 12 months respectively (Fig. 4).

Finally, when we consider coverage including all the taxa, again the two factors *installation month*, *immersion period*, and their interactive effects were significant (Table 3, Fig. 4). In the May installation set, there was an abrupt increase from the beginning until the sixth month of immersion (November, 105 ± 9%) when the total cover reached a 'steady state'. However, in the November installation set there was a notably lower increase until the sixth month of immersion (May), when it accelerated to attain values close to those of the May installation set at 12 months (November, 89 ± 4%).

3.3. Diversity

Immersion period and *installation month* had no significant effects on the Shannon-Wiener index except their interaction (Table 4). Thus, in the November installation set, at three months' immersion (February) there was a fall in diversity, attaining minimal values at six months (May, 1.3 ± 0.1), when few Cyanobacteria species gained quantitative importance. Then the index recovered (2.5 ± 0.2 at 12 months), when species other than Cyanobacteria recruited. The May installation set showed a rather steady pattern during the whole study, with slightly higher values at 24 months (2.6 ± 0.15, Fig. 5).

Table 4
ANOVA of the effect of the *installation month* (*D*) and *immersion period* (*T*) on the Shannon-Wiener index. C. test, Cochran test; Trans, transformation used; df, degrees of freedom; MS, mean squares; F, *F* test statistic; P, *P*-value.

Shannon-Wiener diversity index			
Source of variation	df	MS	F
D	1	0.038	0.148
T	3	0.325	1.251
D × *T*	3	0.930	3.580*
Residual	16	0.260	
Trans		none	
C. test		P > .05	
*P < .05			

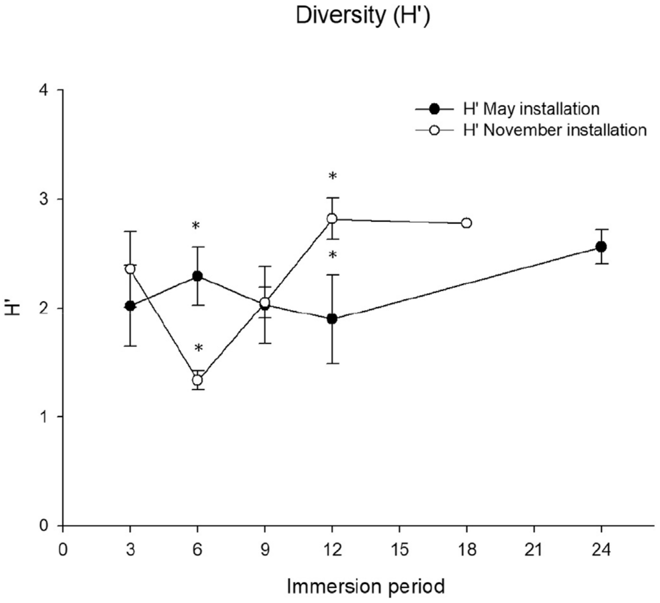

Fig. 5. Shannon-Wiener diversity index (H′) through *immersion period*. Asterisks indicate significant differences in SNK tests between *installation month*. Only one plate remained for the last November set (18 months of immersion). All the results are shown as the mean and standard error (mean ± SE).

4. Discussion

It is known in ecology that scale matters when we want to understand patterns and processes. When studying succession, there are still two main perspectives on how communities are being shaped. The community may be viewed as a result of local processes and historical events that drive the community to a certain stable point among multiple possible ones (Sutherland, 1974; Menge et al., 2017), or otherwise, deterministic forces are thought to drive the community to a unique endpoint (Clements, 1916; Stewart, 1989; Vance, 1988). However, in many cases the two approaches are "the flip side of the same coin", and communities can be perceived as mosaics of succession stages where local constraints (recruitment limitation, predation, stress, abiotic disturbances) hamper other unidirectional processes (competition, habitat complexity), which operate in a deterministic way (Boudouresque, 1973; Boudouresque and Cinelli, 1976; Connell, 1978; Sousa, 1979; Bulleri and Benedetti-Cecchi, 2006). This is also true for bioconstructions like vermetid reefs. Thus, natural disturbances (storms, bioeroders) frequently destroy part of these frameworks, so succession restarts permanently even when there is no underlying anthropogenic factor (Antonioli et al., 1999). Nevertheless, vermetid reefs can be dominant when conditions are appropriate, constituting climactic assemblages (Pérès and Picard, 1964). Therefore any better understanding of the deterministic processes fostering such reefs, supported by empirical evidence, is of use to help improve management and restoration strategies (Sinclair et al., 2018). Despite its relatively short duration, our work reveals some general patterns also found in other successional studies, and provides insights to better understand and protect this Mediterranean natural heritage.

4.1. Installation time and the role of recruitment

The season when the plates are installed has strong effects on community succession during the first nine months, accelerating or delaying the recovery rate. This phenomenon has been observed elsewhere in temperate subtidal systems (Serisawa et al., 1998; Antoniadou et al., 2011) and is probably greatly conditioned by the temporal pattern of recruit supply (Fraschetti et al., 2002). The greater abundance of the main reef-builders (*D. lebeche* and *N. brassica-florida*) in the set deployed in May is in agreement with their phenology (Calvo et al., 1998; Bressan et al., 2003) and it is also true for *Hydrolithon* spp. (Reyes and Afonso-Carrillo, 1995). Thus, winter could be a limiting season for the recruitment of the engineering species that contribute most to that bioconstruction. This lack of recruitment by the main engineering species in winter could be harnessed by Cyanobacteria, which showed more quantitative importance in November installation sets than in those of May.

Colonization by recruitment rather than by lateral encroachment seems the dominant strategy used not only by crustose corallines, but also the remaining taxa. This is because most early identified patches of organisms are localized within the plate area rather than entering from the periphery (Fig. 1). This was also true for those turf species that are also distinctive for their capacity to develop vegetative axes invading clearings (Airoldi, 2000a, 2000b). The importance of both strategies has been reported (Asnaghi et al., 2015; Fava et al., 2016). Nonetheless, other studies also describe recruitment as the main colonization process, even in small clearings (Benedetti-Cecchi and Cinelli, 1994; Bulleri, 2005). The use of plates a few cm high instead of artificial clearings involves an additional difficulty for those species capable of lateral expansion to invade from the periphery, through either crusts or lateral axes. It means that recruitment by diaspores (zygotes, propagules, spores, vegetative fragments) is probably the main source of organisms from which the succession proceeds (in our time window), as reported in other studies using colonization plates (Sangil, 2011; Pacheco et al., 2011). Finally, most of the taxa identified (Appendix, Table A.1) were previously detected in these abrasion platforms (Terradas-Fernández et al., 2018). This is in line with other studies that point out the important role of neighbouring assemblages in determining the succession patterns in natural habitats (Bulleri and Benedetti-Cecchi, 2006).

4.2. Immersion period

The converging successional pattern of assemblages observed between plates installed at different times of the year seems to be general (Niell, 1979). Antoniadou et al. (2011) distinguished one initial phase in which seasonality in the recruit supply masks the immersion period, and a second phase in which established colonizers drive the succession towards a predictable endpoint. Pacheco et al. (2011) did not detect any seasonal effect in an analogous experimental design after a year of deployment.

The increase in total cover up to a certain steady stage was achieved during the first year or earlier, like other studies carried out in shallow subtidal communities (Boudouresque, 1973; Benedetti-Cecchi and Cinelli, 1996; Milazzo et al., 2004) and faster than others carried out in the deeper sublittoral assemblages (Antoniadou et al., 2010; Teixidó et al., 2013). These differences could be explained by the productivity potential of each assemblage (sensu Steneck and Dethier, 1994). Thus, factors like upwelling could speed up the succession processes and recovery in some subtidal communities (Pacheco et al., 2011 and references therein). Likewise, the lesser productivity potential of the Mediterranean circalittoral rocky benthos (Ballesteros, 1989; Garrabou et al., 2002) could affect the resilience of those deeper communities, slowing down their cover recovery rate.

As for the main reef builders, it is known that coralline algae are able to colonize at the first successional stage (Airoldi, 2000b; Asnaghi et al., 2015), which is in line with this study. However, in our study coralline crusts show different successional patterns, depending on their thickness. Thus, the thin crusts of *Hydrolithon* spp. disappear in the late stages of succession, probably outcompeted by the thicker *N. brassica-florida*. These competitive interactions seem to occur even at the early stages of succession when there is a great availability of free space (Fig. 6). Cyanobacteria also seemed to impair and delay the spread of *Neogoniolithon* once this coralline alga recruited successfully in the warm season (Fig. 6).

The better competitive capacity of both *D. lebeche* and *N. brassica-florida* appears to be the main reason for their increase through time. However, facilitation processes could also be involved. The limpets detected on some plates could foster the dominance of coralline algae through their grazing activity (Littler et al., 1995). Another facilitation process could be the above-mentioned potential enhancement of the vermetid recruitment by coralline algae (Spotorno-Oliveira et al., 2015). Alongside this, the limited dispersal ability of vermetids and their ability to easily make aggregations (Calvo et al., 1998; Pacheco et al., 2011) points to a probable increase in the recovery rate through time, with new recruits settling from the parents previously installed on the plates. The observation of aggregates of *D. lebeche* and *N. brassica-florida* on the older immersed plates, including recent recruits on top of them (Fig. 7), reinforces that hypothesis, as does the observed exponential tendency in vermetid abundance. These aggregates probably also restrict competition with erect algae during the time when the bioconstruction is growing in height and depth decreases. Moreover, the fact that the surface of the plates was some cm higher than the floor of the abrasion platform would also hamper the establishment of erect algae capable of hindering coralline and vermetid growth (Galil, 2013; Badreddine et al., 2019). In most cases, erect algae only attained moderate cover and if competitive interaction with coralline algae and vermetids arose, it would not be enough to halt the increase of both engineering species in the studied location (Table A.1).

4.3. The diversity pattern and its relationship to increased cover of the engineering guilds

Shannon-Wiener index is related to the different temporal recruitment patterns discerned for the two installation seasons, with fewer species recruited during late autumn and winter months and more in later spring and summer months. The lack of a clear increase in diversity -beyond a year- could also be related to the intrinsic properties of these assemblages. Thus, the higher increase rates in the cover of both engineering guilds over the other taxa suggest that a diversity increase would be difficult to achieve in mature communities (considering our methodology based on cover abundance of visually detectable taxa). On healthy reefs in Sicily, *Neogoniolithon* cover values were between 40% and 77% and the density values of the living vermetid individuals were around 250–530 indiv./100 cm^2 (*D. cristatum* instead of *D. lebeche*) (Fine et al., 2016). Similar values (200–800 indiv./100 cm^2) were found at Nueva Tabarca for *D. lebeche* (Bayle-Sempere and Sánchez-Jerez, 2004). In our study, the maximum *Dendropoma* density of 290 indiv./100 cm^2 was reached on a May installed plate, immersed for two years. These values are rather low but comparable to those for healthy reefs.

4.4. Considerations for management and restoration strategies

Despite the relatively small time window of this study, some of our results could aid in management and restoration procedures. The observed cover increase of *N. brassica-florida* on the colonization plates was fast. Moreover, in two years the density of *D. lebeche* was comparable to that found in healthy vermetid reefs. However, this system was far from being a true vermetid reef (Fig. 7). The three-dimensional growth of the bioconstruction was almost nil on all the plates, even in those with higher coverage of *N. brassica-florida* and vermetids. However, some aggregates of *Neogoniolithon* and *Dendropoma* formed patches of a few cm^2, reaching up to 3–4 mm high on the oldest plates (Fig. 7).

As already stated, some bioconstructions are dated at 400–700 years old (Antonioli et al., 1999; Silenzi et al., 2004; Chemello and Silenzi, 2011), with an accretion rate estimated at about 0.86 mm per year^{-1} (Sisma-Ventura et al., 2009). This estimation is in line with those found

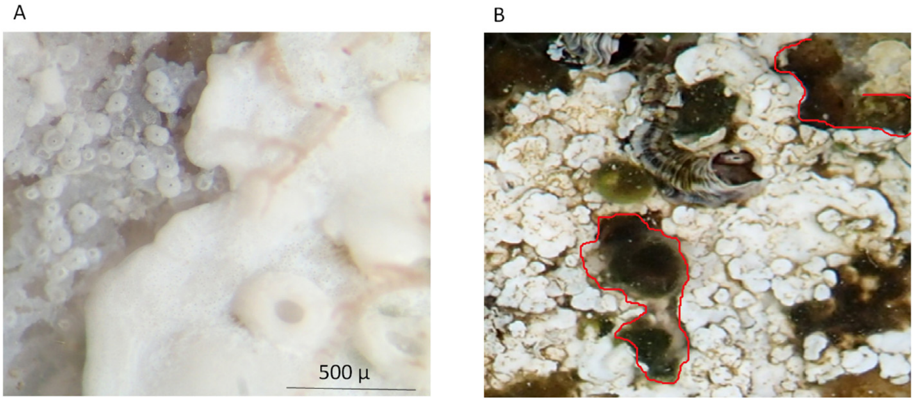

Fig. 6. Possible competitive interactions. A: *N. brassica-florida* (right) encroaching on *Hydrolithon* sp. (left) in a plate deployed in May 2015 and retrieved in November 2016 (6 months later). This pattern was seen in many plates (also in the three-month extraction set with a high proportion of free space), where usually *Hydrolithon* was encroached by *Neogoniolithon*. B: Margins of *N. brassica-florida* (red lines) stopping just at the perimeter of hemispheric cyanobacteria (*Rivularia* sp.) on a plate deployed in November 2015 and retrieved in May 2017 (after 18 months). This could again indicate a competitive interaction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

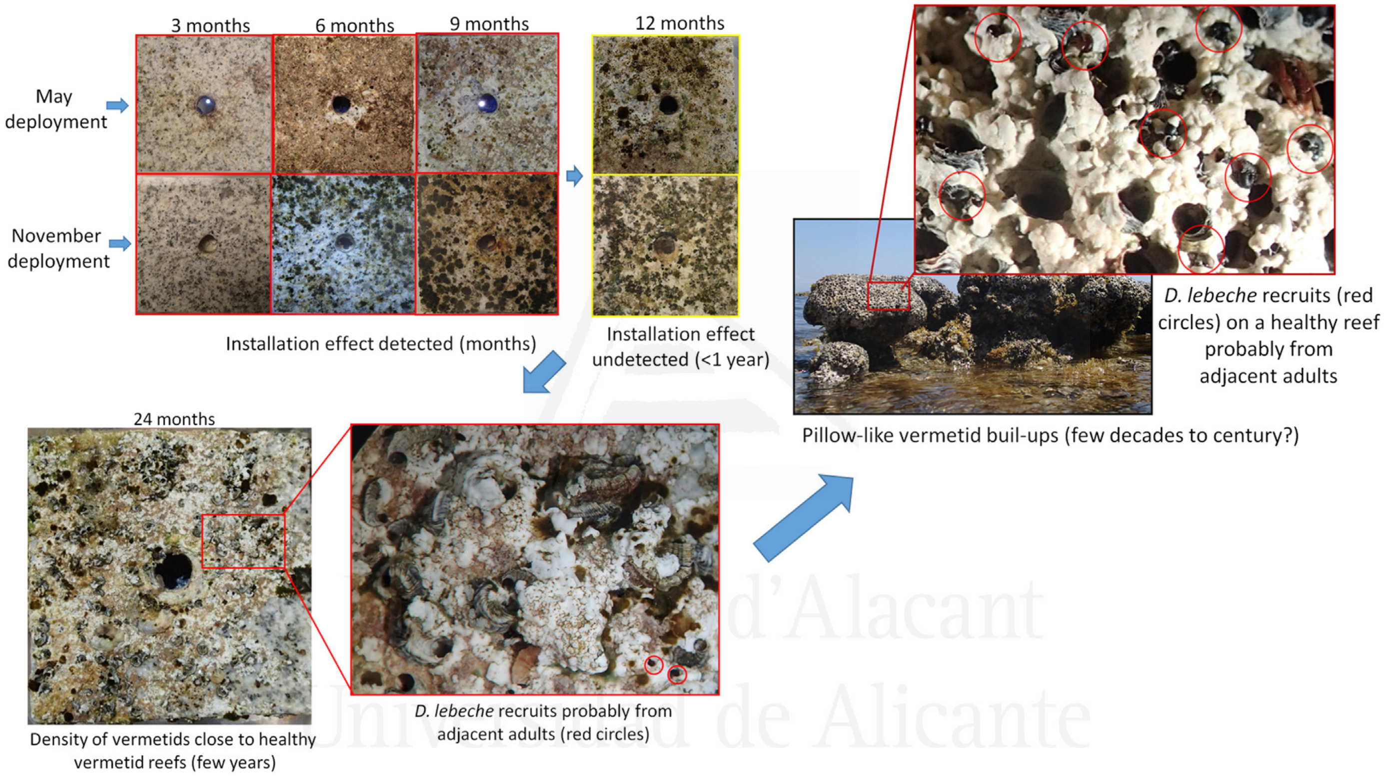

Fig. 7. Successional pattern showing representative plates (left) and the possible length of time at each stage. The effect of seasonal *installation time* was detected during the first nine-months. Plates removed at 24 months showed vermetid densities close to those reported in healthy Mediterranean vermetid reefs. Pillow-like formations (10–20 cm high) adjacent to the experimental set-up (right). According to the literature it takes from several decades to over a century to generate these bioconstructions. See text.

in shallow Rhodophyta concretions (< 5 m depth, Sartoretto et al., 1996 and references therein). It means that any build-up that is 10–15 cm high (easy to find in such reefs) takes at least several decades. However, the recruitment of both these engineering guilds on artificial plates is relatively easy to achieve without any disruption of the adjacent natural community. Artificial plates can thus be viewed as a source of recruits when restoration is required, particularly after anthropogenic drivers have affected and damaged these reefs to the extent they become discontinuous. Thus, when the anthropogenic impacts diminish, the artificial colonized plates can be transplanted as recruitment enhancers. This technique would permit the restoration of the reef, avoiding direct transplantation of pieces from healthy reef formations. The use of recruitment enhancer sources (instead of direct transplantation) deserves further study and application since it has proven successful in other Mediterranean habitat-forming communities threatened by anthropogenic pressures (Verdura et al., 2018).

5. Conclusions

Our results referring to an early succession on a vermetid reef point to general patterns already found in other studies on community succession. There is a significant seasonal effect on benthic succession, and the succession proceeds faster on plates deployed in May, coinciding with the putative recruitment window for the local engineering species. This seasonal effect is dampened in less than a year, when a convergent pattern is shown when both engineering species increase in cover. The high cover values of *N. brassica-florida* and *D. lebeche* on the older plates, along with the harmless effect of the settled plates on the vermetid reef, show that this technique could be applied in restoration procedures using the plates as recruitment enhancers.

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Appendix A

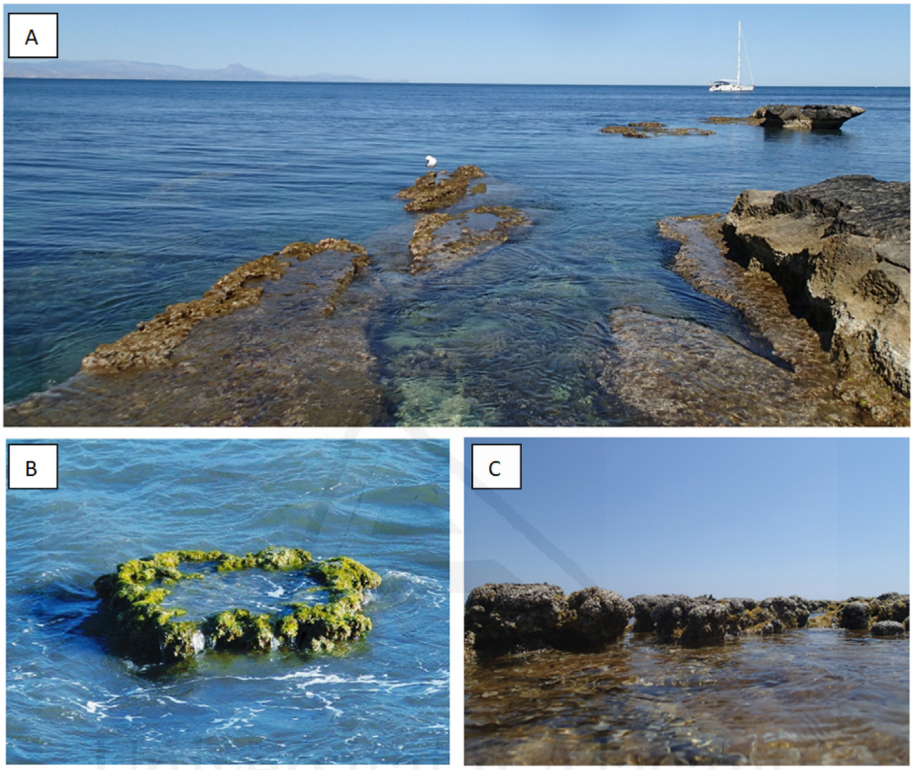

Fig. A.1. Different types of vermetid formations along Nueva Tabarca Island. An outer vermetid rim on calcarenitic platforms (A), a micro-atoll (B) and pillow-like outcrops on metagabbro rocks (C). (Photos: A, C: M Terradas Fernández, B: F Quijada).

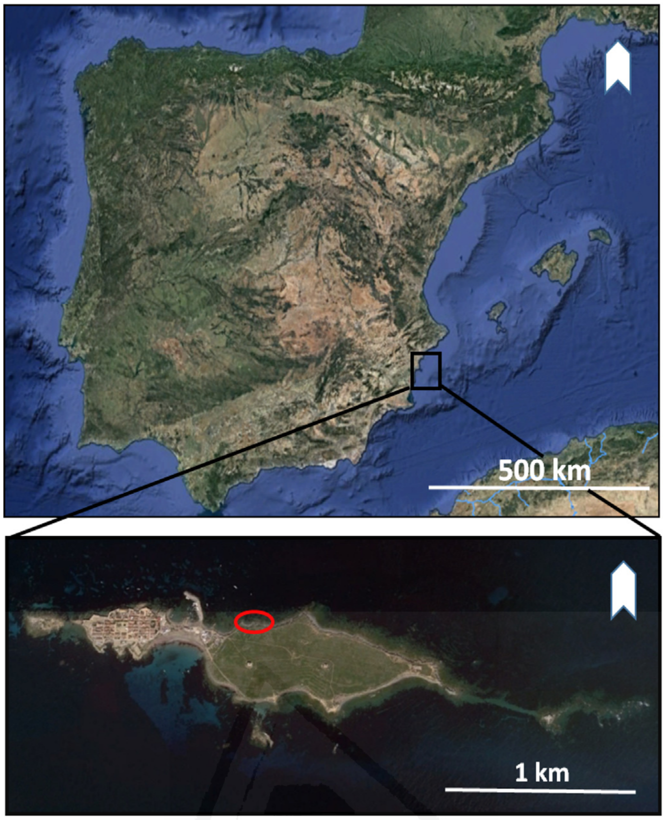

Fig. A.2. Study location (red circle) where the field experiment took place. Modified from Google Earth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

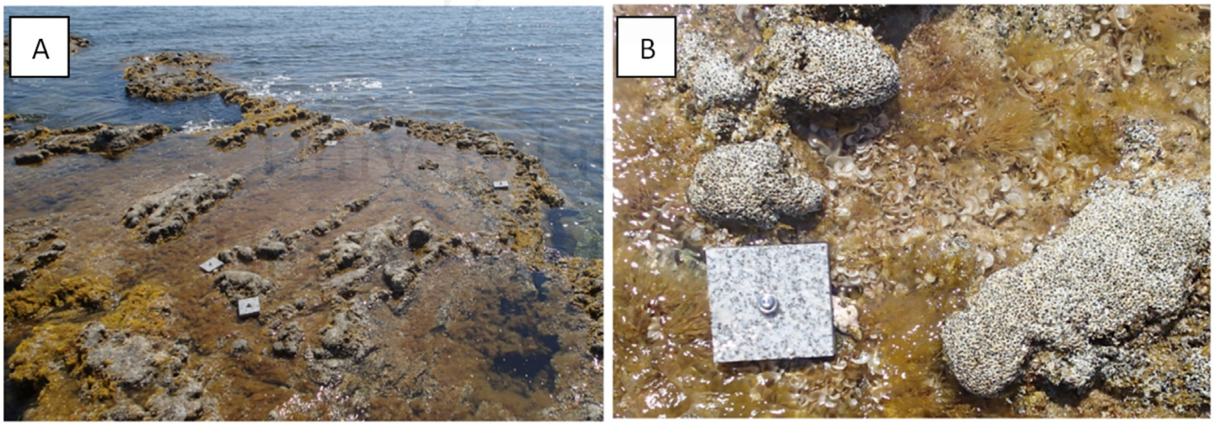

Fig. A.3. Plate sets adjacent to the pillow-like vermetid formations (A). The installation was set on the platform adjacent to the vermetid pillow-like formations, to avoiding damaging them (B).

Table A.1
Checklist for taxa recorded from plates per immersion period (months) at each installation month: A. May, B. November. Mean (% cover value), SE (standard error). There was only one plate left for the immersion period in the 18th month, from the set installed in November.

Immersion period	3		6		9		12		24	
Installation month	*May*		*May*		*May*		*May*		*May*	
Taxa	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Acinetospora crinita (Carmichael) Sauvageau					1.20	1.20				
Blennothrix lyngbyacea (Kützing ex Gomont) Anagnostidis & Komárek									0.28	0.28
Calohtrix spp.	2.51	1.26	9.84	4.38	5.91	2.87	4.04	1.20	6.25	3.75
Ceramium spp.					0.05	0.05	0.03	0.03	0.01	0.01
Chondria capillaris (Hudson) Wynne			0.43	0.43	0.01	0.01				
Chrococcales unidentified	0.57	0.57	2.98	1.62	4.05	2.35	4.83	2.84	6.31	4.13

(*continued on next page*)

Table A.1 (*continued*)

Immersion period	3		6		9		12		24	
Installation month	*May*		*May*		*May*		*May*		*May*	
Taxa	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Chroodactylon ornatum (Agardh) Basson							0.00	0.00		
Chthamalus stellatus (Poli, 1791)	0.03	0.03	0.32	0.30	0.10	0.10	0.28	0.20	0.11	0.08
Cladophora albida (Nees) Kutzing			0.00	0.00						
Cladophora dalmatica Kützing	0.00	0.00	0.03	0.02	0.84	0.56			0.01	0.01
Cladophora sp.	0.01	0.01								
Corallinaceae unidentified									0.14	0.14
Dendropoma lebeche Templado et al., 2016	0.20	0.14	0.24	0.12	0.28	0.14	1.65	0.60	10.42	4.00
Bacillariophyceae unidentified			0.25	0.25	0.23	0.23	0.94	0.94		
Dictyota sp.	0.10	0.10			0.91	0.56				
Dictyota fasciola (Roth) Lamouroux									1.79	1.79
Dictyota mediterranea (Schiffner) Furnari							6.70	6.70		
Entophysalis sp.									4.80	4.80
Feldmannia irregularis (Kützing) Hamel					4.79	4.79				
Foraminifera unidentified			0.13	0.12						
Gelidiella lubrica cf.									0.80	0.80
Gelidiella sp.							0.04	0.04		
Hydrolithon cruciatum (Bressan) Chamberlain	1.72	0.82	7.52	3.71	0.30	0.18	0.13	0.13		
Hydrolithon boreale cf.	0.35	0.20	0.53	0.32	0.00	0.00			0.24	0.24
Hyella sp.			0.12	0.12						
Isactis plana Thuret ex Bornet & Flahault			0.12	0.10						
Jania adhaerens Lamouroux	0.01	0.01	0.43	0.39	0.10	0.05	0.08	0.08	3.38	3.38
Laurencia sp.	0.02	0.00			0.38	0.24			0.80	0.78
Lophosiphonia spp.	1.15	0.36	9.59	7.25	0.79	0.29	3.14	1.83	0.39	0.23
Lyngbya spp.	0.32	0.25	2.56	0.64	1.05	0.25	0.15	0.15	1.49	0.81
Nemacystus flexuosus (Agardh) Kylin					0.02	0.02				
Neogoniolithon brassica-florida (Harvey) Setchell & Mason	11.79	9.40	53.02	2.32	65.99	9.93	65.24	14.40	37.01	9.34
Oscillatoria sp.							0.03	0.03	0.59	0.30
Padina pavonica (Linnaeus) Thivy			0.17	0.14	0.10	0.05	6.02	6.02	0.15	0.15
Palisada tenerrima (Cremades) Serio, Cormaci, Furnari & Boisset			0.03	0.03			0.04	0.04		
Patella sp.					0.08	0.08	1.03	1.03	0.54	0.54
Phaeophila dendroides (Crouan & Crouan) Batters	0.38	0.19	8.06	5.45	5.41	1.30	2.64	0.92	1.46	0.76
Polysiphonia opaca (C.Agardh) Moris & De Notaris	0.44	0.44	2.16	2.16	3.34	1.62	0.85	0.85	0.30	0.15
Polysiphonia sp.	0.02	0.02								
Rivularia spp.	0.80	0.47	1.11	0.80	3.85	0.33	12.57	6.12	6.85	3.38
Scytosiphon sp.					0.01	0.01				
Sphacelaria spp.			0.56	0.33	1.13	0.69	0.03	0.03		
Spirorbinae unidentified	0.01	0.01	0.02	0.02	0.01	0.01	0.00	0.00		
Stylonema alsidii (Zanardini) Drew			0.12	0.12						
Titanoderma pustulatum (Lamouroux) Nägeli	0.06	0.06			0.17	0.17				
Vermetidae *unidentified*			0.32	0.27	0.04	0.04	0.02	0.02	0.05	0.05
Vermetus triquetrus Bivona-Bernardi, 1832			4.30	3.86	3.07	3.07	2.56	0.99	5.00	2.68

B

Immersion period	3		6		9		12		18	
Installation month	*Nov*		*Nov*		*Nov*		*Nov*		*Nov*	
Taxa	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Anadyomene stellata (Wulfen) Agardh					0.02	0.02				
Anotrichum sp.							0.01	0.01		
Blennothrix lyngbyacea (Kützing ex Gomont) Anagnostidis & Komárek							0.18	0.18		
Brachytrichia sp.					1.71	1.71	3.37	3.20	2.88	-
Calohtrix spp.	0.08	0.03	2.61	1.89	10.41	4.57	17.73	5.16	13.07	-
Ceramium ciliatum (Ellis) Ducluzeau							0.01	0.01		
Ceramium siliquosum (Kützing) Maggs & Hommersand							0.02	0.01		
Chondria capillaris (Hudson) Wynne					0.01	0.01	3.47	3.47		
Chrococcales unidentified	0.06	0.06	0.31	0.16	5.28	2.51	1.52	1.31	2.38	-
Chroodactylon ornatum (Agardh) Basson										
Chthamalus stellatus (Poli, 1791)	0.04	0.04	0.13	0.10	0.09	0.02	0.19	0.07	0.44	-
Cladophora dalmatica Kützing	0.01	0.01			0.11	0.06	0.08	0.06		
Corallinaceae unidentified	0.11	0.10	0.01	0.01	0.17	0.13	4.58	4.49		
Cystoseira sp.							0.00	0.00		
Dendropoma lebeche Templado et al., 2016			0.02	0.02	0.28	0.09	1.34	0.59	3.93	-
Bacillariophyceae unidentified	0.01	0.01					0.46	0.46		
Dictyota fasciola (Roth) Lamouroux									0.03	-
Entophysalis sp.			0.71	0.71			3.25	3.25	1.38	-
Feldmannia irregularis (Kützing) Hamel							0.03	0.03		
Feldmannia sp.					0.20	0.20				

(*continued on next page*)

Table A.1 (*continued*)

B

Immersion period	3		6		9		12		18	
Installation month	*Nov*		*Nov*		*Nov*		*Nov*		*Nov*	
Taxa	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Gayliella flaccida (Harvey ex Kützing) Cho & McIvor					0.01	0.01				
Hydrolithon cruciatum (Bressan) Chamberlain					0.01	0.01	1.52	0.41	0.02	-
Hydrolithon farinosum (Lamouroux) Penrose & Chamberlain							0.24	0.16		
Hydrolithon boreale cf.	0.05	0.05	0.22	0.22	0.00	0.00	0.11	0.11	0.28	-
Jania adhaerens Lamouroux	0.01	0.01			0.01	0.01	0.40	0.38		
Kuetzingiella battersii (Bornet ex Sauvageau) Kornmann	0.03	0.03								
Laurencia sp.					0.00	0.00	0.16	0.15		
Lophosiphonia spp.					0.93	0.26	1.23	1.03		
Lyngbya spp.	0.06	0.05	0.01	0.00	0.71	0.09	1.85	1.15	2.38	-
Neogoniolithon brassica-florida (Harvey) Setchell & Mason					0.69	0.34	23.03	8.75	24.88	-
Padina pavonica (Linnaeus) Thivy							0.13	0.06		
Phaeophila dendroides (Crouan & Crouan) Batters	0.06	0.04			2.15	1.53	1.71	1.23	1.19	-
Polysiphonia opaca (Agardh) Moris & De Notaris							3.97	3.03	2.67	-
Polysiphonia scopulorum Harvey					0.30	0.23	1.15	1.15		
Polysiphonia sp.							0.03	0.02		
Rivularia spp.	0.07	0.00	7.34	4.22	21.47	2.03	16.66	3.75	7.15	-
Scytosiphon sp.	0.01	0.01								
Sphacelaria spp.							0.03	0.03		
Spirorbinae unidentified	0.02	0.02			0.00	0.00	0.00	0.00	0.14	-
Titanoderma pustulatum (Lamouroux) Nägeli							0.07	0.07		
Vermetidae *unidentified*			0.02	0.02	0.03	0.03	0.04	0.04		
Vermetus triquetrus Bivona-Bernardi, 1832					0.07	0.07	0.49	0.49	1.00	-

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Title: Response to small pulse disturbances of phytobenthos on vermetid platforms with distinct ecological status.

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Abstract

Succession was evaluated in macroalgal assemblages on shallow vermetid platforms with distinct ecological status at two different starting points in the year. Using cleared and unmanipulated control plots, we simulated small pulse disturbances from which the succession starts. The possible effect of position on the platform was also considered by sampling in two parallel inner and outer zones. Clearings were performed at two different times, in October and May, and the study lasted 20 months. The growth of opportunistic ephemerals was higher in the low status condition. Additionally, results showed that assemblages in cleared plots tended to converge to control ones before the end of the study regardless of their ecological status. Specifically, similarities between controls and cleared plots were achieved faster when clearing treatments were carried out in the inner zones or during May in the outer ones. This is due to the growth of opportunistic and stress-tolerant species in control and cleared plots under harsher conditions. Different species and morpho-functional groups could play complementary roles in situations

that differ by their ecological status . The acute seasonality of the main species strengthens the determinism found in both ecological situations after small pulse disturbances.

Introduction

Understanding structuring mechanisms that shape assemblages is a key goal in ecology. A good starting point can be creating controlled and replicable gaps within assemblages. This simulates natural disturbances that frequently affect communities allowing the study of secondary succession (Vance, 1988; Farrell, 1991). On shallow rocky shores such gaps are usually produced by wave action (Shanks & Wright, 1986; Seymour et al., 1989), grazing (Sousa et al., 1981; Sala & Boudouresque, 1997) and emersion periods (Stewart, 1989; Bertocci et al., 2007). Local or geographical factors such as battering by drift logs (Dayton, 1971), ice scouring (Pugh & Davenport, 1997) or substrate fracturing (Foster, 2003) can also be relevant, along with some anthropogenic disturbances like trampling (Keough & Quinn, 1998; Milazzo et al., 2004). When these gaps are relatively low in intensity and frequency, the inherent properties of the community are barely altered (Margalef, 1977). Thus, experiments dealing with relatively small pulse disturbances can help evaluate and compare resilience among communities, while leaving important previous community properties unaltered (population structure, recruitment supply). However, abiotic factors (light, temperature, nutrients) usually show a seasonal pattern, conditioning resilience depending on when a disturbance takes place, not only in temperate seas (Serisawa et al., 1998; Kim et al., 2017) but also in tropical ones (Hutchinson & Williams, 2003; Mayakun et al., 2010). Moreover, depending on the season when a pulse disturbance occurs, different priority effects could drive the community towards possible “multiple stable” or “transient stable” points (Fukami, 2015). These priority effects are intensified when such disturbances coincide with the recruitment period of either the main canopy-forming species or their competitors (Benedetti-Cecchi, 2000; Menge et al., 2017).

As Kim et al. stated (2017), there is a need to identify habitat-specific patterns of community resilience in rocky shores. This is not only important for basic research but can also improve the management of natural heritage.

The present study focuses on vermetid platforms, a distinctive habitat on warm Mediterranean seashores (Pérès & Piccard, 1964; Safriel, 1975; Kelletat 1997). Vermetid abrasion platforms, largely ignored until recently, especially in the western basin (Milazzo et al., 2016), have some attributes, beyond their accessibility, which facilitate studies into the role of abiotic disturbances as drivers in rocky shores. Thus, due to their extremely shallowness, grazing seems to be a minor driver, since large macrograzers are usually only found in pools, crevices and deeper refugia. Correlational studies carried out in such systems appear to point to bottom-up processes as being more important drivers than top-down ones (Einav et al., 1998; Terradas-Fernández et al., 2018). By contrast, in deeper subtidal systems, both processes seem to be relevant (Hereu et al., 2008), as in intertidal assemblages (Benedetti-Cecchi, 2000). Thus, we can assume that grazing pressure is highly attenuated in such a way that the effects of interaction between grazing and abiotic disturbances could be low. However, this should be tested experimentally.

The platform flatness allows the recruitment of many subtidal algae that thrive over the entire platform. These algae are rarely exposed to emersion periods in other geographical areas (Chappuis et al., 2014; Cefalí et al., 2016). However, they are affected by recurrent long-lasting emersion events in these systems (Einav & Israel., 2007; Zamir et al., 2018). Besides, subtidal algae are usually distributed in parallel to the shore, forming wider belts or zones than those usually found on the littoral fringe of tideless seas like the western Mediterranean (Mariani et al., 2016). All this facilitates the manipulative experimentation of each belt. Hydrodynamism, usually more intense towards the outer margin, and depth seem to be the main components of the environmental gradient driving such a zonal pattern. Thus, large canopy-forming fucoids thrive especially on the outer exposed margins (or in deep poles and crevices), whereas lower laying algae such as *Dictyota* spp. and *Padina pavonica* (Linnaeus) Thivy are distinctive on the mid-platform and the innermost zones, respectively (Einav et al., 1998; Terradas-Fernández et al., 2018). Besides, such platforms show an acute seasonal pattern with different macroalgal groups dominating according to the time of the year. Thus, during summer and autumn stress-tolerant species such as articulated corallines gain quantitative importance, whereas corticated dictyotacean are more abundant during winter and spring (Terradas-Fernández et al., 2018).

Vermetid platforms are also affected by many anthropogenic stressors as is distinctive of upper subtidal assemblages (Pinedo & Ballesteros, 2019). These pressures have produced a critical decimation of such natural heritage in recent years, encompassing large geographical areas where their existence is threatened (Galil, 2013; Badredine et al., 2019). These changes include a phase shift where vermetid rims and macroalgal pristine communities are replaced by opportunistic and stress-tolerant species (Badredine et al., 2019). The Southeastern Iberian Peninsula hosts paradigmatic examples of such seascapes, especially on limestone shores (Terradas-Fernández, 2018). Vermetid platform regression can also be detected, especially in urban areas, probably due to persistent eutrophication and other anthropogenic stressors (Aranda et al., 1994; Ramos-Esplà et al., 2008; Terradas-Fernández et al., in prep.).

The objective of this study is to evaluate succession, after a small pulse disturbance, of the most abundant assemblages on vermetid platforms showing distinct ecological status. The annual timing when the pulse disturbance takes place and its position related to the outer platform margin are also assessed.

Materials and methods

Experimental design

The current study was carried out at two locations close to Alicante (SE Spain): Cabo de las Huertas (38°21'10.22''N, 0°25'06.04''W) and Playa de Aguamarga (38°18'06.21'' N 0°31'05.08'' W) (Fig. 1). Both locations have shallow abrasion platforms which are differentiated by their ecological status. Cabo de las Huertas has a high ecological status with fucoid algae and vermetid reefs dominating the outer margin of the platforms (Terradas-Fernández et al., 2018). On the contrary, Playa de Aguamarga have platforms dominated by articulated corallines, Ulvacean algae and other taxa distinctive of low ecological status (Ballesteros et al., 2007). In addition, they are depleted of vermetid reefs, and only some scattered dead remnants show their existence in the recent historical past. This low status is attributed to the influence of the Port of Alicante and seawage outfalls discharge close to Aguamarga (Aranda et al., 1994).

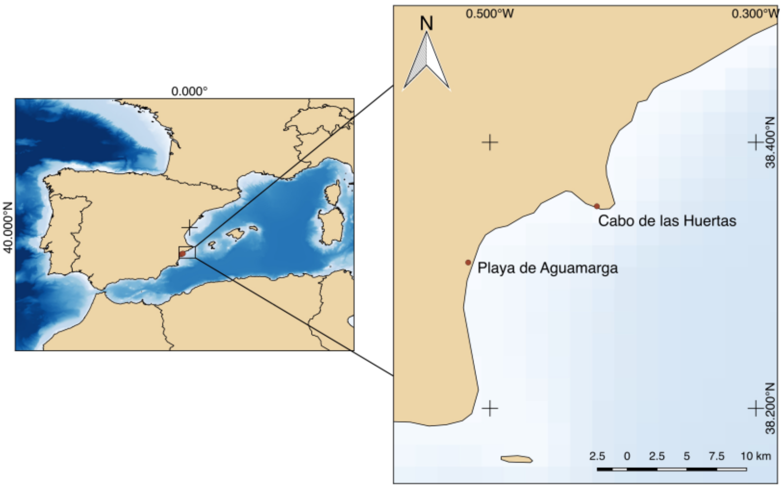


Fig. 1 Locations included in this study. Playa de Aguamarga, south of Alicante city, has a low ecological status. Conversely, Cabo de las Huertas (Cap de l'Horta) located just north from Alicante houses assemblages of good ecological status.

During autumn 2016, prior to the study, the assemblages to be studied were checked. In both locations, two main zones or seaweed belts were distinguished, over the entire platform width (ca. 8 m), according to the macroalgal dominant groups: an inner platform zone and a mid-platform zone. A third outer zone dominated by vermetid reefs was also distinguished in Cabo de las Huertas. However, this outer zone was not included in the study. In Cabo de las Huertas, the inner zone of the platform (ca. 2 m width) was dominated by articulated corallines of the genus *Jania* Lamouroux along with the *Laurencia* complex (mainly *Palisada tenerrima* (Cremades) Serio et al.) and *Padina pavonica* (Linnaeus) Thivy. The mid-platform zone (ca. 5 m width) was dominated by *Jania* spp. and Dictyotacean algae (*P. pavonica*, *Dictyota* spp.). In Aguamarga, both zones show similar widths to Cabo de las Huertas, and were dominated by *Ellisolandia elongata* (Ellis & Solander) Hind & Saunders and *Ulva* spp (the latter was more abundant in the inner zone). Another important group found in both locations consisted of unidentifiable turf comprising small filamentous algae. This turf was considered as an operative group despite its taxonomic heterogeneity (including Ceramiales, Ulvales, Cladophorales, Erythropeltidales and other small caespitose algae).

We established various trials in these two zones. Each trial consisted of eight plots of which four were untreated controls, and four were cleared using a hammer and chisel to create a pulse disturbance in the community. After clearing, only bare space was recognizable to the naked eye (without ruling out the persistence of some very small thalli and crusts). Every plot (25 × 25 cm) was one to two meters apart from each other. Control and cleared plots were randomly distributed in every trial. Using epoxy-putty (IVERGOR), plots were marked at their corners. Taxa cover and bare space were estimated using a frame of 20 × 20 cm with 25 sub-quadrats. In each sub-quadrat, a score was given from 0 to 4 following the criteria of Dethier et al. (1993).

In October 2016, one trial was established in the inner zone of both locations, and the same was carried out in May 2017. As for the mid-platform zones, trials were set up in October 2017 and May 2018 respectively. In each trial, the sampling started two months after the clearing treatment and lasted 18 months (20 months since the clearing treatment). The sampling frequency was monthly until the sixth month after the clearing treatment. From then onwards, the sampling frequency was approximately quarterly.

Additional sampling was carried out during January 2017 in the inner zone from Aguamarga because a bleaching event was detected, which provided an opportunity to evaluate the recovery pattern of the affected plots.

Data analysis

To evaluate differences between assemblages of treated and control plots over time, a multivariate PERMANOVA test was carried out on the untransformed data of coverage for every taxon (Anderson et al., 2008). Factors considered were *treatment* with two levels: control and cleared plots; *location* with two levels: affected location and unaffected location; *zone* with two levels: inner zone and mid-platform zone; *trial timing* with two levels: October and May. For simplicity, *time* since pulse treatment was considered according to five intervals as follows: 2 months since treatment, 3 - 4 months since treatment, 5 - 8 months since treatment, 9 - 15 months since treatment, 16 - 20 months since treatment. All factors were considered as fixed. *A posteriori* pairwise test was carried out regarding the largest significant term for pairs of levels of factor *treatment.*

Taxa responsible for differences among treatment levels were identified using SIMPER analysis (Table S1). Those taxa with cumulative contributions with up to 90 % similarity were further evaluated individually by univariate PERMANOVA test from a Euclidean distance matrix, using the same factorial design. *A posteriori* pairwise test was also carried out.

These taxa were plotted with error bars incorporated (mean ± SE). Analyses were run using PRIMER 7 and PERMANOVA+ software (Clarke and Gorley, 2015). Scatter plots were performed using SigmaPlot 10.0.1.

Results

Regarding species composition, all fixed factors showed an interaction according to the permutational multivariate analysis (($P < 0.05$), Table 1). Both locations recovered fast from the clearing treatments, and a convergence pattern with the controls was detected. In all cases, significant *treatment* effects were undetectable in the oldest-aged plots.

In the October trials, the inner zones recovered faster than the mid-platform ones, especially in Cabo de las Huertas where significant differences were only shown in the first interval (2 months since treatment). In Aguamarga, such differences lasted until the second interval (3 - 4 months since treatment). As for the mid-platform zones, such differences were maintained until the third interval (5 - 8 months since treatment) in both locations.

Those plots from the May trials, in both zones and in both locations, showed significant differences in the first interval. In some plots, significant differences reappeared, especially in the mid-platform zones, coinciding with optimum growth for the Dictyotacean and *E.elongata* in Cabo de las Huertas and Aguamarga, respectively.

In order to better understand the algal abundance patterns, we describe them below for every experimental trial separately. The main significant differences between cleared plots and the control ones are commented (*P* < 0.05, Fig. 2, Table 1). Differences found between the main taxa are also described (Table S2).

Table 1 A) Results of distance-based permutational multivariate analysis PERMANOVA using *treatment* (Tr), *time* since pulse treatment (Ti), *trial timing* (Se), *location* (Lo) and *zone* (Zo) as fixed factors. Df, degrees of freedom; SS, sums of squares; MS, mean squares; Pseudo-F, pseudo-*F* ratio; t, pseudo-*t* statistic; P(perm), permutation *P*-value. **B)** Results of pairwise analyses from the term 'TrxTixSexLoxZo' for pairs of levels of factor *treatment*. P(MC), Montecarlo *P*-value. Significant P(perm) and P(MC) values are in bold.

A)

Main Test

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	15393	15393	13.858	**0.001**	996
Ti	4	46787	11697	10.53	**0.001**	996
Se	1	29098	29098	26.197	**0.001**	998
Lo	1	458700	458700	412.97	**0.001**	998
Zo	1	61307	61307	55.194	**0.001**	998
TrxTi	4	10298	2574.5	2.3178	**0.001**	999
TrxSe	1	4459.6	4459.6	4.015	**0.001**	999
TrxLo	1	15784	15784	14.21	**0.001**	998
TrxZo	1	8983.3	8983.3	8.0877	**0.001**	997
TixSe	4	131310	32828	29.555	**0.001**	999
TixLo	4	38608	9652	8.6897	**0.001**	999
TixZo	4	42297	10574	9.5199	**0.001**	998
SexLo	1	13323	13323	11.994	**0.001**	997
SexZo	1	8076.2	8076.2	7.271	**0.001**	998
LoxZo	1	73273	73273	65.967	**0.001**	997
TrxTixSe	4	8190.9	2047.7	1.8436	**0.006**	998
TrxTixLo	4	14453	3613.1	3.2529	**0.001**	998
TrxTixZo	4	7813	1953.3	1.7585	**0.007**	999
TrxSexLo	1	2418.4	2418.4	2.1773	**0.027**	998
TrxSexZo	1	4158.3	4158.3	3.7437	**0.002**	999
TrxLoxZo	1	10475	10475	9.4305	**0.001**	999
TixSexLo	4	61857	15464	13.922	**0.001**	999
TixSexZo	4	39240	9810.1	8.832	**0.001**	997
TixLoxZo	4	34359	8589.7	7.7333	**0.001**	998
SexLoxZo	1	8973.4	8973.4	8.0787	**0.001**	999
TrxTixSexLo	4	8160	2040	1.8366	**0.007**	999
TrxTixSexZo	4	5245.6	1311.4	1.1807	0.234	998
TrxTixLoxZo	4	4999.4	1249.9	1.1252	0.311	998
TrxSexLoxZo	1	4171.6	4171.6	37556	**0.001**	998
TixSexLoxZo	4	24761	6190.2	5.573	**0.001**	998
TrxTixSexLoxZo	4	7063.3	1765.8	1.5898	**0.029**	999
Res	563	625350	1110.7			

B)

Pairwise Test	October setting (Inner Zone)		October setting (Mid Zone)		May setting (Inner Zone)		May setting (Mid Zone)	
	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	**0.02**	**0.006**	**0.004**	**0.002**	**0.036**	**0.032**	**0.029**	**0.028**
3-4 months	0.084	**0.002**	**0.004**	**0.005**	0.094	0.060	0.728	0.337
5-8 months	0.094	0.799	**0.013**	**0.001**	0.078	0.129	**0.038**	**0.049**
9-15 months	0.236	0.329	0.088	0.37	**0.050**	0.552	0.227	0.242
16-20 months	0.17	0.657	0.235	0.234	0.455	0.323	0.103	0.711

Temporal pattern in the control plots from inner trials

Cabo de las Huertas

Control plots showed an acute temporal pattern analogous in both trials. The group of *Jania* spp. was most abundant during mid-summer and autumn months attaining cover values over 60 %, while the remaining algal groups (mostly *P. pavonica* and the *Laurencia* complex) showed fewer fluctuations over the year with cover below 40%. The low values of *Jania* spp. coincided with high values of bare space. Small individuals of fucoid algae (dominated by *Cystoseira humilis* Schousboe ex Kützing) were more abundant during spring and early summer months with a higher spike in May 2018.

Aguamarga

In the control plots, *Ulva* spp. showed higher cover in mid-winter and spring months, when it became dominant in some cases. By contrast, *E.elongata* was dominant during autumn and early winter months occupying most of the substrate. The group of *Jania* spp. showed a similar pattern as the one in Cabo de las Huertas, more abundant in summer and autumn months. However, the high spikes in Cabo de las Huertas were not found in Aguamarga. Thus, possible interactive effects with *E. elongata* or *Ulva* spp. cannot be ruled out. Major bleaching events ocurred in early winter during 2017 and 2018. In 2017, twenty days after the first bleaching event, *E. elongata* recovered attaining cover close to previous levels (Fig. S1, Fig. S2).

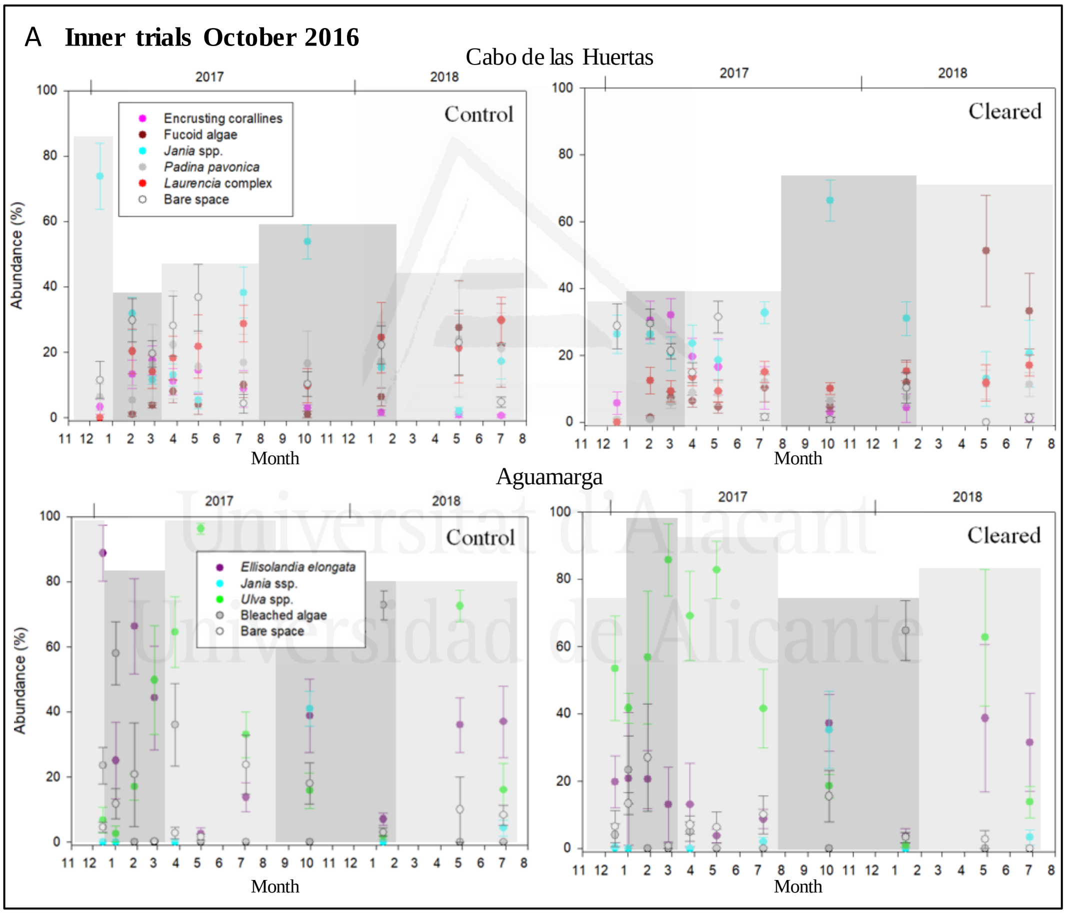
Temporal pattern in the control plots from Mid-platform trials

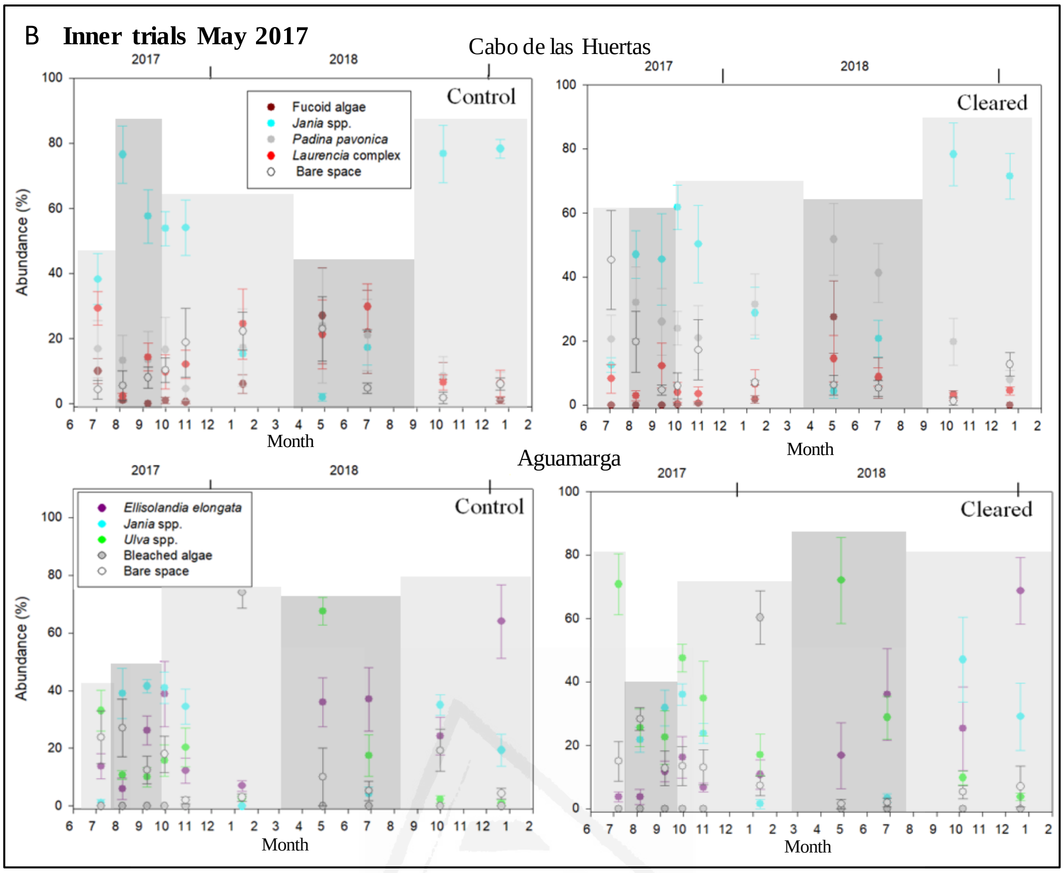
Cabo de las Huertas

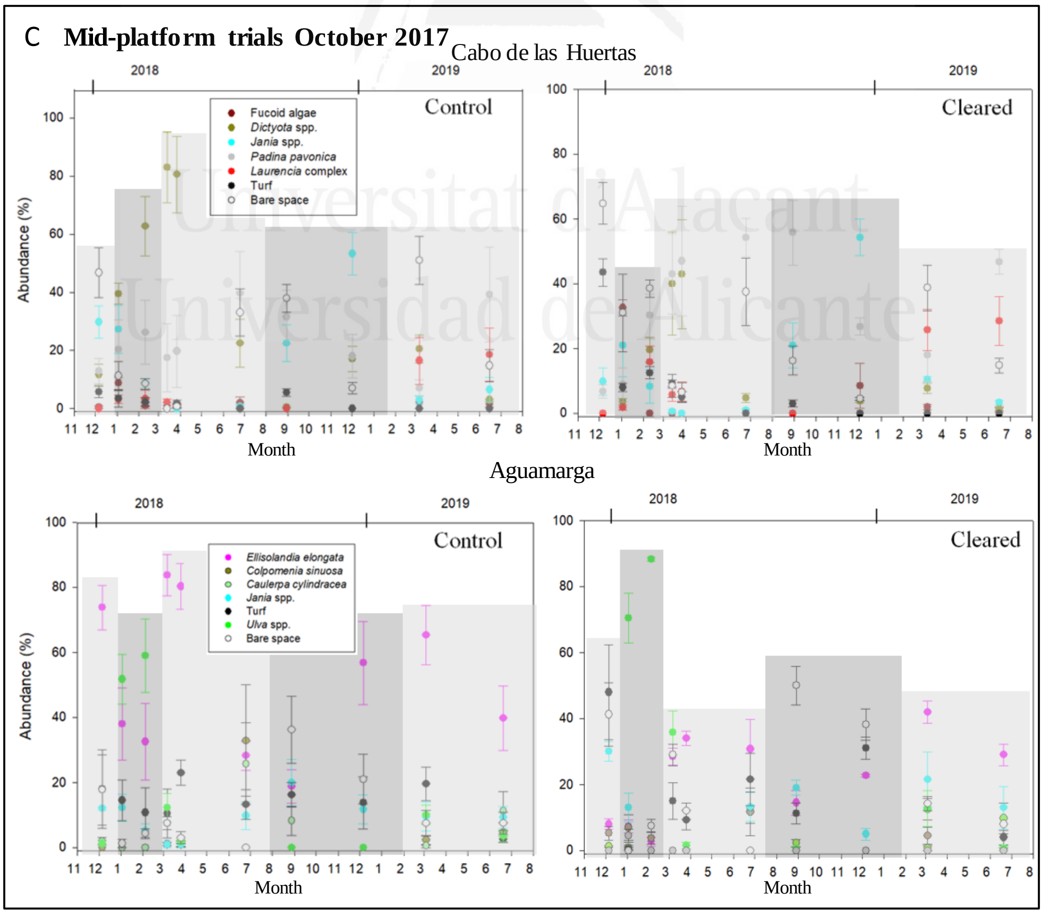
The group of *Dictyota* spp. grew during winter and spring 2018 attaining values of over 80 % cover with a substantial decrease in summer and almost nil values during autumn. There was a slight recovery during 2019 but showing lower values than the previous year. *Padina pavonica* was easily detectable during all the annual cycle with higher values during summer months (ca. 40%). As for *Jania* spp., this group was more abundant from late summer to early winter. The *Laurencia* complex showed moderate values (below 20 %) and turf algae always had low cover, though it was more abundant in July and December 2019. Bare space exhibited higher values when the main canopy forming species such as *Dictyota* spp., *Jania* spp. or *Padina pavonica* were at low values.

Aguamarga

Ellisolandia elongata showed higher values in winter and spring (over 60% cover). However, in January 2018, the low sea episode detected, affecting mostly the inner zone, coincided with an acute decrease in *E. elongata* in the mid-platform plots (however, bleaching in this zone was hardly detected at the time of the surveying). This decrease, probably due to the same low sea episode, was harnessed by *Ulva* spp. attaining levels of over 50 % cover. During March 2018, the cover values of *E. elongata* were restored. Thin articulated *Jania* spp. showed low abundance except in late summer and autumn months (over 40 % in August 2018). Turf rarely surpassed 20 % cover and *Colpomenia sinuosa* (Roth) Derb. et Sol spikes in July 2018, with values close to 40 % and then decreasing abruptly onwards. The alien species *Caulerpa cylindracea* Sonder also showed a peak in summer 2018 and was codominant with *Jania* spp. in August of the same year. It showed a decrease during autumn and reappeared in 2019 (April) though showing low cover. Bare space occupied higher values during autumn months and showed moderate to low values in the rest of the surveys.




B Inner trials May 2017
Cabo de las Huertas
2017
2018
Control
Cleared
Fucoid algae
Jania spp.
Padina pavonica
Laurencia complex
Bare space
Abundance (%)
100
80
60
40
20
0
6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2
Month
Aguamarga
Control
Cleared
Ellisolandia elongata
Jania spp.
Ulva spp.
Bleached algae
Bare space
Abundance (%)
Month


C Mid-platform trials October 2017
Cabo de las Huertas
2018
2019
Control
Cleared
Fucoid algae
Dictyota spp.
Jania spp.
Padina pavonica
Laurencia complex
Turf
Bare space
Abundance (%)
100
80
60
40
20
0
11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8
Month
Aguamarga
Control
Cleared
Ellisolandia elongata
Colpomenia sinuosa
Caulerpa cylindracea
Jania spp.
Turf
Ulva spp.
Bare space
Abundance (%)
Month

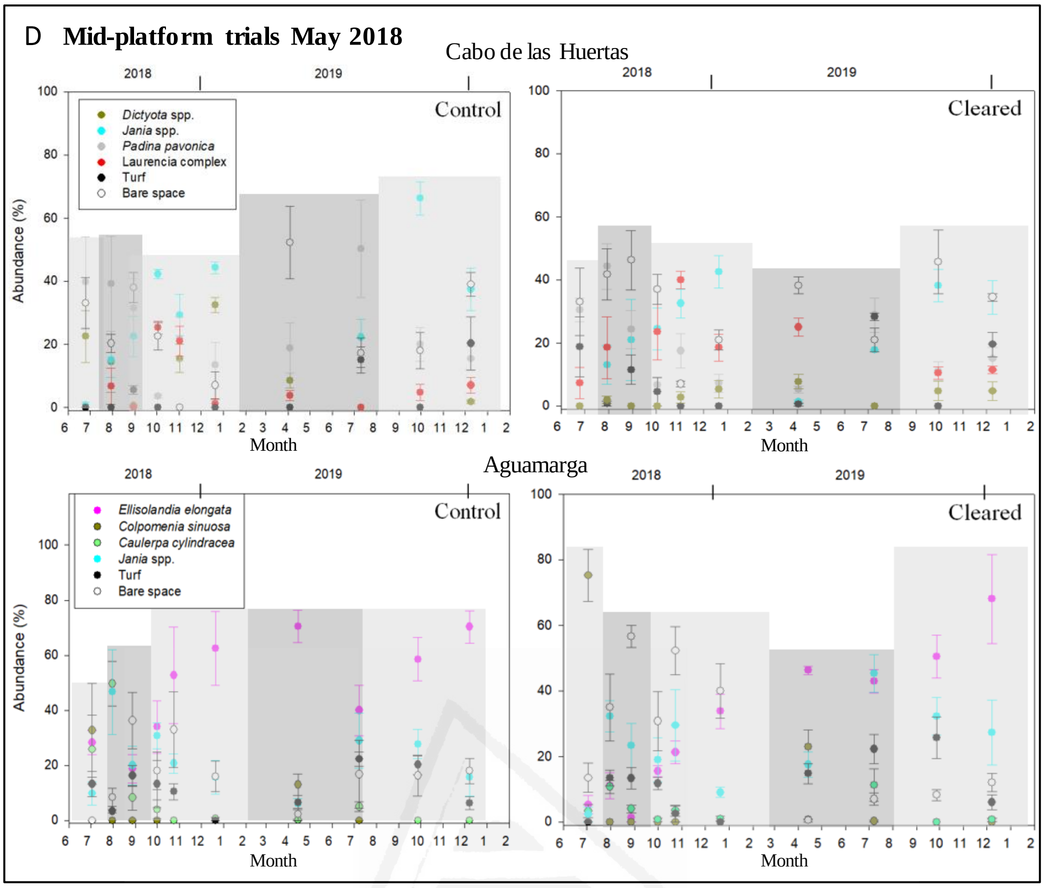


Fig. 2 The abundance pattern of the main algal groups in each trial: A inner trials set up in October 2016, B inner trials set up in May 2017, C mid-platform trials set up in October 2017, D mid-platform trials set up in May 2018. Each grey gamma represents each one of the five-time intervals analyzed. All the results are shown as a mean and standard error (mean ± SE).

Differences between cleared and control plots from inner trials set up in October 2016

Cabo de las Huertas

Significant differences in assemblage composition were only shown in the first interval (2 months since treatment, Table 1B). The dominant *Jania* spp. only showed significantly lower cover in the cleared plots than in the control ones for the first interval. Encrusting corallines, with higher cover in the cleared plots, and the *Laurencia* complex, with higher cover in the control ones, showed differences during the second and third intervals respectively. *Padina pavonica* did not show differences between treatment levels.
Fucoid algae did not show significant differences between treatment levels despite having higher values in the cleared plots. As for bare space, it showed higher values at two months since the treatment in the cleared plots, with minor differences thereafter, despite its fluctuating temporal trend (Fig. 2A, Table S2).

Aguamarga

Significant differences in assemblage composition were shown until the second interval (3-4 months since treatment, Table 1B). In cleared plots, *E. elongata* presented very low coverages (below 25%) compared to the control ones during the same interval (until 4 months since the treatment) coinciding with winter months.

To the contrary, *Ulva* spp. showed higher values in the cleared plots than in the controls, in the same time frame. It occupied most of the space (over 50% cover) except during the bleaching event, in January 2017, when it showed a slight fall and a great deal of *Ulva* stands were bleached (Fig. S2). Neither *Jania* spp. nor bare space showed significant differences in cover between treatment levels (Fig. 2A, Table S2).

Differences between cleared and control plots from inner trials set up in May 2017

Cabo de las Huertas

There were significant differences in assemblage composition during the first interval (2 months since treatment) and marginal differences ($P = 0.05$) reappeared during the fourth interval (9-15 months since treatment, Table 1B). In the cleared plots, *Jania* spp. only showed significantly less abundance in the first interval. Again, *P. pavonica* did not show significant differences between treatment levels, but highest cover values were found in the cleared plots in late spring and summer months (well over 40% cover). As for the *Laurencia* complex, it showed significantly lower values in cleared plots than in the control ones during the first and third intervals. Fucoid algae did not show any treatment effect as encrusting corallines had almost nil values in cleared and control plots. Bare space only showed significantly higher values in the cleared plots during the first interval (Fig. 2B, Table S2).

Aguamarga

Significant differences in assemblage composition were only shown during the first interval (2 months since treatment, Table 1B). In cleared plots, *Ulva* spp. was more abundant up till the first three intervals (5-8 months since treatment) and especially in the first one (surpassing 60% cover). Significant differences reappeared in the last interval (16-20 months since treatment) despite *Ulva* spp. showing low cover values for both treatments. Weak marginal differences in *E.elongata* abundance were detected only during the first interval (2 months since treatment) ($P = 0.07$), whereas the thin articulated *Jania* spp. showed significantly lower values in the cleared plots at the second interval (3-4 months since treatment). Bare space only showed significant effects in the first interval (Fig. 2B, Table S2).

Differences between cleared and control plots from mid-platform trials set up in October 2017

Cabo de las Huertas

Differences in assemblage composition were significant until the third interval (5-8 months since treatment, Table 1B). Some algae showed significantly higher cover values in the cleared plots, among them, turf algae attained values over 40% at two months since the clearing (with nearly nil values in the control plots). Fucoid recruits (mainly *Cystoseira amentacea var. stricta* Montagne) showed a peak in early winter with cover values close to 40 % in January 2018 (being below 10 % in the control plots). Such differences were significant in January 2018 when all surveying months were taken separately as factor levels (data not shown), but still, such trend was perceived, yet not significant, in the second interval (3-4 months since treatment, $P = 0.14$; Fig. 2 C, Table S2). To the contrary, *Dictyota* spp. had significantly lower values in cleared plots in all but the last time interval. The thin articulated coralline group (*Jania* spp.) did not show differences between control and cleared plots and only minor differences were detected in the *Laurencia* complex. *Padina pavonica* showed higher marginally significant values in the cleared plots in the third interval ($P = 0.056$), coinciding with the spike of *Dictyota* in the control ones. Bare space showed higher values in the cleared plots in the third interval (5-8 months since treatment) (Fig. 2 C, Table S2).

Aguamarga

Differences in assemblage composition were significant until the third interval (5-8 months since treatment, Table 1B). In the cleared plots, *Ulva* spp. had significantly higher values in the second interval (3-4 months) surpassing 60% cover. Probably, its abundance was previously underestimated, being ascribed as turf. Cleared plots also showed higher abundance of *Jania* spp. in the first interval (up to 30 % cover) without any differences between treatment levels from then on. *Colpomenia sinuosa was* not detected in winter in the control plots, but it appeared, in low abundance, in the cleared ones so that differences were significant in the first and second intervals.

By contrast, *E. elongata* showed significantly lower values in the cleared plots until the third interval. However, when every month was considered as a separate factor level, such differences were significant during all the study period except in summer months (data not shown). As for the alien *C. cylindracea*, its values were significantly lower in the cleared plots with almost nil cover values. However, it peaked in the control ones during July and August 2018 with values over 30% cover. Bare space was significantly higher in the cleared plots during the third interval coinciding with an acute decrease in *Ulva* spp. and a moderate recover in *E. elongata* (Fig. 2 C, Table S2).

Differences between cleared and control plots from mid-platform trials set up in May 2018

Cabo de las Huertas

Differences between control and cleared plots were significant in the first interval (2 months since clearing) and in the third one (5-8 months since treatment, Table 1B). In both treatment levels, *Dictyota* spp. showed lower values than in the October trial. Such low cover of *Dictyota* spp. was more acute in the cleared plots where it never surpassed 10 % cover. The *Laurencia* complex had higher values in the cleared plots, such differences were significant from the third interval (5-8 months) onwards. *Padina pavonica* values were very close to those from the control ones, with no significant differences. The group of *Jania* spp. did not show differences between controls and cleared plots. Bare space showed significantly higher values at the cleared plots in the third interval coinciding with the moderate spike of *Dictyota* spp. in the control plots (Fig. 2 D, Table S2).

Aguamarga

Differences between control and cleared plots were significant in the first and third intervals (Table 1B). In cleared plots, *E. elongata* showed lower values than in the control ones with a recovery trend from the beginning to the end of the experiment. The first and third intervals were the only ones with significant differences regarding the control plots. As for the second interval, it is worth noting that coincided with summer months when *E. elongata* showed low values in both treatment levels.

In the case of *Jania* spp, no effect was detected. Conversely, *C. sinuosa* was benefited by the clearing treatment monopolizing the cleared plots during the first time interval. This alga disappeared one month later showing the same pattern found in the control plots thereafter. *Caulerpa cylindracea* showed lower values in the cleared plots with the same seasonal pattern as in the control ones. Finally, bare space showed significantly higher values in cleared plots during the first interval (2 months since treatment) and the third one (5-8 months). The second interval coincided with late summer months, when algal cover decreased in both treatment levels (Fig. 2 D, Table S2).

Discussion

Seasonal pattern

The seasonal pattern found in the unaffected location is in line with that already observed in shallow vermetid platforms (Terradas-Fernández et al., 2018). This pattern is generalizable to what occurs in shallow Mediterranean subtidal assemblages, where two main stages can be detected during a year: First, there is a community stage culminating at the end of a period when productivity potential is high and dominated by phaeophycean algae like Fucales or Dictyotaceae. Second, a subsequent community stage comes from a period of maximum stress when coralline algae gain quantitative importance. In shallow Mediterranean subtidal, the first stage is usually found in spring, whereas the second one usually occurs in autumn (Ballesteros, 1991).

In the altered location (Aguamarga), however, the phaeophycean stage is replaced by the dominance of thick articulated corallines, mainly *E. elongata,* as occurs in other littoral altered systems (Soltan et al., 2001; Pinedo et al., 2015; Pinedo et al., 2019). *Ellisolandia elongata* decreases in summer whereas *Jania* spp., along with other seasonal species like *C. sinuosa* and the alien *C. cylindracea,* increase their cover. The decrease in *E. elongata*, during summer, has been reported in other communities from the littoral fringe and could be produced by summer stress on *E. elongata* stands (Guerra-García et al., 2011; Bertocci et al., 2012; Terradas-Fernández et al., in prep.).

Bleaching events

In our study, bleaching events (due to prolonged emersion periods) were detected mainly in the inner zone. They affect mostly the location of Aguamarga, especially during winter, when low sea level episodes are more frequent in Western Mediterranean (Duarte et al., 1999). These episodes are even described in some literary works (Joan Maragall, 1891, *Les minves del Gener*; Josep Pla, 1984, *Els últims dies del Gener*) highlighting their historical recurrence. The lack of an outer vermetid healthy reef, able to retain water, may contribute (along with some slight differences with depth and platform slope) to the greater severity of such low sea episodes in Aguamarga than in Cabo de las Huertas (Fig. S1).The effect of the outer rim maintaining water within the platform, even at times of low sea episodes, has been already pointed out by Safriel (1975).

In the plots surveyed during January 2017, bleaching affected mostly the erect parts of *E.elongata* and *Ulva* spp.. Both species recovered in a few weeks from the regrowth of the basal living parts (Stewart, 1989; Einav et al., 1995; Zamir et al., 2018; Fig. S2).

The interannual fluctuations in the abundance of some taxa could also be conditioned by the intensity of low sea level episodes and mean sea level fluctuations between years. This could explain the low cover of *Dictyota* spp and the low abundance of fucoid recruits observed in 2019 compared to 2018, because of their higher sensitivity to stress than other algae such as *P.pavonica* and the *Laurencia* complex. Unfortunately, as most trials are carried out in different years, the interannual effect cannot be correctly assessed.

Succession after clearings

Clearings promote higher growth of ephemerals in Aguamarga than in Cabo de las Huertas. This is in agreement with studies showing that either nutrient enrichment or anthropogenic affectation increase the occupancy of ephemerals in cleared patches (Benedetti-Cecchi et al., 2001; Bokn et al., 2002; Gagnon et al., 2016; Bertocci et al., 2017).Thus, in Aguamarga, Ulvaceae are the main group favored in the inner zone after the clearing treatments, whereas in the mid-platform zone different taxa recruit according to the time of year. Thus, *C. sinuosa* is fostered in those plots cleared in May and Ulvaceae in those cleared in October. The lower stress of the mid-platform zone could allow the effective seasonal recruitment of more species than in the inner zone. In line with this, other studies have demonstrated that stress (due to high temperature and emersion periods) influences negatively the diversity and success of recruits (Kaehler and Williams., 1997; Viejo., 2009).

The fact that *C. cylindracea* is not benefited -and even impaired- by artificial clearings indicates that morpho-functional strategies could be involved in the recovery success, even when possible competitors are eliminated. Thus, despite the proved role of canopy-forming species hampering the invasiveness of *C. cylindracea*, the presence of scattered erect algae seems to promote the growth of *C. cylindracea* by acting as anchoring points for the attachment of its stoloniferous axes (Bulleri & Benedetti-Cecchi., 2008). Moreover, clearing treatment probably destroys the cryptic stolons from which population regrowth occurs seasonally, as vegetative growth and clonal fragmentation seems to be the main mechanism from which such alga spreads in the Mediterranean sea (Cecherelli & Piazzi, 2001; Varela-Álvarez et al., 2012).

When productivity potential decreases, the recruitment window for ephemeral species –in cleared plots- gets constrained, weakening their growth (Buschmann, 1990; Hutchinson & Williams, 2001; Mayakun et al., 2019). This can occur to some extent in Cabo de las Huertas, presumably because of the lower nutrient availability (Terradas-Fernández et al., in prep.). Moreover, the lower hydrodynamism of the inner zone could impair even more the growth of ephemerals in this zone. This could explain why those clearings from Huertas, especially in the inner zones, are re-occupied mainly by preexistent species, whereas ephemeral ones are only slightly promoted. However, other non-opportunistic species such as fucoid algae seem to take advantage of clearings produced in Huertas in the mid-platform zone in line with other studies showing that clearings could promote the growth of fucoid algae, especially when it coincides with their recruitment window (Perkol-Finkel and Airoldi., 2010; Piazzi and Ceccherelli., 2017). The source of fucoid recruits (mainly *C. amentacea* and *C. humilis*) probably are scattered adult individuals distributed over the platform along with the stable populations thriving in the outer margin only a few meters from the plots.

Resilience and similarity between treatment levels

In most cases, clearing treatments only showed significant differences with controls during a few months. This pattern is also found in the lower intertidal from the neighbouring Atlantic and in the littoral fringe from other geographical regions dominated by similar morpho-functional groups (Milazo et al., 2010; Oliveira et al., 2015; Kim et al., 2017; Martins et al., 2018).

Thus, resilience, after a small pulse disturbance, seems to be analogous and fast in both locations despite their distinct ecological status. However, the similarity between treatments shows some variability related to the location, zone and trial timing.

The higher stress affecting the inner zones and summer months promotes a few rather opportunistic and stress-tolerant species (thin articulated corallines, *Ulva* spp.) that are able to colonize fast both cleared and control plots increasing their similarity. This pattern is in line with other studies pointing out stress as an enhancer of the resilience of preexistent stress-tolerant species submitted to a pulse disturbance (Viejo, 2009; Kim et al., 2017). When stress is too high, also for local stress-tolerant organisms, resilience is negatively affected (Bertness et al., 2006; Viejo, 2009). In extreme situations like tropical intertidal shores, summer season could even act as a die-off event from which succession restarts annually (Hutchinson and Williams, 2003).

However, in our study, similarity and resilience can be confused with each other, especially when such similarity underestimated the real status of the slowest species to recover, usually included in more complex morpho-functional groups. Thus, the apparent higher resilience and the faster convergent pattern in the mid-platform zone, in those clearings carried out before the harsh summer, looks like a "mirage effect". Once in the production phase, during winter and spring, dissimilarities reappeared in mid-aged plots when structurally more complex species (*Dictyota* spp, *E. elongata*) increase more in the controls than in the cleared plots.

These results strengthen the relevance of taxa composition, and their biological traits, to understand better the resilience of assemblages along with the local constraints affecting them (Schiel., 2006; Viejo., 2009; Balata et al., 2011, Pinedo and Ballesteros., 2019). Thus, two vermetid platforms, corresponding to two-phase states, have complementary morpho-functional groups responding similarly to small pulse disturbances. Thin articulated corallines (Jania spp.) show a rather seasonal "opportunistic" behavior in both locations. Meanwhile, thick articulated corallines (*E. elongata*) (yet considered stress-tolerant in a broader context) and Dictyotacean thrive in less stressed situations in the affected Aguamarga and the unaffected Cabo de las Huertas, respectively. The opportunistic trend of thinner articulated corallines over the thicker ones has been pointed out in previous works (Stewart., 1989) and is analogous to what happens in crustose corallines (Stenneck., 1986).

Seasonality of species and some possible hierarchical competitive interactions explain the convergence pattern

The strong seasonality of the main species of both locations could explain the fast convergence pattern found among cleared plots and controls. There are neither similar competitors able to monopolize the space for extended periods generating multiple "stable states" (Foster et al., 2003; Menge et al., 2017; Martins et al., 2018) nor ephemerals hindering the recruitment for long periods (Kim et al., 2017). In the case of Aguamarga (low ecological status), when conditions are optimal for *E. elongata*, *Ellisolandia elongata* tends to occupy and persist over most of the platform, whereas the same seems to be true for Dictyotacean in the unaltered Cabo de las Huertas.

Despite the two Dictyotacean overlapping their temporal and spatial ranges, *Padina pavonica* seems less competitive and more stress-tolerant. Thus it thrives better than *Dictyota* in the inner parts and copes better with the harsh summer conditions (Terradas-Fernández et al., 2018; this study). When they overlap, *Dictyota* spp. seems to be a superior competitor judging by the higher cover of *P.pavonica* in cleared plots, where the control ones show a *Dictyota* dominance. The latter situation being more probable when seasonal conditions are optimal for *Dictyota* growth and are accompanied by less stressful local abiotic factors.

The role of competition deserves further study on dominant species to better understand their possible role on the structure of these assemblages. Thus, dominance, even when space is saturated by a single persistent species, not necessarily mean competitive exclusion takes place. In a mid-intertidal from California, Stewart (1989) showed experimentally that dominance of *Corallina* species was not the result of exclusion of other secondary taxa. On the contrary, the ephemeral pattern and low cover of secondary species was due to their incapacity to cope with abiotic stressors, whereas interactive effects between species were inexistent. In our study, it cannot be rule out that during most of the winter, the same process could explain the dominance of *E. elongata* with respect to *Jania* spp. in Aguamarga (despite the possibility that interactive processes could act in autumn and early winter as has been pointed out above). This is due to the apparent low ability of *Jania* spp. to cope with winter conditions (Bressan et al., 2003; Terradas Fernández et al., 2018, this study).

Summer stress acts as a brake for most dominant and relatively structurally complex species in both locations (*E. elongata, Dictyota* spp.), despite differences between ecological status. This allows the restart of a growth cycle during winter. However, such cyclic determinism could be weakened when disturbance regime increases. Thus, large spatial perturbations could drive intertidal and subtidal systems from a unique endpoint to multiple stable ones (Petraitis et al., 2009; Rindi et al., 2017). The increased trend in extreme events like great storms or prolonged emersion periods in the last decades (Easterling et al., 2000, Zamir et al., 2018;) make long-term monitoring studies and experimental manipulations, including temporal and spatial variability on the intensity of the disturbances, a paramount goal for further research in the comprehension of the role of disturbances as drivers of these very shallow communities.

Conclusions

Our study supports that most macroalgal assemblages thriving in shallow vermetid platforms recover fast after a small pulse disturbance. The convergence between control and cleared plots is achieved before the end of the study (20 months) in most cases regardless of the ecological status of the vermetid platforms. As expected, the growth of ephemerals is higher in the low ecological status condition, and it is probably related to anthropogenic stressors (eutrophication, sedimentation, etc.) that usually affect urban areas. Regardless of ecological status, abiotic stressful situations, occurring in the inner zones or during summer months, increase the similarity between cleared and control plots due to the increase in fast growing species in both treatment levels, whereas more structurally complex species show lower cover values in the same situations. The temporal pattern of assemblages seems to prevent the establishment of multiple "prolonged states" regardless of when the pulse disturbance occurs. The biological traits of the main taxa are key points to understand the successional and temporal pattern between locations where different morpho-functional groups have a complementary role.

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Supplementary Material

Title: Response to small pulse disturbances of phytobenthos on vermetid platforms with distinct ecological status.

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Table S1. Results from SIMPER analysis according to treatment levels (controls and cleared plots). Average abundance of each species and its contribution to Bray-Curtis dissimilarities between treatment levels are shown.

Affected location	Average dissimilarity = 65.52				
Treatment	Control plots	Cleared plots			
Species	Average abundance (%)	Average abundance (%)	Average dissimilarities	Contribution (%)	Cumulated percentages
Ellisolandia elongata	38.35	22.48	17.69	26.99	26.99
Ulva spp.	17.3	25.86	17.24	26.32	53.31
Jania spp.	13.77	14.35	10.24	15.62	68.93
Turf	9.91	10.49	7.75	11.82	80.76
Colpomenia sinuosa	2.24	3.24	2.89	4.4	85.16
Caulerpa cylindracea	3.34	1.92	2.66	4.06	89.22
Mytilaster minimus	2.04	2.1	2.07	3.16	92.38
Cladophora spp.	0.86	2.4	1.66	2.53	94.91
Encrusting corallines	1.05	1.83	1.63	2.48	97.39
Gelidium crinale/pusillum	0.47	0.27	0.43	0.66	98.05
Derbesia tenuissima	0.36	0.3	0.4	0.61	98.66
Acinetospora crinita	0.47	0.31	0.38	0.58	99.24
Laurencia complex	0.41	0.19	0.3	0.45	99.69
Amphiroa beauvoisii	0.01	0.14	0.08	0.12	99.81
Gymnogongrus griffithsiae	0	0.13	0.07	0.1	99.91
Petalonia fascia	0.06	0.01	0.03	0.05	99.97
Hypnea musciformis	0.03	0	0.02	0.03	99.99
Gastroclonium clavatum	0	0.01	0	0.01	100

Unaffected location	Average dissimilarity = 62.65				
Treatment	Control plots	Cleared plots			
Species	Average abundance (%)	Average abundance (%)	Average dissimilarities	Contribution (%)	Cumulated percentages
Jania spp.	29.08	26.34	16.55	26.41	26.41
Padina pavonica	19.69	21.91	13.29	21.21	47.62
Laurencia complex	11.49	10.51	8.18	13.06	60.68
Dictyota spp.	10.94	3.89	7.63	12.18	72.86
Cystoseira spp.	4.5	5.41	4.9	7.82	80.68
Turf	2.49	5.42	4.14	6.61	87.29
Encrusting corallines	3.25	4.21	3.85	6.15	93.43
Cladophora spp.	0.99	1.56	1.37	2.19	95.63
Vermetus sp.	0.56	0.35	0.52	0.83	96.46
Hypnea musciformis	0.06	0.73	0.44	0.69	97.16
Chondria spp.	0.21	0.38	0.36	0.57	97.73
Rivularia spp.	0.33	0.19	0.3	0.47	98.2
Halopteris scoparia	0.2	0.27	0.26	0.42	98.62
Caulerpa cylindracea	0.24	0.18	0.23	0.37	98.99
Ulva spp.	0.16	0.16	0.18	0.29	99.27
Alsidium corallinum	0.16	0.03	0.12	0.2	99.47
Chaetomorpha spp.	0.09	0.03	0.08	0.12	99.59
Spyridia filamentosa	0	0.09	0.05	0.08	99.68
Ellisolandia elongata	0.04	0.03	0.04	0.07	99.74
Scytosiphon lomentaria	0.01	0.06	0.04	0.06	99.81
Gastroclonium clavatum	0	0.06	0.03	0.05	99.86
Colpomenia sinuosa	0	0.05	0.03	0.05	99.91
Dascycladus vermicularis	0.02	0.02	0.02	0.03	99.94
Mytilaster minimus	0.02	0.01	0.02	0.03	99.96
Acetabularia acetabulum	0.03	0	0.01	0.02	99.99
Gelidium crinale/pusillum	0.01	0.01	0.01	0.01	100

Table S2. Results of distance-based permutational univariate analysis PERMANOVA for the main species and bare space. Main test is shown for each species using *treatment* (Tr), *elapsed time* since pulse treatment (Ti), *season trial* (Se), *location* (Lo) and *zone* (Zo) as fixed factors. Below the main test, the results of pairwise analyses are shown. To facilitate the visualization of the results, the term 'TrxTixSexLoxZo' for pairs of levels of factor *treatment* is always shown. When significant, the next largest term that includes *treatment* is also shown All other interactions are omitted. Species are represented in alphabetical order. df, degrees of freedom; SS, sums of squares; MS, mean squares; Pseudo-F, pseudo-*F* ratio; t, pseudo-*t* statistic; P(MC), Montecarlo *P*-value. Significant P(perm) and P(MC) values are in bold.

Main test *C.cylindracea*

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	162.8	162.8	72.149	**0.004**	997
Ti	4	328.98	82.245	36.449	**0.009**	998
Se	1	170.66	170.66	75.634	**0.002**	997
Lo	1	959.85	959.85	42.538	**0.001**	998
Zo	1	718.09	718.09	31.824	**0.001**	999
TrxTi	4	216.76	54.19	24.016	**0.044**	998
TrxSe	1	46.475	46.475	20.597	0.152	997
TrxLo	1	144.57	144.57	64.072	**0.011**	998
TrxZo	1	203.83	203.83	90.333	**0.004**	997
TixSe	4	681.5	170.38	75.507	**0.001**	998
TixLo	4	260.54	65.136	28.867	**0.016**	999
TixZo	4	364.25	91.062	40.356	**0.001**	999
SexLo	1	227.6	227.6	10.087	**0.002**	996
SexZo	1	142.62	142.62	63.205	**0.012**	995
LoxZo	1	1021.1	1021.1	45.252	**0.001**	995
TrxTixSe	4	313.85	78.462	34.773	**0.004**	998
TrxTixLo	4	222.63	55.657	24.666	**0.038**	999
TrxTixZo	4	172.6	43.151	19.124	0.097	998
TrxSexLo	1	55.039	55.039	24.392	0.108	996
TrxSexZo	1	114.74	114.74	50.851	**0.025**	999
TrxLoxZo	1	234.38	234.38	10.387	**0.001**	996
TixSexLo	4	768.68	192.17	85.165	**0.001**	999
TixSexZo	4	741.78	185.44	82.185	**0.001**	997
TixLoxZo	4	442.85	110.71	49.065	**0.002**	998
SexLoxZo	1	92.59	92.59	41.034	**0.043**	998
TrxTixSexLo	4	380.74	95.186	42.184	**0.001**	999
TrxTixSexZo	4	363.59	90.897	40.284	**0.003**	999
TrxTixLoxZo	4	175.92	43.98	19.491	0.106	998
TrxSexLoxZo	1	102.21	102.21	45.299	**0.04**	997
TixSexLoxZo	4	664.94	166.24	73.672	**0.001**	998
TrxTixSexLoxZo	4	301.16	75.291	33.367	**0.013**	999
Res	563	12704	22.564			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
C.cylindracea	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	0.644	0.359	-	0.507	0.345	0.336	-	0.121
3-4 months	0.203	-	0.338	0.143	0.165	0.344	0.309	**0.054**
5-8 months	-	-	-	**0.036**	0.327	0.214	-	0.87
9-15 months	0.31	0.426	-	0.277	0.153	-	-	0.325
16-20 months	0.484	-	-	0.884	0.255	-	0.188	0.199

Main test *C.sinuosa*

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	209.78	209.78	83.673	**0.007**	995
Ti	4	2698.7	674.67	26.91	**0.001**	997
Se	1	762.07	762.07	30.397	**0.001**	997
Lo	1	2233.9	2233.9	89.102	**0.001**	997
Zo	1	2159.6	2159.6	86.14	**0.001**	996
TrxTi	4	525.34	131.33	52.385	**0.001**	999
TrxSe	1	178.74	178.74	71.296	**0.009**	996
TrxLo	1	194.99	194.99	77.774	**0.009**	998
TrxZo	1	217.74	217.74	8.685	**0.004**	998
TixSe	4	2527.1	631.78	25.2	**0.001**	998
TixLo	4	2733.3	683.33	27.256	**0.001**	997
TixZo	4	2716.7	679.18	27.09	**0.001**	999
SexLo	1	791.05	791.05	31.552	**0.001**	998
SexZo	1	785.49	785.49	31.331	**0.001**	996
LoxZo	1	2208.2	2208.2	88.078	**0.001**	998
TrxTixSe	4	359.18	89.796	35.817	**0.011**	998
TrxTixLo	4	528.56	132.14	52.706	**0.001**	999
TrxTixZo	4	524.78	131.19	52.329	**0.001**	999
TrxSexLo	1	192.92	192.92	76.949	**0.003**	999
TrxSexZo	1	195.68	195.68	7.805	**0.003**	995
TrxLoxZo	1	233.35	233.35	93.078	**0.002**	999
TixSexLo	4	2502.7	625.68	24.956	**0.001**	999
TixSexZo	4	2468.7	617.19	24.618	**0.001**	999
TixLoxZo	4	2683	670.74	26.754	**0.001**	999
SexLoxZo	1	756.61	756.61	30.179	**0.001**	997
TrxTixSexLo	4	341.65	85.412	34.068	**0.008**	999
TrxTixSexZo	4	362.11	90.528	36.109	**0.006**	999
TrxTixLoxZo	4	520.67	130.17	51.919	**0.002**	997
TrxSexLoxZo	1	181.4	181.4	72.356	**0.009**	996
TixSexLoxZo	4	2493	623.24	24.859	**0.001**	999
TrxTixSexLoxZo	4	379.82	94.954	37.874	**0.005**	999
Res	563	14115	25.071			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
C.sinuosa	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	-	-	-	**0.031**	-	0.372	-	**0.056**
3-4 months	0.258	-	-	**0.019**	-	-	-	-
5-8 months	0.308	0.336	-	0.106	-	-	-	-
9-15 months	-	-	-	0.373	-	0.341	-	0.409
16-20 months	-	0.371	-	0.676	-	-	-	-

Main test *Dictyota* spp.

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	1889.4	1889.4	47.26	**0.001**	999
Ti	4	6075.8	1519	37.994	**0.001**	998
Se	1	2507.8	2507.8	62.727	**0.001**	998
Lo	1	7741	7741	193.63	**0.001**	996
Zo	1	7463.4	7463.4	186.68	**0.001**	998
TrxTi	4	1002.7	250.68	62.704	**0.001**	999
TrxSe	1	406.81	406.81	10.176	**0.002**	998
TrxLo	1	1889.4	1889.4	47.26	**0.001**	998
TrxZo	1	1989	1989	49.752	**0.001**	995
TixSe	4	4578.6	1144.7	28.632	**0.001**	999
TixLo	4	6075.8	1519	37.994	**0.001**	999
TixZo	4	5933.3	1483.3	37.103	**0.001**	999
SexLo	1	2507.8	2507.8	62.727	**0.001**	997
SexZo	1	2394.3	2394.3	59.889	**0.001**	996
LoxZo	1	7463.4	7463.4	186.68	**0.001**	994
TrxTixSe	4	418.94	104.73	26.198	**0.029**	997
TrxTixLo	4	1002.7	250.68	62.704	**0.001**	998
TrxTixZo	4	1104.1	276.03	69.044	**0.001**	999
TrxSexLo	1	406.81	406.81	10.176	**0.006**	999
TrxSexZo	1	472.91	472.91	11.829	**0.002**	998
TrxLoxZo	1	1989	1989	49.752	**0.001**	999
TixSexLo	4	4578.6	1144.7	28.632	**0.001**	997
TixSexZo	4	4403.6	1100.9	27.537	**0.001**	998
TixLoxZo	4	5933.3	1483.3	37.103	**0.001**	999
SexLoxZo	1	2394.3	2394.3	59.889	**0.001**	997
TrxTixSexLo	4	418.94	104.73	26.198	**0.03**	999
TrxTixSexZo	4	449.25	112.31	28.093	**0.028**	999
TrxTixLoxZo	4	1104.1	276.03	69.044	**0.001**	999
TrxSexLoxZo	1	472.91	472.91	11.829	**0.001**	997
TixSexLoxZo	4	4403.6	1100.9	27.537	**0.001**	998
TrxTixSexLoxZo	4	449.25	112.31	28.093	**0.024**	999
Res	563	22508	39.979			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
Dictyota spp.	P(MC) Unaffected	P(MC) Affected	P(MC) Unaffected	P(MC) Affected	P(MC) Unaffected	P(MC) Affected	P(MC) Unaffected	P(MC) Affected
2 months	0.366	-	**0.015**	-	-	-	**0.035**	-
3-4 months	0.087	-	**0.001**	-	-	-	0.239	-
5-8 months	0.099	-	**0.011**	-	-	-	**0.007**	-
9-15 months	-	-	**0.022**	-	0.307	-	0.876	-
16-20 months	-	-	0.137	-	-	-	0.067	-

Main test *E.elongata*

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	12282	12282	72.128	**0.001**	998
Ti	4	13124	3281	19.269	**0.001**	997
Se	1	1069.4	1069.4	6.2802	**0.012**	997
Lo	1	1.38E+05	1.38E+05	808.19	**0.001**	997
Zo	1	3662.4	3662.4	21.508	**0.001**	997
TrxTi	4	4443.9	1111	6.5244	**0.001**	998
TrxSe	1	2655.7	2655.7	15.596	**0.001**	998
TrxLo	1	12282	12282	72.128	**0.001**	996
TrxZo	1	1170.2	1170.2	6.8723	**0.013**	998
TixSe	4	10396	2599.1	15.264	**0.001**	998
TixLo	4	13255	3313.8	19.461	**0.001**	999
TixZo	4	9736.2	2434	14.295	**0.001**	999
SexLo	1	1108.6	1108.6	6.5105	**0.01**	996
SexZo	1	158.61	158.61	0.93147	0.344	996
LoxZo	1	3662.4	3662.4	21.508	**0.001**	999
TrxTixSe	4	2326.4	581.6	3.4156	**0.008**	999
TrxTixLo	4	4427.1	1106.8	6.4998	**0.001**	998
TrxTixZo	4	1964.2	491.05	2.8838	**0.026**	999
TrxSexLo	1	2655.7	2655.7	15.596	**0.001**	998
TrxSexZo	1	148.79	148.79	0.87379	0.368	998
TrxLoxZo	1	1211.2	1211.2	7.1131	**0.006**	994
TixSexLo	4	10470	2617.4	15.371	**0.001**	999
TixSexZo	4	3209.6	802.39	4.7123	**0.002**	998
TixLoxZo	4	9940.4	2485.1	14.594	**0.001**	999
SexLoxZo	1	158.61	158.61	0.93147	0.341	998
TrxTixSexLo	4	2290.5	572.63	3.3629	**0.007**	996
TrxTixSexZo	4	628.9	157.22	0.92334	0.454	999
TrxTixLoxZo	4	1994.4	498.61	2.9282	**0.022**	998
TrxSexLoxZo	1	134.64	134.64	0.79074	0.367	998
TixSexLoxZo	4	3117.7	779.43	4.5774	**0.006**	999
TrxTixSexLoxZo	4	603.82	150.95	0.88652	0.489	999
Res	563	95867	170.28			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
E.elongata	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	-	**0.002**	-	**0.001**	-	0.07	-	**0.007**
3-4 months	-	**0.031**	-	**0.002**	-	0.14	0.327	0.342
5-8 months	-	0.518	-	**0.001**	0.203	0.212	-	**0.006**
9-15 months	-	0.839	-	0.143	-	0.376	-	0.188
16-20 months	-	0.887	-	0.069	-	0.715	-	0.689

Encrusting corallines

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	118.17	118.17	4.5419	**0.025**	997
Ti	4	316.06	79.016	3.0371	**0.015**	998
Se	1	462.96	462.96	17.795	**0.001**	997
Lo	1	605.05	605.05	23.256	**0.001**	996
Zo	1	541.7	541.7	20.821	**0.001**	996
TrxTi	4	64.484	16.121	0.61964	0.671	998
TrxSe	1	79.657	79.657	3.0617	0.08	997
TrxLo	1	5.5389	5.5389	0.2129	0.661	995
TrxZo	1	10.278	10.278	0.39504	0.539	997
TixSe	4	878.73	219.68	8.4438	**0.001**	999
TixLo	4	403.21	100.8	3.8745	**0.006**	998
TixZo	4	2307.4	576.85	22.172	**0.001**	997
SexLo	1	554.31	554.31	21.306	**0.001**	995
SexZo	1	981.66	981.66	37.731	**0.001**	998
LoxZo	1	170.85	170.85	6.5669	**0.01**	994
TrxTixSe	4	247.13	61.783	2.3747	**0.061**	999
TrxTixLo	4	253.36	63.34	2.4346	**0.061**	999
TrxTixZo	4	113.68	28.42	1.0924	0.356	999
TrxSexLo	1	42.565	42.565	1.636	0.196	996
TrxSexZo	1	357.85	357.85	13.754	**0.001**	998
TrxLoxZo	1	2.7118	2.7118	0.10423	0.742	998
TixSexLo	4	1023.7	255.92	9.8365	**0.001**	999
TixSexZo	4	797.17	199.29	7.66	**0.001**	999
TixLoxZo	4	1509.7	377.43	14.507	**0.001**	999
SexLoxZo	1	196.73	196.73	7.5615	**0.009**	999
TrxTixSexLo	4	328.76	82.191	3.1591	**0.014**	999
TrxTixSexZo	4	86.179	21.545	0.8281	0.507	999
TrxTixLoxZo	4	280.81	70.203	2.6984	**0.033**	997
TrxSexLoxZo	1	65.923	65.923	2.5339	0.104	999
TixSexLoxZo	4	1072.4	268.11	10.305	**0.001**	999
TrxTixSexLoxZo	4	224.26	56.065	2.155	0.088	999
Res	563	14648	26.017			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
Encrusting corallines	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	0.549	0.288	-	-	0.169	0.819	0.339	-
3-4 months	**0.006**	0.133	0.328	-	0.143	**0.014**	-	0.367
5-8 months	0.432	0.723	0.331	0.336	0.08	0.719	0.26	0.206
9-15 months	0.554	0.513	0.345	0.338	0.679	0.346	0.354	0.351
16-20 months	0.683	-	0.403	-	0.415	0.105	0.554	0.301

Main test fucoid algae

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	12.535	12.535	0.30052	0.573	999
Ti	4	1381.9	345.47	8.2825	**0.001**	996
Se	1	361.55	361.55	8.668	**0.005**	993
Lo	1	3319.2	3319.2	79.577	**0.001**	996
Zo	1	1489.8	1489.8	35.718	**0.001**	997
TrxTi	4	191.36	47.84	1.1469	0.343	998
TrxSe	1	317.77	317.77	7.6184	**0.009**	998
TrxLo	1	12.535	12.535	0.30052	0.586	996
TrxZo	1	4.2228	4.2228	0.10124	0.748	997
TixSe	4	2422.1	605.53	14.517	**0.001**	999
TixLo	4	1381.9	345.47	8.2825	**0.001**	999
TixZo	4	2242.4	560.61	13.44	**0.001**	998
SexLo	1	361.55	361.55	8.668	**0.005**	992
SexZo	1	11.674	11.674	0.27987	0.621	993
LoxZo	1	1489.8	1489.8	35.718	**0.001**	998
TrxTixSe	4	115.67	28.918	0.69329	0.585	999
TrxTixLo	4	191.36	47.84	1.1469	0.336	999
TrxTixZo	4	178.35	44.587	1.069	0.387	999
TrxSexLo	1	317.77	317.77	7.6184	**0.005**	997
TrxSexZo	1	77.687	77.687	1.8625	0.166	996
TrxLoxZo	1	4.2228	4.2228	0.10124	0.761	997
TixSexLo	4	2422.1	605.53	14.517	**0.001**	998
TixSexZo	4	2433	608.25	14.583	**0.001**	999
TixLoxZo	4	2242.4	560.61	13.44	**0.001**	998
SexLoxZo	1	11.674	11.674	0.27987	0.587	995
TrxTixSexLo	4	115.67	28.918	0.69329	0.607	996
TrxTixSexZo	4	245.28	61.32	1.4701	0.204	999
TrxTixLoxZo	4	178.35	44.587	1.069	0.368	999
TrxSexLoxZo	1	77.687	77.687	1.8625	0.168	995
TixSexLoxZo	4	2433	608.25	14.583	**0.001**	998
TrxTixSexLoxZo	4	245.28	61.32	1.4701	0.192	999
Res	563	23483	41.711			

Pairwise test	October trial (inner zone)		October trial (mid Zone)		May trial (inner zone)		May trial (mid zone)	
Fucoid algae	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	-	-	0.352	-	**0.047**	-	0.336	-
3-4 months	0.256	-	0.104	-	0.082	-	0.328	-
5-8 months	0.885	-	0.327	-	0.185	-	-	-
9-15 months	0.237	-	0.4	-	0.585	-	-	-
16-20 months	0.222	-	0.845	-	0.418	-	-	-

Main test *Jania* spp.

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	752.05	752.05	3.7969	**0.042**	998
Ti	4	8689.8	2172.4	10.968	**0.001**	998
Se	1	17978	17978	90.767	**0.001**	996
Lo	1	24583	24583	124.11	**0.001**	996
Zo	1	6794.1	6794.1	34.301	**0.001**	997
TrxTi	4	3078.6	769.64	3.8857	**0.001**	999
TrxSe	1	234.27	234.27	1.1828	0.268	996
TrxLo	1	1217.6	1217.6	6.1471	**0.018**	997
TrxZo	1	222.62	222.62	1.124	0.284	996
TixSe	4	61503	15376	77.628	**0.001**	998
TixLo	4	1826.1	456.52	2.3049	0.066	998
TixZo	4	2260.9	565.22	2.8536	**0.027**	999
SexLo	1	82.401	82.401	0.41602	0.536	995
SexZo	1	663.82	663.82	3.3515	0.062	998
LoxZo	1	19318	19318	97.531	**0.001**	995
TrxTixSe	4	712.08	178.02	0.89878	0.472	999
TrxTixLo	4	3040.5	760.11	3.8376	**0.005**	999
TrxTixZo	4	1464.8	366.19	1.8488	0.103	998
TrxSexLo	1	0.0047568	0.0047568	2.40E-05	0.995	996
TrxSexZo	1	6.2796	6.2796	0.031704	0.857	998
TrxLoxZo	1	55.037	55.037	0.27787	0.582	997
TixSexLo	4	12023	3005.7	15.175	**0.001**	998
TixSexZo	4	12131	3032.9	15.312	**0.001**	998
TixLoxZo	4	2301.6	575.39	2.905	**0.02**	997
SexLoxZo	1	2.3835	2.3835	0.012034	0.908	993
TrxTixSexLo	4	2195.2	548.8	2.7707	**0.03**	998
TrxTixSexZo	4	1132.9	283.22	1.4299	0.227	997
TrxTixLoxZo	4	1285.2	321.29	1.6221	0.17	998
TrxSexLoxZo	1	66.667	66.667	0.33658	0.559	996
TixSexLoxZo	4	2315.7	578.94	2.9229	**0.027**	999
TrxTixSexLoxZo	4	272.08	68.02	0.34342	0.828	997
Res	563	1.12E+05	198.07	0.343	0.828	997

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
Jania spp.	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	**0.009**	0.331	**0.031**	**0.001**	**0.02**	0.237	0.383	0.157
3-4 months	0.755	-	0.694	0.624	0.058	**0.032**	0.823	0.534
5-8 months	0.329	0.194	0.316	0.141	0.507	0.535	0.256	0.533
9-15 months	0.207	0.815	0.994	0.698	0.64	0.796	0.772	0.145
16-20 months	0.342	0.89	0.449	0.18	0.711	0.352	0.062	0.35

Main test *Laurencia* complex

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	54.252	54.252	1.0211	0.318	996
Ti	4	1244.7	311.19	5.8571	**0.001**	998
Se	1	26.904	26.904	0.50639	0.518	998
Lo	1	14291	14291	268.99	**0.001**	998
Zo	1	973.94	973.94	18.332	**0.001**	999
TrxTi	4	93.542	23.386	0.44016	0.762	998
TrxSe	1	3.4022	3.4022	0.064036	0.8	996
TrxLo	1	29.803	29.803	0.56096	0.472	995
TrxZo	1	1831.4	1831.4	34.471	**0.001**	997
TixSe	4	2704.6	676.15	12.727	**0.001**	999
TixLo	4	1174.6	293.64	5.527	**0.001**	998
TixZo	4	1405.9	351.47	6.6154	**0.001**	999
SexLo	1	28.732	28.732	0.54079	0.441	996
SexZo	1	164.16	164.16	3.0898	0.078	997
LoxZo	1	619.74	619.74	11.665	**0.001**	998
TrxTixSe	4	68.35	17.087	0.32162	0.866	998
TrxTixLo	4	71.624	17.906	0.33703	0.85	999
TrxTixZo	4	125.85	31.464	0.59221	0.651	999
TrxSexLo	1	0.018543	0.018543	0.00034901	0.983	997
TrxSexZo	1	102.29	102.29	1.9253	0.165	998
TrxLoxZo	1	1671.9	1671.9	31.468	**0.001**	997
TixSexLo	4	2700.3	675.08	12.706	**0.001**	998
TixSexZo	4	1298.4	324.61	6.1098	**0.001**	999
TixLoxZo	4	1118.8	279.7	5.2646	**0.001**	997
SexLoxZo	1	159.75	159.75	3.0068	0.081	996
TrxTixSexLo	4	113.22	28.305	0.53276	0.731	999
TrxTixSexZo	4	425.98	106.5	2.0045	0.092	998
TrxTixLoxZo	4	93.226	23.307	0.43868	0.795	995
TrxSexLoxZo	1	139.76	139.76	2.6306	0.113	998
TixSexLoxZo	4	1700.8	425.2	8.0032	**0.001**	998
TrxTixSexLoxZo	4	546.01	136.5	2.5693	**0.038**	999
Res	563	29912	53.129			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
Laurencia complex	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	-	-	-	-	**0.017**	0.253	0.187	-
3-4 months	0.223	-	0.18	-	0.915	-	0.388	-
5-8 months	**0.029**	0.316	**0.024**	-	**0.035**	-	**0.047**	0.487
9-15 months	0.509	0.254	-	-	0.072	-	**0.044**	-
16-20 months	0.114	-	0.202	-	0.225	-	**0.043**	-

Main test *P.pavonica*

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	63.754	63.754	0.40477	0.551	998
Ti	4	2237.2	559.3	3.551	**0.015**	999
Se	1	711.67	711.67	4.5184	**0.036**	998
Lo	1	58889	58889	373.88	**0.001**	995
Zo	1	3126.7	3126.7	19.851	**0.001**	998
TrxTi	4	480.76	120.19	0.76307	0.523	999
TrxSe	1	74.448	74.448	0.47266	0.518	997
TrxLo	1	63.754	63.754	0.40477	0.569	998
TrxZo	1	17.404	17.404	0.1105	0.744	998
TixSe	4	4532.7	1133.2	7.1944	**0.001**	999
TixLo	4	2237.2	559.3	3.551	**0.013**	999
TixZo	4	390.86	97.714	0.62038	0.652	999
SexLo	1	711.67	711.67	4.5184	**0.033**	997
SexZo	1	1119.6	1119.6	7.1085	**0.011**	997
LoxZo	1	3126.7	3126.7	19.851	**0.001**	999
TrxTixSe	4	336.27	84.068	0.53374	0.708	998
TrxTixLo	4	480.76	120.19	0.76307	0.566	999
TrxTixZo	4	564.24	141.06	0.89557	0.451	998
TrxSexLo	1	74.448	74.448	0.47266	0.499	997
TrxSexZo	1	2925.2	2925.2	18.572	**0.001**	998
TrxLoxZo	1	17.404	17.404	0.1105	0.739	995
TixSexLo	4	4532.7	1133.2	7.1944	**0.001**	999
TixSexZo	4	2327.1	581.78	3.6937	**0.006**	999
TixLoxZo	4	390.86	97.714	0.62038	**0.638**	999
SexLoxZo	1	1119.6	1119.6	7.1085	**0.004**	996
TrxTixSexLo	4	336.27	84.068	0.53374	0.725	998
TrxTixSexZo	4	894.47	223.62	1.4197	0.242	998
TrxTixLoxZo	4	564.24	141.06	0.89557	0.482	998
TrxSexLoxZo	1	2925.2	2925.2	18.572	**0.001**	997
TixSexLoxZo	4	2327.1	581.78	3.6937	**0.011**	998
TrxTixSexLoxZo	4	894.47	223.62	1.4197	0.226	998
Res	563	88676	157.51			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
P.pavonica	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	0.227	-	0.27	-	0.772	-	0.579	-
3-4 months	0.26	-	0.689	-	0.111	-	0.926	-
5-8 months	0.224	-	**0.056**	-	0.082	-	0.581	-
9-15 months	0.217	-	0.068	-	0.065	-	0.135	-
16-20 months	0.266	-	0.456	-	0.231	-	0.252	-

Main test turf

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	1029.4	1029.4	11.826	**0.001**	999
Ti	4	3657.9	914.48	10.505	**0.001**	999
Se	1	121.88	121.88	1.4001	0.244	996
Lo	1	4757.5	4757.5	54.653	**0.001**	997
Zo	1	2255.2	2255.2	25.907	**0.001**	998
TrxTi	4	1287.1	321.78	3.6965	**0.01**	999
TrxSe	1	1071.1	1071.1	12.305	**0.001**	998
TrxLo	1	534.84	534.84	6.1441	**0.012**	999
TrxZo	1	492.21	492.21	5.6544	**0.016**	995
TixSe	4	4835.7	1208.9	13.888	**0.001**	999
TixLo	4	920.96	230.24	2.6449	**0.031**	999
TixZo	4	2445.6	611.39	7.0235	**0.001**	999
SexLo	1	159.49	159.49	1.8322	0.182	998
SexZo	1	130.89	130.89	1.5036	0.212	995
LoxZo	1	1.1818	1.1818	0.013577	0.913	998
TrxTixSe	4	2044.7	511.19	5.8724	**0.001**	999
TrxTixLo	4	1169.8	292.46	3.3597	**0.008**	998
TrxTixZo	4	1178	294.49	3.383	**0.014**	999
TrxSexLo	1	91.288	91.288	1.0487	0.301	998
TrxSexZo	1	7.6767	7.6767	0.088188	0.765	998
TrxLoxZo	1	341.05	341.05	3.9179	**0.049**	998
TixSexLo	4	1959.7	489.94	5.6283	**0.001**	998
TixSexZo	4	3632.4	908.1	10.432	**0.001**	999
TixLoxZo	4	1255.5	313.87	3.6056	**0.007**	999
SexLoxZo	1	1045.7	1045.7	12.012	**0.002**	998
TrxTixSexLo	4	677.55	169.39	1.9459	**0.09**	999
TrxTixSexZo	4	641.9	160.47	1.8435	0.115	999
TrxTixLoxZo	4	191.06	47.764	0.5487	0.693	999
TrxSexLoxZo	1	14.9	14.9	0.17117	0.669	998
TixSexLoxZo	4	1471.4	367.86	4.2259	**0.003**	999
TrxTixSexLoxZo	4	315.49	78.871	0.90605	0.442	998
Res	563	49009	87.049			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
Turf	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	0.149	0.293	**0.001**	0.15	0.341	0.088	0.089	**0.028**
3-4 months	0.874	0.654	**0.003**	**0.017**	0.905	0.89	0.313	0.783
5-8 months	0.685	0.698	**0.002**	0.428	0.737	0.917	0.325	0.396
9-15 months	0.785	0.245	0.433	0.155	0.832	0.667	0.285	0.355
16-20 months	0.235	0.258	-	0.704	0.347	0.5	0.956	0.798

Main test *Ulva* spp.

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	3499	3499	23.199	**0.001**	997
Ti	4	8487.3	2121.8	14.068	**0.001**	998
Se	1	6006	6006	39.821	**0.001**	995
Lo	1	60874	60874	403.61	**0.001**	994
Zo	1	20552	20552	136.26	**0.001**	998
TrxTi	4	2689.7	672.42	4.4584	**0.002**	998
TrxSe	1	55.656	55.656	0.36902	0.523	997
TrxLo	1	3513.7	3513.7	23.297	**0.001**	996
TrxZo	1	1437.1	1437.1	9.5287	**0.004**	997
TixSe	4	23257	5814.2	38.55	**0.001**	999
TixLo	4	8619.9	2155	14.288	**0.001**	997
TixZo	4	9520.9	2380.2	15.782	**0.001**	999
SexLo	1	5842.1	5842.1	38.735	**0.001**	998
SexZo	1	650.08	650.08	4.3102	**0.036**	998
LoxZo	1	19995	19995	132.57	**0.001**	998
TrxTixSe	4	1504.6	376.15	2.494	**0.048**	999
TrxTixLo	4	2705.8	676.44	4.485	**0.002**	999
TrxTixZo	4	1569.7	392.43	2.6019	**0.029**	999
TrxSexLo	1	71.833	71.833	0.47627	0.487	996
TrxSexZo	1	138.11	138.11	0.91574	0.302	996
TrxLoxZo	1	1401.7	1401.7	9.2937	**0.004**	996
TixSexLo	4	22295	5573.9	36.956	**0.001**	999
TixSexZo	4	10845	2711.2	17.976	**0.001**	999
TixLoxZo	4	9385.5	2346.4	15.557	**0.001**	998
SexLoxZo	1	613.98	613.98	4.0709	**0.055**	998
TrxTixSexLo	4	1408.8	352.2	2.3352	**0.047**	999
TrxTixSexZo	4	542.56	135.64	0.89933	0.439	999
TrxTixLoxZo	4	1480	370	2.4532	**0.039**	999
TrxSexLoxZo	1	128.4	128.4	0.85132	0.376	998
TixSexLoxZo	4	10208	2552	16.92	**0.001**	998
TrxTixSexLoxZo	4	476.47	119.12	0.78978	0.542	999
Res	563	84913	150.82			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
Ulva spp.	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	-	**0.024**	0.359	0.153	-	**0.015**	-	0.358
3-4 months	0.177	**0.001**	0.139	**0.013**	-	**0.019**	-	-
5-8 months	0.235	0.99	0.323	0.139	-	**0.006**	-	0.311
9-15 months	-	0.788	-	0.29	0.438	0.63	-	0.392
16-20 months	0.549	0.571	-	-	-	**0.026**	-	-

Main test bare space

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Tr	1	3002.8	3002.8	15.48	**0.001**	997
Ti	4	8141.5	2035.4	10.493	**0.001**	998
Se	1	643.61	643.61	3.3179	**0.058**	997
Lo	1	12282	12282	63.316	**0.001**	999
Zo	1	16423	16423	84.663	**0.001**	996
TrxTi	4	5118.6	1279.6	6.5968	**0.001**	998
TrxSe	1	20.026	20.026	0.10324	0.741	999
TrxLo	1	85.595	85.595	0.44126	0.493	993
TrxZo	1	1445.9	1445.9	7.4537	**0.009**	999
TixSe	4	4360	1090	5.6191	**0.001**	999
TixLo	4	6154.9	1538.7	7.9324	**0.001**	998
TixZo	4	3237.5	809.38	4.1725	**0.002**	999
SexLo	1	1411.9	1411.9	7.2786	**0.01**	992
SexZo	1	87.666	87.666	0.45193	0.516	999
LoxZo	1	866.42	866.42	4.4665	**0.03**	994
TrxTixSe	4	526.44	131.61	0.67847	0.634	999
TrxTixLo	4	2124.9	531.23	2.7386	**0.03**	998
TrxTixZo	4	1369.7	342.42	1.7652	0.122	998
TrxSexLo	1	436.39	436.39	2.2496	0.127	992
TrxSexZo	1	71.743	71.743	0.36984	0.543	998
TrxLoxZo	1	334.6	334.6	1.7249	0.177	995
TixSexLo	4	3839.4	959.86	4.9482	**0.002**	998
TixSexZo	4	10618	2654.5	13.684	**0.001**	998
TixLoxZo	4	9865.8	2466.5	12.715	**0.001**	998
SexLoxZo	1	1930.9	1930.9	9.954	**0.004**	999
TrxTixSexLo	4	1102.8	275.7	1.4213	0.214	999
TrxTixSexZo	4	364.48	91.12	0.46974	0.76	998
TrxTixLoxZo	4	2031.4	507.84	2.618	**0.036**	999
TrxSexLoxZo	1	163.77	163.77	0.84427	0.373	998
TixSexLoxZo	4	1077.9	269.47	1.3892	0.252	999
TrxTixSexLoxZo	4	1007.6	251.91	1.2986	0.277	999
Res	563	1.09E+05	193.98			

Pairwise test	October trial (inner zone)		October trial (mid zone)		May trial (inner zone)		May trial (mid zone)	
Bare space	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)	P(MC)
	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected	Unaffected	Affected
2 months	**0.015**	0.308	0.157	0.152	**0.037**	0.466	1	**0.017**
3-4 months	0.878	0.809	**0.001**	0.62	0.379	0.921	0.072	0.239
5-8 months	0.373	0.518	**0.006**	**0.004**	0.181	0.363	**0.036**	**0.018**
9-15 months	0.182	0.715	0.393	0.258	0.19	0.255	0.575	0.396
16-20 months	0.403	0.744	0.552	0.674	0.355	0.25	0.14	0.14

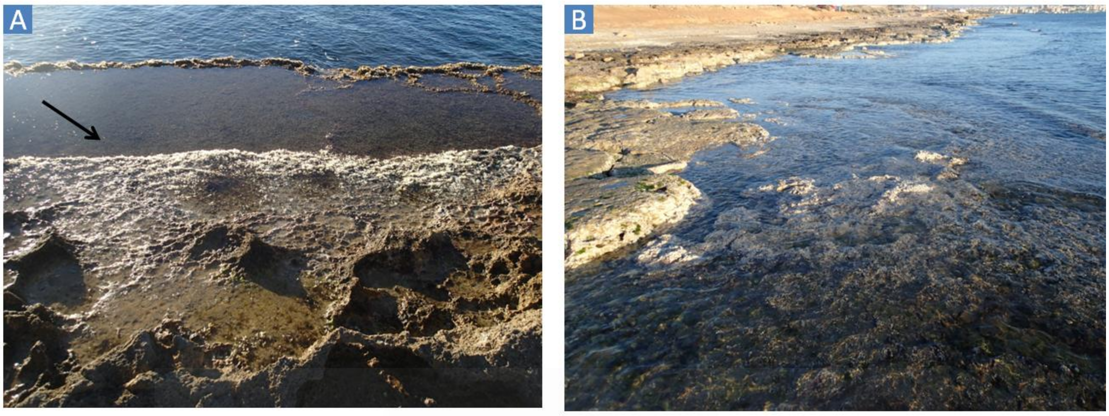

Fig. S1 Bleached algae due to a low sea level episode in Cabo de las Huertas (A) and Playa de Aguamarga (B). In Cabo de las Huertas a mid-littoral belt of bleached *Laurencia* is observed, which continues along the platform’s inner zone (arrow). An outer vermetid rim is also observed. Notice that the platform is full of water despite the low sea level. In Aguamarga, large part of the platform shows bleached algae even in the outer margin lacking the vermetid rim.

Fig. S2 A cleared plot from Aguamarga. A) Two months after the clearing treatment and affected by a low sea level episode during January 2017 (02 01 2017). B) The same plot twenty six days later.

RESUMEN GLOBAL Y DISCUSIÓN DE LOS RESULTADOS

Esta tesis aporta nueva información sobre la dinámica, la resiliencia, y algunos condicionantes (*drivers*) implicados en la estructura de las comunidades que se desarrollan en las plataformas de vermétidos y algas calcáreas. También se ha visto que el estado ecológico del sistema es importante en su respuesta a otras amenazas antrópicas como las especies invasoras. Finalmente, algunos resultados de esta tesis pueden contribuir a la mejora de la gestión y restauración de este patrimonio natural.

Algunas dudas previas al desarrollo de esta tesis han quedado sin respuesta, y otras se han generado a lo largo del trabajo.

A continuación, se resumen y discuten los principales resultados encontrados y algunas de las dudas más relevantes que quedan abiertas.

1. Dinámica del fitobentos asociado a las plataformas de abrasión de algas y vermétidos

En condiciones de no alteración, la dinámica de estos sistemas tiene semejanzas y diferencias respecto a los estudios realizados en otras comunidades del infralitoral superior mediterráneo. Se puede observar una fase otoñal, dominada por algas tolerantes al estrés, en donde el género *Jania* presenta especial relevancia. También se puede observar una fase desarrollada (con algas de mayor porte), dominada generalmente por dictiotáceas, entre primavera y principios de verano. La discriminación en dos fases (estadio desarrollado y estadio "decaído"), encajaría con el esquema ya observado por Niell (1976) en el intermareal de Vigo y el propuesto por Ballesteros (1992) para las comunidades del Mediterráneo Noroccidental. Sin embargo, el estadio desarrollado puede subdividirse dependiendo del óptimo estacional de las distintas especies dominantes. En este sentido, se pueden detectar tres principales facies según la época del año: i) una facies otoñal dominada por *Jania* spp.; ii) una facies primaveral dominada por *Dictyota* spp.; y iii) una facies tardo-primaveral y temprano-estival dominada por *Padina pavonica* (si bien *Jania* spp. empieza a ganar importancia durante el verano).

La observación de varias facies a lo largo del año se ha observado en distintos sistemas sublitorales, tanto templados como tropicales, donde no hay una especie dominante perenne clara (Lirman y Biber, 2000; Skriptsova y Levenets, 2012). Cuando esto ocurre, no puede hablarse de una fase de decaimiento que coincida con una fase de diversificación por la pérdida de biomasa de la especie principal (Ballesteros, 1992; Wernberg y Goldberg, 2008). En cambio, al solaparse la fase de desarrollo invernal y primaveral con el óptimo (o sub-óptimo) de muchas especies, el periodo de desarrollo coincide con el de diversificación (aunque se pueden generar monopolios en el momento de máximo desarrollo de las especies que determinan las distintas facies). Este patrón (visto en la primera publicación) parece similar al de las plataformas de vermétidos del Mediterráneo Oriental, donde la diversidad es máxima durante el invierno (Zamir *et al*, 2018). La coincidencia de la fase de desarrollo con valores de diversidad elevados también se ha observado en zonas fotófilas mediterráneas con posible afectación del alga potencialmente dominante por herbivoría (Martí *et al*., 2005) o en la zona circalitoral donde la falta de luz dificulta la dominancia de una única especie (Ballesteros, 1990). Por lo tanto, cierto descenso en el potencial productivo, como ocurre en las plataformas por la amortiguación del oleaje, la escasísima profundidad, y los periodos de bajamar, dificultaría el establecimiento de una fase desarrollada dominada por una única especie. En cambio, más allá del margen externo o en zonas muy expuestas se han observado cinturones densos de fucales que probablemente presentan un ciclo análogo al descrito para el Mediterráneo Noroccidental, con las correspondientes fases de producción y diversificación.

En cambio, en la zona alterada de Aguamarga, *Ellisolandia elongata* genera "monopolios", dominando la plataforma durante gran parte del año y con una pérdida de biomasa de mayor intensidad durante el verano (salvo en las partes más internas donde los periodos de bajamar invernales también la afectan), tal como se ha observado en otros enclaves superficiales (Guerra-García *et al*., 2011; Bertocci *et al*., 2012). Esta pérdida de biomasa se aprovecha por especies secundarias como *Jania* spp., e incluso por especies exóticas como *C. cylindracea* que crecen durante este periodo estival. En este caso, la fase de decaimiento de la especie principal coincide con una fase de diversificación.

2. Principales condicionantes (drivers) de las plataformas de abrasión de algas y vermétidos

A partir de los estudios correlativos, y mediante el análisis DISTLM (Publicación 1), se refuerza la hipótesis que la dinámica de estos sistemas está controlada, sobre todo, por la oferta de recurso (*bottom-up control*) que, en parte, sigue una pauta estacional en su disponibilidad. Así, los primeros factores explicativos de la dinámica y la variabilidad encontrada a lo largo de la plataforma han sido la profundidad y el fotoperiodo. La profundidad, en nuestro caso, nos indica la disponibilidad hídrica teniendo en cuenta la escasísima profundidad del sistema, sin una relación entre disponibilidad lumínica y profundidad que afecte sensiblemente a la productividad (Einav e Israel, 2007). Además, nos indica la probabilidad de sufrir perturbaciones vinculadas a eventos de bajamar, generalmente más importantes en las zonas menos profundas (Publicación 4). El hidrodinamismo, relacionado con la distancia al margen de la plataforma, también es un buen informador del potencial productivo y explica en gran medida la variabilidad encontrada.

El fotoperiodo y la temperatura (en menor grado) son, después de la profundidad, las mejores variables explicativas. Al existir una correlación entre el fotoperiodo y la temperatura, es imposible discriminar el papel específico de estas variables. La leve ventaja del fotoperiodo (frente a la temperatura) como variable informadora del patrón anual iría en línea con los resultados de Gunnarson y Ingólfsson (1995), si bien ambas parecen tener un peso importante en las plataformas de vermétidos, igual que en muchas comunidades fitobentónicas (Lüning 1990 y referencias). La fase de desarrollo estaría ligada al incremento del fotoperiodo, mientras que las altas temperaturas estarían ligadas al estrés estival que marca el decaimiento de la comunidad.

Las algas de las plataformas parecen responder a la disponibilidad del recurso de acuerdo con el modelo ligado al potencial de productividad propuesto por Steneck y Dethier (1994). Así, cuando el fotoperiodo se alarga, a partir del invierno, y en las zonas de "mayor" profundidad o de hidrodinamismo elevado (cerca del margen exterior), empiezan a desarrollarse las algas de mayor porte (fucales y *Dictyota* spp.) mientras que las de menor porte quedan relegadas a las partes más internas de las plataformas (coralináceas y *P. pavonica*) o se desarrollan durante el estrés estival y cuando el fotoperiodo se acorta (*Jania* spp.).

El caso del "monopolio" de la comunidad alterada (Publicaciones 2 y 4), por parte de *E. elongata* (calcárea y articulada, y de porte mayor que *Jania* spp.), puede depender de determinados estresores característicos de las zonas antropogenizadas, como la sedimentación y la eutrofización (Gorgula y Connell, 2004), que pueden facilitar directa o indirectamente el desarrollo de *E. elongata* (Pinedo y Ballesteros, 2019).

Finalmente, destacamos la bajísima densidad de herbívoros que se mantiene durante todo el año y su papel relativamente residual (Publicación 1). Solamente en el piso mediolitoral la abundancia de algunos herbívoros (Patellidae, Littorinidae, Trochidae) ha sido relativamente elevada, y su papel como condicionantes clave en este piso se ha demostrado en otros enclaves mediterráneos (Benedetti-Cecchi, 2000). Como en las observaciones previas (Terradas-Fernández, 2014), la norma ha sido una escasa cobertura de herbívoros a lo ancho de la plataforma. Esto corrobora la hipótesis de partida: que los principales macroherbívoros (salpas y erizos) tienen un rol irrelevante, salvo en las cubetas y grietas más profundas donde pueden presentarse. Queda así reforzada la hipótesis de que este sistema está poco controlado "desde arriba" en comparación con otros sistemas infralitorales más profundos (Sala, 1996; Hereu *et al*., 2008; Ferrari *et al*., 2012).

3. El estado ecológico y su posible relación con la expansión de especies exóticas

La distinta dinámica de las comunidades asociadas a las plataformas de algas y vermétidos, en base a su estado de alteración, parece clave para la expansión de posibles especies invasoras (Publicación 2). Aprovechando que la especie exótica *C. cylindracea* fue detectada al mismo tiempo en dos localidades con un estado ecológico contrastado (Pena *et al*., 2003, Ramos Esplá, com.pers), podemos evaluar su éxito en ambas localidades e inferir si puede existir una causa subyacente, dependiente de la comunidad receptora, que explique potenciales diferencias en su abundancia.

Atendiéndonos a los resultados de la segunda publicación, en situaciones de alteración un menor grupo de especies dominan la dinámica anual, con un protagonismo de *E. elongata* como ocurre en otras zonas alteradas del infralitoral mediterráneo (Arévalo *et al*., 2007; Ballesteros *et al*., 2007). Algunos estresores como la sedimentación y la eutrofización podrían explicar el éxito de *E. elongata* en estas condiciones (Steneck y Dethier, 1994; Pinedo y Ballesteros, 2019). Con todo, las mediciones de nutrientes y de sedimentación (con un método de aproximación visual) no son, a diferencia de lo que esperábamos, tan desiguales entre las localidades (a pesar de que ambas variables tienden a tener valores más altos en la localidad alterada). En cualquier caso, la dinámica marcada tan claramente por la especie dominante (*E. elongata*) implica que cuando ésta pierde abundancia, otras especies de tendencia oportunista, reforzadas por la posible eutrofización, prosperen (esto último queda también reforzado por el mayor crecimiento de efemerofíceas observado en los clareos de la localidad alterada en la Publicación 4). Entre ellas, *C. cylindracea*, que parece encajar más como "pasajera del cambio" que como "condicionadora" del mismo (MacDougall y Turkington, 2005). Sin embargo, también se ha visto en otros trabajos que *C. cylindracea*, incluso con bajas coberturas, puede afectar la recuperación de la comunidad (Bulleri *et al*., 2017), así como interaccionar positivamente con estresores como la sedimentación (Piazzi *et al*., 2007) y la eutrofización (Gennaro y Piazzi, 2011).

Que el decaimiento de *E. elongata* tienda a generarse durante el estrés estival favorece positivamente a *C. cylindracea* que presenta su óptimo térmico en estas fechas (Samperio-Ramos *et al.,* 2015). Otra especie exótica *Codium fragile* (Suringar) Hariot, también forma manchas abundantes en la misma localidad afectada y su éxito, en parte, también podría explicarse por la disminución de cobertura de *E. elongata,* aunque esta especie no ha sido estudiada (sus mayores poblaciones quedaban fuera de la plataforma).

En cambio, en la localidad menos alterada del Cabo de las Huertas, un mayor recambio de especies generadoras de dosel y que mantienen una cobertura elevada a lo largo del año, junto a la posible menor eutrofización, dificultaría el éxito de *C. cylindracea* (y posiblemente de otras exóticas). Por lo tanto, el éxito de las especies exóticas, en estas plataformas, puede estar determinado, en gran parte, por su estado ecológico.

4. La resiliencia de las comunidades asociadas a las plataformas de abrasión.

Antes de tratar la resiliencia, hay que saber a qué nos referimos, cómo la definimos. En este trabajo, la entendemos como la capacidad de recuperación de una comunidad tras una perturbación (*disturbance*) que ha generado una pérdida de biomasa. Esta definición es una de las acepciones encontradas en la bibliografía (Montefalcone *et al*., 2011) y es operativamente válida para muchos experimentos bentónicos en los que se quiere evaluar la recuperación tras una perturbación controlada.

En realidad, definir "recuperación" y medirla es una operación complicada. La recuperación no es una propiedad inmutable de cada comunidad concreta; depende de su estado constitutivo (la densidad de los organismos, su estado de fertilidad, etc.) y ello influirá en la resiliencia mostrada. Dicha resiliencia, a la vez, dependerá del tipo e intensidad de la perturbación, pudiéndose además generar múltiples estados estabilizados (*multiple stable points*) sin una recuperación hacia un único estado final (*endpoint*) (Sutherland, 1974; Petraitis *et al*., 2009; Rindi *et al*, 2017). En nuestro caso, las perturbaciones generadas han sido puntuales, inmediatas y pequeñas. En este sentido, encajarían con el concepto de "*pulse disturbance*" donde, tras el clareo o por instalación de placas, se genera una pérdida inmediata de cobertura de especies a partir de la cual empieza la recolonización (Glasby y Underwood, 1996). Sin embargo, al ser el clareo (o la placa) de pequeño tamaño, las propiedades de la comunidad ligadas a su resiliencia (estructura poblacional, aporte de reclutas), en el momento de efectuar la perturbación, apenas quedan afectadas (Margalef, 1977).

Para medir la resiliencia hemos evaluado la varianza en distintos intervalos temporales desde el inicio de la perturbación, tanto desde la perspectiva multivariante (de toda la comunidad) como univariante (de las especies que presentan mayor relevancia), ateniéndonos a si existía un patrón convergente de recuperación en función del tiempo.

En la tercera publicación, la comunidad a estudiar fue el propio arrecife de algas y vermétidos. Para ello, buscamos un enclave accesible pero a la vez con poca concurrencia de gente (Reserva Marina de Tabarca). Las bioconstrucciones presentaban un buen desarrollo. El arrecife estaba libre, en gran medida, de algas epífitas y se distribuía generando discontinuidades donde se podían instalar las placas sin afectarlo. Las especies generadoras de la bioconstrucción reclutaron con relativa rapidez; sin embargo, el factor estacional fue importante en el proceso de la sucesión. Esto lo atribuimos a la importancia de la oferta de reclutas determinada por la fenología de ambas especies ingenieras (y bioconstructoras) que coincide con los periodos más cálidos (Calvo *et al*., 1998; Bressan *et al*., 2003). Esto se tradujo en una mayor rapidez en la ocupación del espacio por parte del alga bioconstructora (*N. brassica-florida*) en la instalación hecha en mayo que en la realizada en noviembre mientras que el menor crecimiento del vermétido no permitió ver diferencias significativas ligadas al momento de instalación. El proceso de convergencia fue rápido y a los 9 meses no había diferencias significativas, a nivel de comunidad, entre las placas instaladas en uno u otro periodo. Las especies ingenieras tuvieron una tendencia a incrementar su cobertura en función del tiempo. Las densidades del vermétido llegaron a unos niveles comparables, a la baja, a los que presentan los arrecifes maduros. Por este motivo, y por la relativa velocidad en generarse densidades altas del vermétido (1-2 años) y altas coberturas del alga (9-12 meses), pensamos que el uso de placas podría ser útil en procesos de restauración, utilizándolas como potenciadores del reclutamiento (*recruitment enhancers*).

En esta tercera publicación también se pone de manifiesto que la composición específica no es suficiente para evaluar la resiliencia de estas bioconstrucciones. Debido a su crecimiento por acreción en tres dimensiones, es necesario considerar otras variables informadoras de la estructura (grosor, altura, etc.) en estudios a largo plazo, además de tener en cuenta los organismos endobiontes. Gracias a algunos estudios de datación por radiocarbono, y de tasas de acreción estimadas en periodos cortos, se puede inferir que un arrecife desarrollado puede necesitar des de varias decenas a varios centenares de años en generarse (Sartoretto et al., 1996; Antonioli *et al.*, 1999; Silenzi *et al.*, 2004).

En la cuarta publicación, focalizada en las fitocenosis que prosperan en el interior de la plataforma, se observa un proceso convergente rápido entre los controles y los clareos (generalmente de menos de un año) independientemente del estado ecológico de las plataformas. Sin embargo, este proceso convergente, medido a partir de la variabilidad en la abundancia de las especies entre las parcelas control y las clareadas, no siempre indica una recuperación real. Se confunde también con el incremento de especies de crecimiento relativamente rápido, como el de las algas del género *Jania* spp., que colonizan rápidamente todas las parcelas (independientemente del tratamiento). Estas últimas llegan a ser muy abundantes tras el "estresante" filtro estival. Es por ello que los clareos hechos en mayo (justo antes del verano) o en la parte interna de la plataforma (con menor hidrodinamismo) parece que tengan una sucesión más rápida al aumentar este tipo de algas, tanto en los controles como en los susodichos clareos. Sin embargo, en la fase de producción (invierno y primavera), las diferencias se vuelven a acentuar cuando las especies estructuralmente más complejas (*E. elongata* en el caso de la localidad con bajo estado ecológico y dictyotales en el caso de la localidad con buen estado) crecen más en los controles. Esto implica que en el periodo desfavorable, estas especies ya deben presentar una mayor cobertura "críptica" en los controles, a modo de costra o ejes postrados. Por lo tanto, una vez más, la recuperación real no siempre se mide correctamente sólo a partir de la semejanza y variabilidad entre tratamientos. Tampoco parece que el estado ecológico implique una recuperación a distinta velocidad. Así, distintas especies pertenecientes a distintos grupos funcionales pueden presentar un rol semejante en zonas que difieren por su estado ecológico. En ambas situaciones, el verano actúa de estación limitante perjudicando a las especies más complejas, que decaen, y promoviendo especies de carácter más oportunista (Ulvales y *Jania* spp. entre otras). Este "filtro estival" es comparable, pero menos extremo, al observado en zonas intermareales tropicales donde el verano no permite ni siquiera la existencia de especies oportunistas, y donde cada año la sucesión empieza de "cero" (Hutchinson y Williams, 2003).

La fuerte estacionalidad de las especies dominantes, tanto en la localidad de bajo estado ecológico como en la de buen estado, junto a la falta de especies competidoras que puedan ocupar el espacio al mismo tiempo y por largos periodos, implica que el proceso convergente sea rápido y los efectos prioritarios (*priority effects*) poco intensos. Este patrón parece común en comunidades someras con especies de porte parecido al del presente estudio, donde se tiende a una convergencia hacia un estado final de recuperación (*endpoint*) previsible (Milazzo *et al*., 2004; Martins *et al*., 2018).

5. Aspectos abiertos

Tras el desarrollo de esta tesis han surgido nuevas preguntas a partir de los resultados observados. Los principales aspectos que pensamos que cabría investigar y clarificar los resumimos a continuación.

5.1 *El papel del herbivorismo por pequeños ramoneadores y otros herbívoros*

Al haber realizado una aproximación correlativa, cabe la posibilidad de haber subestimado el impacto real del herbivorismo en las plataformas de abrasión de algas y vermétidos. Sin embargo, pensamos que el papel de los grandes herbívoros (erizos y salpas) sólo puede ser relevante en las plataformas que presenten cierta profundidad o que tengan una proporción elevada de cubetas o grietas "profundas". En nuestras observaciones, incluso de noche, no hemos sido capaces de detectar erizos pastando en las zonas planas de las plataformas. De hecho, un experimento de exclusión de erizos sería inasumible en muchas de estas plataformas, sencillamente porque están ausentes. Por lo que respecta a las salpas (*Sarpa salpa*) se han visto en periodos de nivel del mar alto y en contadísimas ocasiones. Sin embargo, se han observado frecuentemente pequeños peces de roca (Blenniidae, Tripterygiidae, Gobiidae). Pensamos que su papel como condicionantes de la vegetación debe ser mínimo por su baja densidad (quizá sobrestimada). Sin embargo, está descrito su papel como consumidores de algas (Zander y Hagemann, 1989; Monteiro *et al*., 2005).

Durante la noche, se ha observado un incremento de caracolas (*Stramonita haemastoma*) junto a cangrejos. Ambos pueden tener un rol como consumidores de algas. En el caso de la caracola, la bibliografía indica que son principalmente carnívoras (Rilov *et al*., 2004a). Sin embargo, hemos detectado presencia de algas en ejemplares examinados durante la noche (sin dañarlos). En el caso de los cangrejos (sobretodo *P. marmoratus*), ya se indicó en la introducción, que su papel parece localizado en las cercanías de sus madrigueras (Safriel, 1975).

Finalmente, la abundancia de pequeños moluscos en la plataforma (Columbellidae, Cerithiidae, Skeneopsidae, etc.) se ha subestimado al pasar inadvertidos en el muestreo visual. Por todo ello, sería de sumo interés realizar experimentos manipulativos para detectar un posible papel de todos estos organismos como condicionantes del fitobentos asociado a las plataformas.

5.2 *La posible capacidad competitiva podría estar ligada al potencial productivo determinando la zonación*

En muchas ocasiones se atribuyen factores competitivos para explicar los patrones de distribución. En muchos casos subestimando otros procesos (no excluyentes) que pueden explicar esta distribución como el propio comportamiento de las esporas o de las larvas antes de reclutar (Amsler y Searles, 1980; Grosberg, 1982). Se trata de un aspecto que también explicitó Connell (1961) en sus trabajos clásicos acerca de la zonación de los cirrípedos, a pesar de que le otorgara menos relevancia que a los factores competitivos, predatorios o ligados al estrés.

También se ha visto que incluso la formación de monopolios de determinadas algas no indica necesariamente una exclusión competitiva (Stewart, 1989). A pesar de todo, la norma según la cual a mayor potencial productivo prosperan mejor las especies más competitivas parece de aplicación general tanto en el ambiente terrestre (Grime, 1977) como en el marino (Steneck y Dethier, 1994). Por lo tanto, en las plataformas, aquellas especies que viven en condiciones de menor potencial productivo (poca profundidad y zonas de bajo hidrodinamismo) probablemente también son menos competitivas. Así, en el Cabo de las Huertas, los clareos efectuados en la zona media de la plataforma, durante el óptimo de crecimiento de *Dictyota* spp., tenían una proporción de *Padina pavonica* mucho mayor que los controles monopolizados por *Dictyota* spp. En la zona interna, con menor hidrodinamismo y más sujeta a episodios de bajamar, como ya se ha descrito, la dominancia siempre fue de *P. pavonica*. Por otro lado, en la localidad alterada de Aguamarga, la dominancia de *E. elongata* se hacía más patente en la zona externa (con mayor hidrodinamismo) y los clareos beneficiaban a especies generalmente más restringidas a las zonas internas (Ulvales) o a algas articuladas más delgadas, de crecimiento más rápido (*Jania* spp.), así como a efemerofíceas (*Colpomenia sinuosa*).

Para demostrar interacciones competitivas haría falta realizar experimentos manipulativos que modificaran las abundancias de las especies, también con trasplantes a distintas zonas de la plataforma (Stewart, 1989; Melville y Connell, 2001).

5.3 *Las causas subyacentes al cambio de fase (phase shift) observado entre Cabo de las Huertas (buen estado ecológico) y Aguamarga (mal estado ecológico)*

Los cambios de fase en zonas urbanas son un tema abierto en los estudios bentónicos como ya se explicitó en la segunda publicación (ej: Benedetti-Cecchi *et al*., 2001; Mancuso *et al*., 2018). En nuestro caso, al ser un estudio correlativo, no se pudo demostrar relaciones de causalidad entre los estresores analizados (nutrientes y sedimentación) y las diferencias de composición entre Cabo de las Huertas y Aguamarga. Además, aunque la tendencia fue la esperada (con valores generales superiores en la localidad alterada de Aguamarga), las diferencias fueron menores de lo esperado. En el caso de la sedimentación pensamos que el método usado, una estimación rápida y visual, subestimó los valores de la localidad alterada especialmente durante el otoño y el verano. Además, en estas épocas y en la localidad alterada, observamos zonas dominadas por *Caulerpa cylindracea* muy desarrollada y con una capa de sedimento de varios centímetros de grosor análogas a las ya descritas (Piazzi *et al*., 2007). Por supuesto, métodos de cuantificación en volumen o en masa de sedimento hubieran sido mejores.

En el caso de los nutrientes, la escasa replicación puede haber sido un factor de sesgo o de infravaloración de la cantidad real en la localidad alterada. Pero pensamos que los datos podrían ser cercanos a la realidad (el muestreo fue balanceado y durante varias veces al año). Entonces, ¿por qué tales diferencias en la composición algal entre localidades? El sector alterado de Aguamarga podría presentar grandes fluctuaciones en la carga de nutrientes a partir de entradas masivas en momentos puntuales por emisarios y torrentes ubicados en zonas próximas; posiblemente también acompañadas de entrada de sedimento y de agua dulce. En cambio, el impacto de la desaladora, también próxima, sería irrelevante ya que sus efectos son muy localizados (Javier Aguilar y Fabio Blanco Murillo, com.pers.).

Por lo tanto, para entender estos cambios de fase, objetivo que ha quedado fuera de esta tesis, se requerirían, a nuestro entender, monitoreos continuos capaces de detectar estos posibles "pulsos". Además, el papel de la salinidad, no analizada en esta tesis, también podría ser relevante durante estos eventos (posiblemente ligados a momentos de lluvia intensa) actuando en sinergia con los otros estresores (Buosi y Sfriso, 2017). Los resultados de estos monitoreos se podrían probar experimentalmente mediante experimentos de enriquecimiento de nutrientes, caídas de salinidad e incremento de sedimentación simulando los posibles pulsos encontrados en la localidad alterada, y focalizando el estudio en la respuesta de las especies dominantes (en ambas localidades) a tales estresores (Gennaro *et al*., 2019; Zheng *et al*., 2019).

5.4 *El incremento de los eventos extremos y su interacción con factores antropogénicos podrían afectar la resiliencia de las comunidades asociadas a las plataformas*

En esta tesis, para el cálculo de la resiliencia se han considerado pulsos discretos y pequeños. Es decir, clareos puntuales que apenas afectan a las propiedades de la comunidad. ¿Qué ocurriría bajo perturbaciones más intensas o más recurrentes? Podrían existir respuestas distintas. Así, por ejemplo, Petraitis *et al*., (2009) encontraron que el tamaño del clareo podría determinar el resultado final en el intermareal protegido del golfo de Maine. De este modo, en clareos pequeños la norma era un retorno a la comunidad dominada por *Ascophyllum nodosum*, mientras que los clareos grandes (que simulaban el efecto de la abrasión causada por el hielo durante el invierno) favorecían la instalación de *Fucus vesiculosus* Linnaeus, o del mejillón (*Mytilus edulis*). De este modo, se podía hablar de múltiples estados estables dependiendo del tamaño de la perturbación.

En experimentos realizados en comunidades de *Cystoseira amentacea* (Benedetti-Cecchi *et al*., 2015; Rindi *et al*., 2017), se observó que la respuesta de la comunidad ante un clareo puede estar determinada por el estado del dosel de *Cystoseira*. Si la cobertura del dosel es densa, el clareo se recupera. En cambio, en un estado del dosel alterado, la recuperación se ve dificultada hasta un punto de no retorno. Entonces, se produce un cambio de fase donde la comunidad de *Cystoseira* es sustituida por especies formadoras de "turf".

En el caso de las especies exóticas, también se ha visto que su capacidad de ocupación en un mismo hábitat puede depender de factores externos como el estado ecológico colindante. Así, un estado degradado generalizado puede aumentar la abundancia de una especie exótica, como se ha visto en la segunda publicación, y esto podría incrementar su capacidad de ocupación en otros hábitats (incluso en buen estado) por la mayor presión de propágulos. Esto parece haber ocurrido en el caso del mejillón invasor *Brachydontes pharaonis* en la cuenca oriental del Mediterráneo, cuando en algunas plataformas degradadas la discontinuidad del arrecife de algas y vermétidos permitió aumentar su reclutamiento ocupando estas plataformas. Ello incrementó la oferta de propágulos de *B. paharaonis* acentuando su efecto como invasor incluso en comunidades no alteradas (Rilov *et al*., 2004b; Didham *et al*., 2007).

En un escenario de cambio global donde los fenómenos extremos, como las tormentas y los eventos de bajamar, pueden incrementar su frecuencia (Easterling et al., 2000; Zamir et al., 2018), parece obligado incorporar estos factores de “extremicidad”, junto a los condicionantes antropogénicos, en futuros estudios manipulativos vinculados a las plataformas de abrasión que, por su accesibilidad y fragilidad, pueden jugar un papel, a modo de avanzadilla, de lo que ocurre en otros sistemas bentónicos.

CONCLUSIONES

1. La oferta de recurso (*bottom-up control*) parece de mayor importancia que la herbivoría, como condicionante de la estructura y dinámica del fitobentos asociado a las plataformas de vermétidos y coralináceas. Las algas se distribuyen en función del potencial productivo, tanto espacial como estacionalmente, siendo estructuralmente más complejas, y de mayor porte, cuando dicho potencial resulta mayor.

2. Se observa una fase de desarrollo y otra de decaimiento a lo largo del ciclo anual. Sin embargo, la segunda sólo coincide con un proceso de diversificación en el estado alterado, mientras que en el buen estado ecológico, la fase de desarrollo coincide con un proceso de diversificación.

3. El estado ecológico degradado parece un condicionante clave para la ocupación de *Caulerpa cylindracea* en las plataformas de vermétidos, aprovechando la inestabilidad del dosel, sobre todo en verano, para crecer y ocupar el espacio.

4. Existe una convergencia evidente de todas las comunidades de plataforma analizadas tras una pequeña perturbación discreta (*small pulse disturbance*). La estacionalidad de las especies y la falta de competidores similares, que coincidan en su óptimo temporal, parecen explicar dicha convergencia.

5. La velocidad de recuperación (resiliencia), tras la perturbación, de las comunidades de la plataforma, no parece determinada por el estado ecológico de las localidades estudiadas. Especies y grupos funcionales distintos, en función del grado de alteración, pueden tener un rol parecido que determina la capacidad de recuperación (Dictyotales en zonas no alteradas y *Ellisolandia elongata* en zonas alteradas).

6. El uso de placas experimentales podría tener utilidad como técnica de restauración para potenciar el reclutamiento de las especies ingenieras implicadas en la generación del arrecife de vermétidos. A pesar de la lenta acreción de la bioconstrucción, la relativa facilidad de colonización de dichas especies, en pocos años, lo justificaría (elevada densidad de reclutas de *Dendropoma* y alta cobertura de *Neogoniolithon* en estado fértil).

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