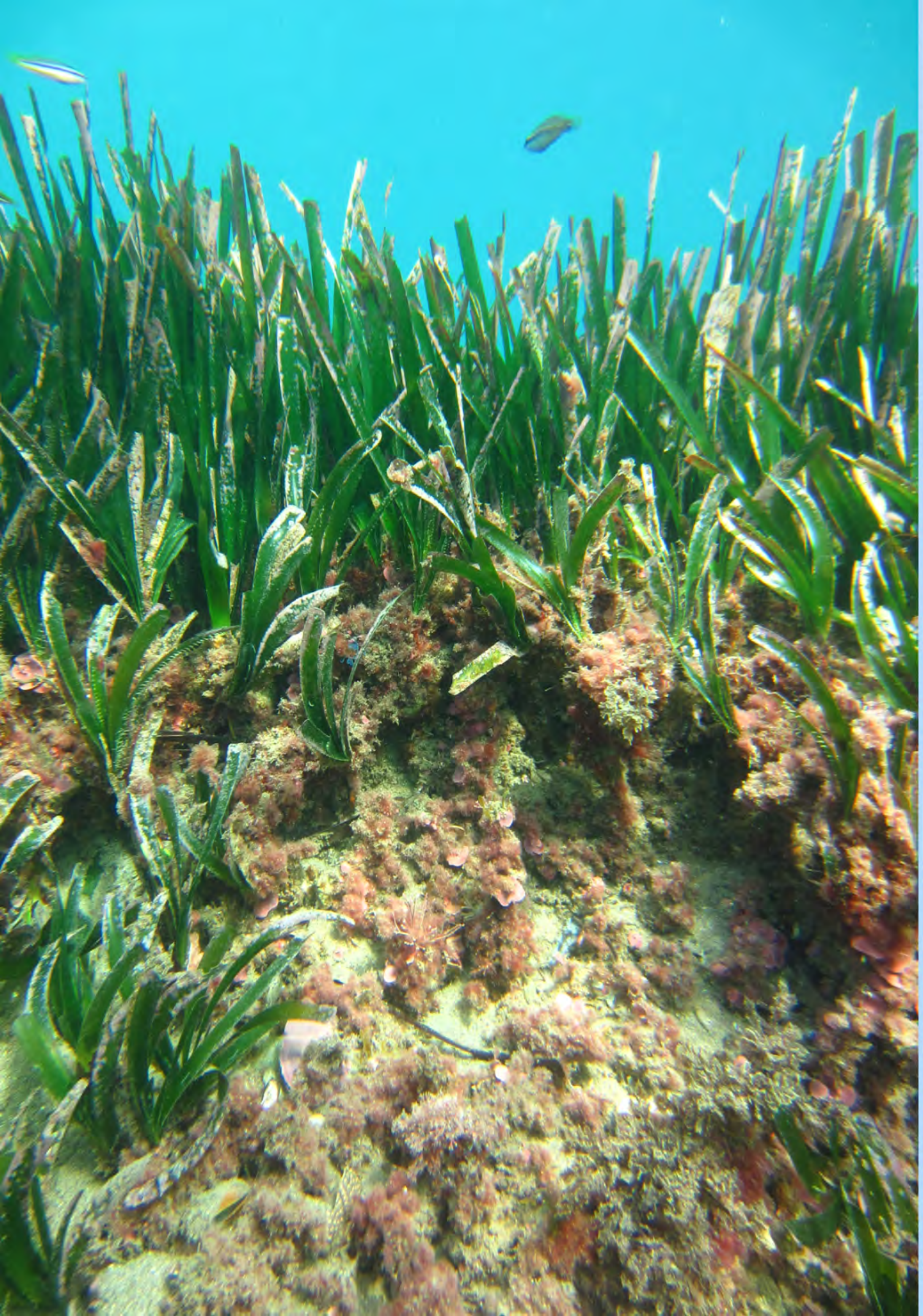


2016

Tesis Doctoral

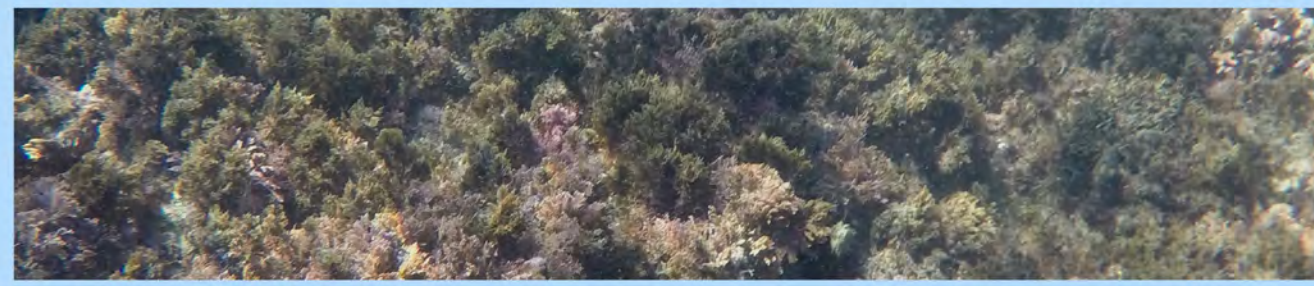
Ángel Mateo Ramírez

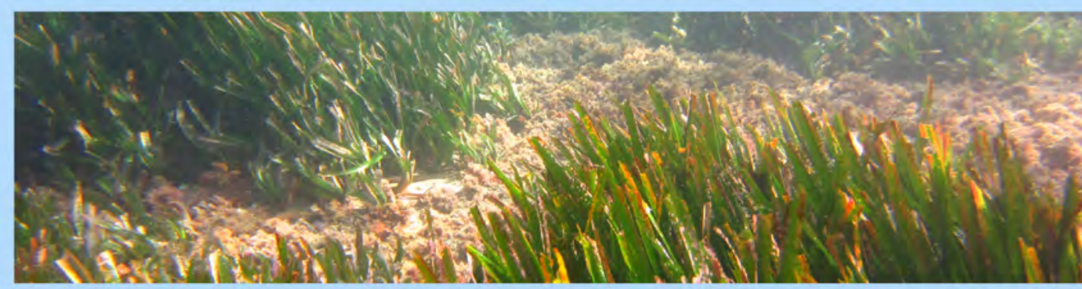
Tesis Doctoral/PhD Thesis

UNIVERSIDAD DE MÁLAGA

Comunidades de crustáceos decápodos asociados a fondos someros de fanerógamas y macroalgas en el sur de España

Crustacean decapod communities associated with shallow bottoms of seagrass meadows and their relation with neighbouring biotopes in South Spain





Ángel Mateo Ramírez

2016

TESIS DOCTORAL

Comunidades de crustáceos decápodos asociados a fondos superficiales de fanerógamas marinas y su relación con biotopos colindantes en el sur de España

PhD Thesis

Crustacean decapod communities associated with shallow bottoms of seagrass meadows and their relation with neighbouring biotopes in South Spain

por/by Don Ángel Mateo Ramírez

dirigida por/supervised by Prof. Dr. José Enrique García Raso

Departamento de Biología Animal

Facultad de Ciencias

Universidad de Málaga

AUTOR: Ángel Mateo Ramírez
http://orcid.org/0000-0002-3825-3279

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Universidad de Málaga

UNIVERSIDAD
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Facultad de Ciencias
Departamento de Biología Animal

D. JOSE ENRIQUE GARCÍA RASO, Profesor Catedrático del Departamento de Biología Animal de la Facultad de Ciencias de la Universidad de Málaga.

CERTIFICA:

Que la presente memoria titulada "**Comunidades de crustáceos decápodos asociados a fondos superficiales de fanerógamas marinas y su relación con biotopos colindantes en el sur de España**" presentada por el Licenciado en Ciencias Biológicas Ángel Mateo Ramírez, ha sido realizada bajo mi dirección y las publicaciones que la avalan no han sido utilizadas en tesis anteriores.

Como director de tesis, considerando que la presente memoria reúne todos los requisitos para ser sometida a juicio de la Comisión correspondiente, por lo que autorizo su exposición y defensa para la obtención del grado de Doctor en Ciencias Biológicas con mención Europea.

Y para que así conste, en cumplimiento de las disposiciones vigentes, firmo la presente acreditación en Málaga, a 09 de noviembre de 2015.

Fdo.: Dr. José Enrique García Raso

UNIVERSIDAD
DE MÁLAGA

Facultad de Ciencias
Departamento de Biología Animal

Visado en Málaga a 09 de noviembre de 2015

El director

Fdo.: Dr. José Enrique García Raso

Prof. Catedrático del departamento de Biología Animal

Universidad de Málaga

Memoria presentada para optar al grado de Doctor en Biología

Fdo.: Ángel Mateo Ramírez

A mis tres Marías, mi padre y hermana

Familia y amigos

"*Muchas personas atacan al mar, yo le hago el amor*". Jacques Cousteau

Agradeciminetos

Enfrentarse a una tesis es duro, y más sin la ayuda de una beca de formación, ya que a los momentos duros a los que todos los doctorandos nos enfrentamos, se le suma el buscar medios para poder sustentarte. Una situación que es difícil de entender y que solo puede mantenerse por la devoción por lo que haces y por el apoyo de todas aquellas personas que han estado cerca ti. Han sido muchas personas las que he conocido en estos ocho años y de las que he aprendido mucho tanto a nivel profesional como personal.

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Y a mis padres y hermana, para los que todo lo que escriba es poco. Me han dado la oportunidad de vivir esta aventura, sin importarles nada y sacrificándose por mi. Por ellos y por todo lo vivido haré que "esto" tenga sentido y pueda ser mi forma vida.

Índice

CAPÍTULO 1

Introducción General

1.1 Praderas de fanerógamas marinas y fondos de algas infralitorales en el mar de Alborán

De las alrededor de las 60 especies de fanerógamas marinas existentes en todo el mundo (Short y Coles 2001), cuatro son las especies presentes en el mar de Alborán: *Posidonia oceanica* (Linnaeus) Delile, *Cymodocea nodosa* (Ucria) Ascherson, *Zostera noltei* Hornemana, *y Zostera marina* Linnaeus.

Las praderas del endemismo mediterráneo *P. oceanica* son las más extensas tanto en el mar Mediterráneo como en Alborán (Figura 1). Dentro de Alborán la mayoría de las praderas y las que mejor estado de conservación presentan, se encuentran en la provincia de Almería, representando un 82% del total de la superficie ocupada en toda Andalucía, unas 6139,56 ha (Junta Andalucía, 2013). En Granada las praderas se concentran en el parte oriental, entre Cala Chilches y Castel de Ferro, presentando un grado de conservación aceptable. En Málaga las praderas aparecen como parches discontinuos con formas y tamaños variables catalogándose como semipraderas. Estas semipraderas aparecen de forma irregular y dispersa sobre sustrato rocoso principalmente y se concentrán en tres sectores: sector oriental, en el tramo comprendido entre Molino de Papel (Paraje Natural de Maro y cerro Gordo)-Nerja; sector central, en el tramo comprendido entre Punta Calaburras-Calahonda; y sector occidental, Estepona y Punta Chullera, donde *P. oceanica* encuentre su límite occidental de distribución. La influencia atlántica y el aumento de la turbidez de las aguas hace que tanto los valores de densidad global (teniendo en cuenta la densidad de haces y la cobertura de la pradera), como el límite inferior de las praderas, disminuyan a medida que nos acercamos al estrecho de Gibraltar, siendo en Málaga, en donde las praderas presentan las densidades globales más bajas. Igualmente el límite inferior sube desde los 30m de profundidad del levante Almeriense, hasta unos 6 m en la zona de Punta Calaburras-Calahonda (Tintoré *et al*. 1988; Moreno y Guirado 2003; Luque y Templado 2004; García Raso *et al*. 2010; Junta de Andalucía 2013).

La floración de *P. ocenica* es un hecho relativamente esporádico, en el cual, la temperatura del agua parece tener un papel importante, pues floraciones masivas se ha detectado tras veranos excesivamente calurosos (Díaz-Alamela *et al*. 2006; Urra *et al*. 2011b). De hecho, en 2009, se detecto una floración masiva a lo largo del litoral andaluz, registrándose unas densidades de flores de entre 40 flores/m^2 en las praderas de Melicena (Granada), 50-200 flores/m^2 en las del Paraje Natural de Maro y Cerro Gordo (Málaga) y 4-184 flores/m^2 en las del LIC de Calahonda (Málaga) (Urra *et al.* 2011b; Junta de Andalucía 2013). En Almería, no obstante se han registrado floraciones durante tres años consecutivos (2001-2003), si bien, las densidades de flores fueron mucho menores (Moreno y Guirado 2006).

La segunda especie en extensión es *C. nodosa,* especie de aguas cálidas (Pérez-Llorents *et al.* 2014), la cual presenta una extensión de 119,38 ha en toda Andalucía, de las cuales 100,43 ha corresponden al mar de Alboran (Almería principalmente) y 18,93 ha a la costa atlántica de Andalucía (Cádiz). Esta especie es la que presenta una distribución más continua a lo largo del litoral andaluz (Figura 2), formando tanto praderas mixtas con *P. oceanica* y *Z. noltei* como praderas monespecíficas. No obstante ha sufrido un elevado grado de regresión durante los últimos años desapareciendo praderas en las provincias de Málaga y Granada (Moreno y Guirado 2003; Junta de Andalucía 2013).

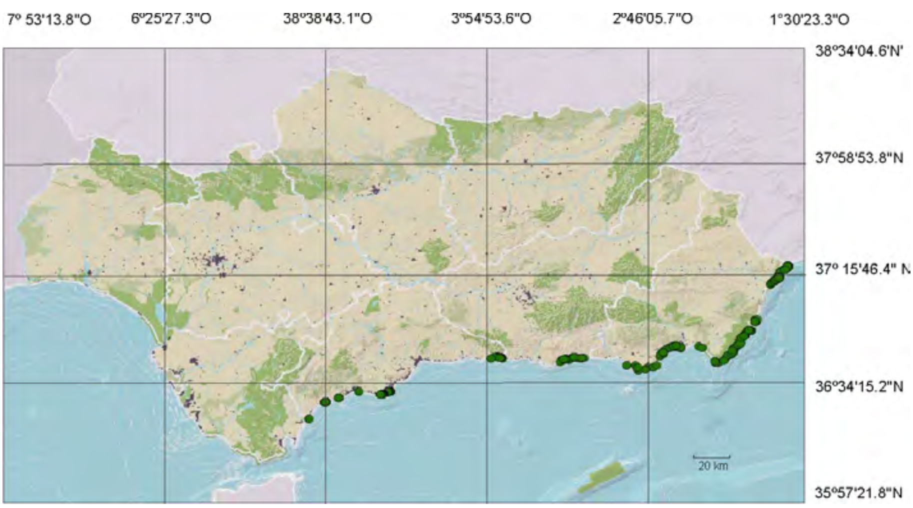

Figura 1. Distribución de *Posidonia oceanica* en el litoral andaluz a partir de las observaciones realizados por el equipo de medio marino del Programa de Gestión Sostenible del Medio Marino Andaluz de la Consejería de Medio Ambiente y Ordenación del Territorio de la Junta de Andalucía entre para el periodo 2004-2013 (Modificada del Informe de Programa de Gestión Sostenible del Medio Marino 2013).

Las dos últimas especies son las menos abundantes. *Z. noltei* es una especie templada que habita tanto aguas atlánticas (desde Noruega hasta Mauritania) como aguas mediterráneas, siendo especialmente abundante en los estuarios de la vertiente atlántica de Andalucía. Dentro de Alborán solo se encuentra en ciertas zonas someras del litoral almeriense y Algeciras (Phillips y Meñez 1988; Luque y Templado 2004) (Figura 3).

Por otro lado, Z. *marina*, que es una especie circumboreal, que encuentra su límite de distribución meridional en una zona cercana a Gibraltar (Philips y Meñez 1988; Luque y Templado 2004; Perez-Llorents *et al.* 2014). La fuerte influencia atlántica que presenta el mar de Alborán hace que su abundancia sea mayor en él que en el resto del mar Mediterráneo (Rueda *et al.* 2008b). Sin embargo esta especie, es la que ha sufrido una regresión más severa, principalmente en Granada y Málaga, donde se considera desaparecida, pudiendose constatar su presencia solamente en el saco interno de la bahía de Cádiz (Junta de Andalucía 2013) (Figura 4).

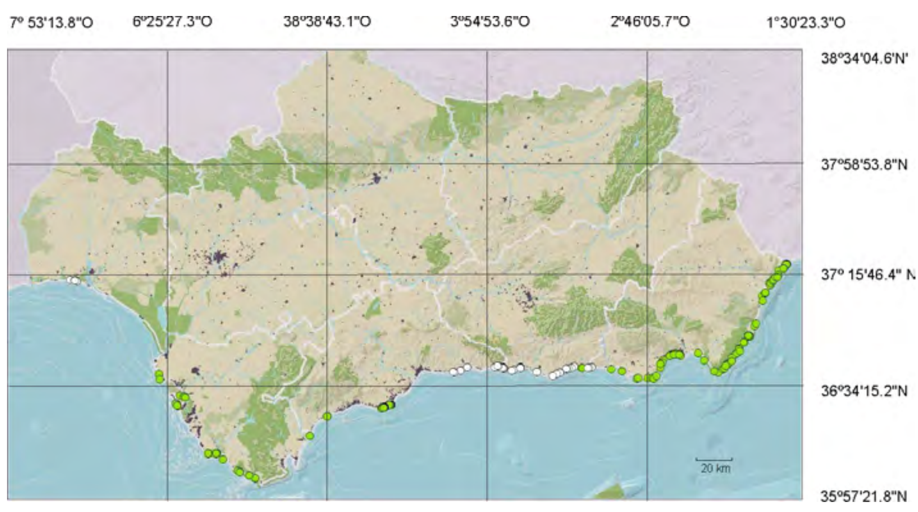

Figura 2. Observaciones de *Cymodocea nodosa* a lo largo del litoral Andaluz a partir de los datos obtenidos por parte del Programa de Gestión Sostenible del Medio Marino Andaluz. En verde se señalan las observaciones correspondientes a la presencia actual de biocenosis de esta especie. En blanco se señalan las biocenosis que por diversos motivos han regresionado y actualmente se consideran desaparecidas (Modificada del Informe de Programa de Gestión Sostenible del Medio Marino 2013).

Figura 3. Observaciones de *Zostera noltei* a lo largo del litoral Andaluz a partir de los datos obtenidos por parte del Programa de Gestión Sostenible del Medio Marino Andaluz. En amarillo se señalan las observaciones correspondientes a la presencia actual de biocenosis de esta especie. En blanco se señalan las biocenosis que han regresionado y actualmente se consideran desaparecidas (Modificada del Informe de Programa de Gestión Sostenible del Medio Marino 2013).

Figura 4. Observaciones de *Zostera marina* a lo largo del litoral Andaluz a partir de los datos obtenidos por parte del Programa de Gestión Sostenible del Medio Marino Andaluz. En verde se señalan las observaciones correspondientes a la presencia actual de esta especie. En blanco se señalan las biocenosis que por diversos motivos han sufrido una regresión y actualmente se consideran desaparecidas (provincias de Málaga y Granada) o que no se puede asegurar su presencia como ocurre en la provincia de Almería (Modificada del Informe de Programa de Gestión Sostenible del Medio Marino 2013).

Por otra parte, las comunidades de algas fotófilas más característica del Mediterráneo occidental son aquellas dominadas por especies pertenecientes al género *Cystoseira*. Estas comunidades son muy diversas y están constituidas por diferentes estratos.1) formas incrustantes y pulviniformes (*Valonia*, *Peyssonnelia*, *Mesophyllum*,…); 2) formas cespitosas (*Halimeda*, *Cladophora*,..); 3) formas erectas bajas o “arbustivas” (*Diginea*, *Dictyopteris*,…) y formas erectas altas o “arbóreas” (*Cystoseira* spp) (Figura 5). Sin embargo, en Alborán, comunidades bien estructuradas con dominancia de especies de *Cystoseira* solo aparecen en Cabo de Gata. A medida que nos acercamos al estrecho de Gibraltar las comunidades de macrófitos van cambiando, aumentando la presencia y la abundancia de especies atlánticas. En las provincias de Málaga y Cádiz son muy abundantes las comunidades de la rodófita invasora *Asparagopsis armata* Harvey, la cual puede llegar a formar un ancho cinturón, desplazando a numerosas especies

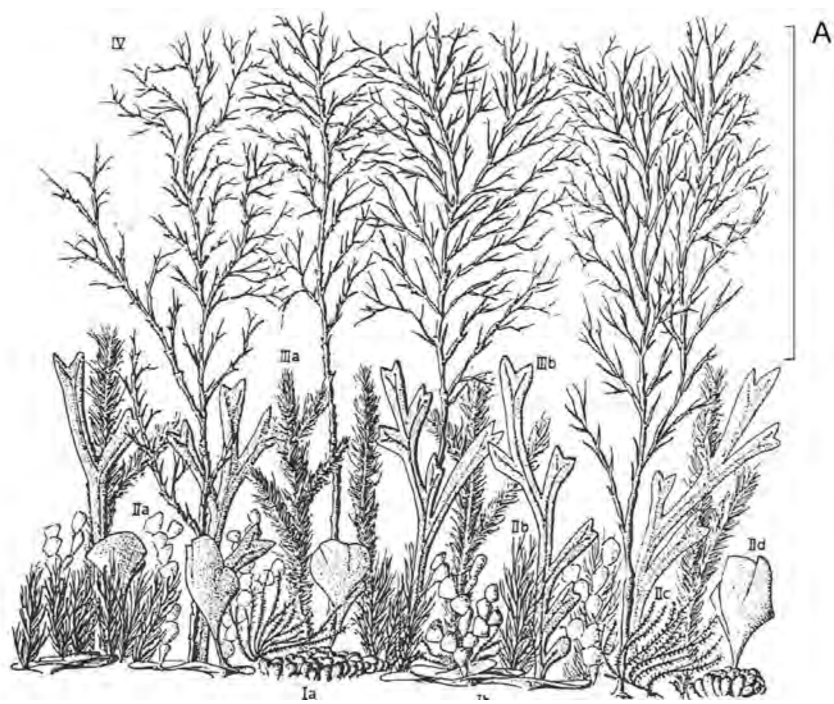

Figura 5. Esquema de la disposición en varios estratos de la vegetación algal de una comunidad de *Cystoseira* infralitoral. I, formas incrustantes y pulviniforme II, formas cespitosas. III, formas erectas bajas “arbustivas”. IV, formas erectas altas “arbóreas”. A, el estrato arbóreo está muy poco desarrollado o ausente en las comunidades de algas del ZEC”Calahonda”(Modificada de Margalef 1989).

de algas autóctonas, tanto de zonas iluminadas como parcialmente umbrías. Además se observa una simplificación y miniaturización de la comunidad, como consecuencia de la sustitución del estrato arbóreo por el arbustivo, el cual se encuentra dominado por especies como la feofita *Halopteris scoparia* (Linnaeus) Sauvageau (Conde y Seoane 1982; Conde 1989; Margalef 1989; Flores-Moya 1989; Ballesteros 1993; Flores-Moya *et al*. 1995; Conde *et al*. 1996; Luque y Templado 2004; Cobos y Ortega 2010).

1.2 Pérdida de hábitat y sus efectos sobre las asociaciones de invertebrados

El mar Mediterráneo, a pesar de representar solamente un 0,8% del volumen total de todos los océanos del mundo, está considerado como un punto caliente u "hot spot" de diversidad marina, presentando un 7% del total de las especies animales y vegetales conocidas actualmente, de las cuales, el 20,2% son endemismos mediterráneos. Las últimas estimaciones indican que en el mar Mediterráneo viven unas 17,000 especies de organismo, siendo los invertebrados los más numerosos con 11,000 especies. Sin embargo esta riqueza de especies no presenta una distribución homogénea, siendo la cuenca noroccidental más rica que la suroriental (Boudouresque 2004; Coll *et al*. 2010). De igual manera las aguas de la plataforma continental, por encima de los 200m, son las que acumulan la mayoría de la biodiversidad, especialmente la zona batimétrica comprendida por encima de los 50m (Fredj *et al*. 1992; Boudouresque 2004; Coll *et al*. 2010). Esta es la zona donde habitan las fanerógamas marinas y algas fotófilas, no obstante, la desaparición de estas marca el límite inferior del piso infralitoral (Pérès y Picard 1964). Desgraciadamente la mayoría de las presiones antropogénicas se concentran principalmente en este piso, impactando sobre las praderas de fanerógamas marinas y los fondos de algas fotófilas. Actividades como el desarrollo costero (construcción de puertos, espigones, etc.), la pesca ilegal con barcos de arrastre a profundidades menores de los 50m o el fondeo de embarcaciones deportivas tienen un efecto directo sobre las praderas de macrófitos y angiospermas marinas, al arrancarlas o eliminar el hábitat donde se desarrollan, ej. los sustratos duros sobre los que crecen las algas. Otras actividades tienen un efecto indirecto, en relación con la calidad del agua. La resuspensión de sedimentos generada por las obras costeras o la regeneración de playas, así como la eutrofización producida por la polución o por los aportes de materia orgánica provenientes de las industrias, emisarios o piscifactorias, traen consigo una reducción en la claridad del agua, disminuyendo la cantidad luz que llega al fondo. Además, las sustancias tóxicas o metales pesados que puedan venir en estos vertidos tienen también un efecto directo sobre la flora y fauna bentónica (Walker y Kendrick 1998; Delgado *et al*. 1999; Duarte 2002; Boudouresque 2006a; González-Correa 2008; Rueda *et al*. 2008a; Kiparissis *et al*. 2010). Otras amenazas relacionadas con actividades antropogénicas son las especies invasoras y el cambio climático, no obstante Boudouresque (2006a) cita que el 6,5% de la flora presente en el Mediterráneo tienen un origen haloctono y Marbà y Duarte (2010) encontraron una correlación positiva entre el calentamiento del Mediterráneo y el aumento de la mortalidad de haces en *P. oceanica*.

Todas estas amenazas y presiones traen consigo una degradación de las praderas de fanerógamas marinas y fondos de macroalgas, pudiendo llegar a provocar la desaparición las mismas. Existen diferentes ejemplos de regresiones de praderas de *P. oceanica* en el Mediterráneo relacionadas principalmente con la polución, como en el Golfo de Trieste o en zonas cercanas del Lago de Venecia, con el desarrollo costero, como ocurrió en la Riviera Francesa o por una combinación de diferentes factores (pesca, regeneración de playas, acuicultura…) como se ha documentado en España, donde el 58% de las praderas de *P. oceanica* y el 52% de las fanerógamas de la costas catalanas y cercanas a Alicante respectivamente, han regresionado en las últimas décadas (Meinesz *et al*. 1991; Caressa *et al*. 1995; Rismondo *et al*. 1997; Airoldi y Beck 2007). En el caso de las praderas macroalgas (en referencia a fucales como *Cystoseira* spp. y *Sargassum* spp.) también hay ejemplos de regresiones locales en el Mediterráneo, tanto en España, Francia, Croacia, Italia como en Rumania (Sfriso 1987; Munda 1993; Rodríguez-Prieto y Polo 1996, Thibaut *et al*. 2005; Zaitsev 2006). Las causas son varias pero principalmente incluyen un aumento desproporcionado en las poblaciones de erizos y una disminución en la calidad del agua, como consecuencia de la polución y/o la sedimentación (Airoldi y Beck 2007). Con frecuencia, estas regresiones son mayores en las zonas más profundas, de manera que lo que se produce es una disminución en su rango batimétrico, convirtiéndolas en fondos de algas más someros. En otras ocasiones estas praderas son sustituidas por lo que se denomina en inglés "urchin barren/barren grounds", la cual suele estar dominada por especies de coralinaceas, bancos de mejillones, macrófitos efímeros y erizos (Munda 1993; Boudouresque y Verlaque 2001; Guidetti *et al.* 2003; Thibaut *et al.* 2005).

Esta degradación del hábitat suelen traer consigo una pérdida de diversidad, no solo a nivel de abundancia o riqueza específica, sino también en relación a la diversidad funcional (en relación con atributos funcionales como: el tamaño o la categoría trófica de las especies) y a la diversidad espacial o entre hábitats (ß diversidad) (en Arioldi y Beck 2007) (Figura 6). Las casusas de esta pérdida de diversidad son: 1) la desaparición de especies propias y el aumento de especies generalistas, lo que también se conoce como "homogenización biótica", 2) la pérdida de fuentes de alimentos ,ya que por ejemplo, las praderas de fanerógamas marinas o los bosques de macroalgas, así como todos los animales asociados a estos hábitats crean un hábitat más complejo con muchos más recursos, parte de los cuales desaparecerían a consecuencia de la degradación del hábitat y por último, 3) la pérdida de funciones y propiedades ecosistemicas, en relación con la influencia de la complejidad estructural del hábitat sobre el medio, como por ejemplo la modificación del hidrodinamismo, de las condiciones lumínicas o de la sedimentación, así como de su función protectora (Mckinney y Lockwood 1999; Airoldi *et al.* 2008) (Figura 6).

Por otro lado hay trabajos que demuestran que hábitats fragmentados formados por diferentes biotopos dan lugar a un hábitat más complejo y diverso (Boström *et al.* 2006; Mateo-Ramírez y García Raso 2012; Urra *et al.* 2013a). Algo similar encontraron Dean y Conell (1987 a, b, c) en comunidades de macroinvertebrados asociados a algas, cuyas máximas abundancias y riqueza de especies se obtuvieron durante las etapas intermedias de la sucesión, en relación con la mayor diversidad de algas y su mayor complejidad (biomasa y área). Esto puede estar relacionado con los efectos de la fragmentación de un hábitat sobre la fauna asociada, los cuales están a su vez condicionados por diferentes factores como 1) el cambio en la configuración del hábitat, 2) la distancia entre esos parches, 3) su tamaño y 4) la diversidad de hábitats presentes entre los diferentes parches (Farhrig, 2003). Boström *et al.* (2006), hicieron una revisión bibliográfica sobre las praderas de fanerógamas y su relación con la fauna asociada, y encontraron que la fragmentación de las fanerógamas no tiene por qué tener un efecto negativo sobre los animales asociados. Por ejemplo si esa fragmentación

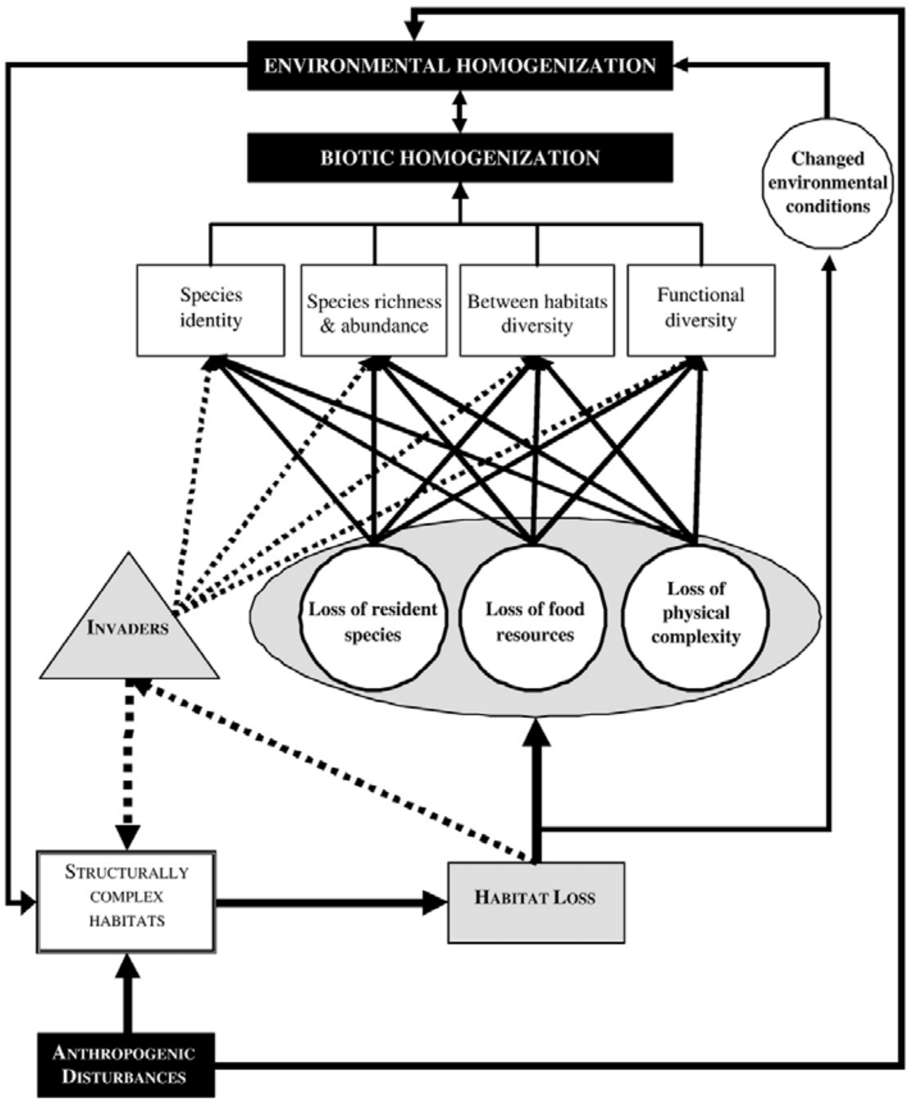

Figura 6. Diagrama mostrando la conexión entre la pérdida de hábitat y los patrones de diversidad, posibles feedbacks entre los diferentes procesos y el resultado global de la homogenización biótica. (Tomado de Airoldi *et al.* 2008).

es consecuencia de la presencia de una especie de alga invasora o por adición de estructuras antropogenicas, estos nuevos hábitats pueden proporcionar beneficos para ciertas especies, pues ambos son hábitats estructurales (Boström *et al*. 2006). Por otro lado esa fragmentación del hábitat puede beneficiar a ciertas especies al disminuir la presión depredadora sobre ellas (ya que la búsqueda de alimento es más difícil en una pradera fragmentada, pues el depredador necesita moverse más y seleccionar el parche adecuado, lo que a su vez lo expone a otros depredadores) (Micheli y Peterson 1999; Hovel y Lipcius 2001) o al permitir la llegada de especies foráneas (Irlandi 1994). No obstante, la fragmentación del hábitat es algo a evitar pues es una amenaza para la conservación de la biodiversidad, tanto en los ecosistemas marinos como en los terrestres, ya que los hace más vulnerables (Bell *et al*. 2001; Tscharntke *et al*. 2002).

1.3 Decápodos y conectividad entre hábitats

Los decápodos son animales que poseen una gran capacidad de desplazamiento, no solo por su capacidad locomotora sino también por su fase plantónica. Estás características les permite poder desplazarse entre diferentes hábitats y/o zonas, que pueden llegar a estar separadas por grandes distancias, estableciendo una conexión poblacional entre ellas (Chiswell *et al*. 2003). El ejemplo más extremo lo representan las especies pertenecientes al infraorden Achelata. Todas estas especies se caracterizan por la presencia de una etapa larvaria denominada filosoma, la cual presenta unas características (cuerpo transparente, dorsoventralmente aplanado y apéndices con muchas setas) que les permiten permanecer durante un largo periodo de tiempo en el plancton. Se ha constatado que filosomas de ciertas especies de langosta como *Jasus edwardsii* (Hutton, 1875), pueden persistir en el plancton hasta 24 meses (Booth 1994; von der Heyden *et al*. 2007). Esto combinado con las corrientes predominantes puede llegar a transportar a las filisomas de esta especie miles de kilómetros, estableciendo una conexión poblacional (Chiswell *et al*. 2003).

Además ciertas especies realizan migraciones entre las zonas de cría y los hábitats donde residen los adultos, como es el caso de la langosta del Caribe, *Panulirus argus* (Latreille, 1804), *Panulirus ornatus* (Fabricius, 1798) o *Panulirus cygnus* George, 1962 (Gillanders *et al*. 2003). Por otra parte los adultos de *P. argus* y de la langosta roja, *Palinurus elephas* (Fabricius, 1787) también realizan ciertas migraciones. En el primer caso están relacionadas con las tormentas otoñales, de manera que las langostas se desplazan hacia aguas más profundas para huir de dichas tormentas (Kanciruk y Herrnkind 1978). Mientras que en el segundo caso ocurre al contrario, durante el periodo pre-reproductivo suben desde aguas profundas a aguas someras para desovar (Ansell y Robb 1977; Goñi *et al*. 2001).

Otros ejemplos bastantes característicos lo representan las especies pertenecientes a la familia Penaidae. En estas especies tanto los adultos como los juveniles viven en hábitats diferentes. Los primeros viven y se reproducen en fondos blandos que pueden llegar a estar localizados a centenares de kilómetros de la costa. Las larvas que surgen de estos ejemplares pasaran al plancton, siendo arrastradas, con la ayuda de las corrientes y las mareas, hacia zonas estuáricas y/o de manglares. A partir de donde subirán río arriba para pasar a la fase de juvenil. Por último, estos juveniles migraran devuelta a los fondos blandos de donde surgieron como larva, donde se convertirán en adultos y cerraran el ciclo (Staples y Vance 1986; Guillanders *et al*. 2003; Ferreira y Freire 2009).

Estos casos son muy llamativos, ya que las especies recorren grandes distancias. Sin embargo hay otras especies que si bien no realizan grandes migraciones, si que hacen un uso diferente de hábitats cercanos. Por ejemplo, *Processa edulis* (Riso 1816), *Sicyonia carinata* (Brünnich, 1768) o *Liocarcinus* spp. son especies asociadas a fondos blandos pero que se desplazan a otros hábitats como praderas de fanerógamas marinas y/o macroalgas para alimentarse, dichos desplazamientos se producen principalmente durante la noche (Chessa *et al*. 1989; García Raso *et al*. 2006a). Estas migraciones o movimientos diarios (día/noche), son frecuentes entre estos biotopos (Ledoyer, 1966, 1984). Otro ejemplo podría ser *Pilumnus hirtellus* (Linnaeus, 1761). Esta especie está asociada principalmente a macroalgas, pero puede utilizar diferentes hábitats cercanos, tales como *P. oceanica* o concrecionamientos de *Meshophyllum alternans* (Fosile) Cabioch & M.L. Mendoza, a modo de "guardería" (García Raso 1988; López de la Rosa y García Raso, 1992; Mateo-Ramírez *et al*. 2015).

Las fanerógamas marinas y ciertas especies de algas presentan una cierta similitud estructural al presentar tanto un estrato superior (hoja-filoide) como otro inferior (rizoma-cauloide y rizoide). Esto hace que ambos hábitats den refugio y alimento a un gran número de especies bentónicas, muchas de las cuales, además, comparten ambos hábitats (Rueda y Salas 2003; López de la Rosa *et al.* 2002,2006; Urra *et al.* 2013a,b). No obstante, entre el 20-25% de todas las especies presentes en el Mediterráneo pueden encontrarse en las praderas de *P. oceanica* (Boudouresque *et al.* 2007).

1.4 Área de estudio

1.4.1 Descripción del Lugar de Interés Comunitario "Calahonda"

El estudio se realizó en dos zonas, Punta Calaburras (36º30'23" N - 04º38'41"W) y Calahonda (36º29'21"N - 04º41'55"W), esta última situada dentro del LIC de "Calahonda". Este espacio fue propuesto por la Junta de Andalucía en Diciembre de 2002 (código ES6170030) y aprobado como LIC por Decisión de la Comisión Europea, el 19 de Julio de 2006 (2006/613/CE). Este LIC fue justificado, en su momento, por la presencia de praderas de *P. oceanica* (hábitat 1120; *Posidonion oceanicae*), las cuales presenta aquí una de las poblaciones más occidentales dentro de su rango de distribución (Luque y Templado 2004).

Sin embargo un estudio posterior, realizado por García *et al.* (2006b), aportó una visión más amplia y detalla de los fondos presentes tanto en el mismo LIC como en zonas aledañas de interés, ampliando el número de hábitat incluidos dentro de la Directiva Hábitats. Añadiendo el hábitat 1110 "Bancos de arena cubiertos permanentemente por agua marina, poco profunda", dentro del cual se incluyen los fondos con pequeñas fanerógamas marinas pertenecientes al *Zosteretum marinae* y *Cymodoceiton nodosae* y el hábitat 1170 "Arrecifes". Según Templado *et al.* (2009), "arrecifes son todos aquellos sustratos duros compactos que afloran sobre fondos marinos en la zona sublitoral (sumergida) o litoral (intermareal), ya sean de origen biogénico o geológico". En el caso del LIC de

"Calahonda" hay dos tipos de fondos que casan perfectamente con esta definición, como son las formaciones rocosas superficiales cubiertas por algas fotófilas, el estrato infrapidícola asociado y el fondo de coralígeno con gorgonias localizado entre 10-25m de profundidad (Laja del Almirante; Cabopino). Además en las rocas infralitorales son abundantes las facies del mejillón *Mytilus galloprovincialis* Lamarck, 1819 e hidrozoos, así como asociaciones de algas como *Cystoseira tamariscifolia* (Hudson) Papenfuss, *Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders, o *Halopteris scoparia*, todas ellas citadas en la descripción del hábitat 1170 (Templado *et al*. 2009; García Raso *et al*. 2010). Esta última especie junto con *Halopteris filicina* (Grateloup) Kützing, forman densas manchas o cinturones de aspecto característico (con forma de brocha), que generan un hábitat predilecto para numerosos especies de moluscos y crustáceos (García Raso *et al*. 2010, Urra *et al*. 2013b).

En estos fondos rocosos también habitan especies protegidas como por ejemplo la lapa *Patella ferruginea* Gmelin, 1791, los gasterópodos pertenecientes a la familia Cypraidae: *Erosaria spurca* (Linnaeus, 1758), *Luria lurida* (Linnaeus, 1758) y *Zonaria pyrum* (Gmelin, 1791) o el bivalvo *Pinna rudis* Linnaeus, 1758. A su vez en los fondos más profundos aparecen especies como el erizo *Centrostephanus longispinus* (Philippi, 1845), el gasterópodo *Charonia lampas* (Linnaeus, 1758), la esponja *Axinella polypoides* Schmidt, 1862 o gorgonias como *Eunicella gazella* Studer, 1878, entre otras, todas ellas incluidas en el Libro Rojo de los Invertebrados de Andalucía de 2008. A todas estas especies protegidas hay que añadirles aquellas cuya explotación está regula como lo son el santiaguiño, *Scyllarus arctus* (Linnaeus, 1758), el centollo *Maja squinado* (Herbst, 1788) o el erizo *Paracentrotus lividus* (Lamarck, 1816) (García Raso *et al*. 2010).

Gracias a toda esta información, se gestionó la ampliación de la extensión del LIC "Calahonda" (Decisión de la Comisión, de 12 de diciembre de 2008. DOUE L43, de 13.2.2009), aumentándose el área marina protegida a un total de 1.094,54 ha entre la Punta Calaburras y Torre de Calahonda, incluyendo los fondos infralitorales hasta una profundidad de 30 metros (Figura 7).

Actualmente el LIC "Calahonda" se ha declarado Zona Especial de Conservación (ZEC), BOJA 153 de 07/08/2015, lo que traerá consigo un plan de gestión que permitirán una mejor conservación de esta zona tan diversa y característica.

1.4.2 Geología y Geomorfología

Desde un punto de vista geológico, la provincia de Málaga pertenece íntegramente a la cordillera Bética, que constituye parte de la cadena de plegamientos alpinos que bordea el Mediterráneo occidental (Serrano y Guerra 2005). Según estos autores el litoral de Málaga se puede dividir en seis sectores (Manilva-Estepona; Ensenada de Marbella; Costa alrededor de Fuengirola; Bahía de Málaga; Costa de los Montes de Málaga y la Costa de Torrox) en función de la composición litológica y estructural de cada zona. De todos estos sectores solo las costas alrededor de Fuengirola y Torrox presentan afloramientos rocosos naturales los cuales están formados por esquistos preorogénicos. Estas formaciones dan lugar a relieves más o menos abruptos, en los que se pueden observar acantilados con pequeñas plataformas de abrasión intercaladas con pequeñas calas (entre P.

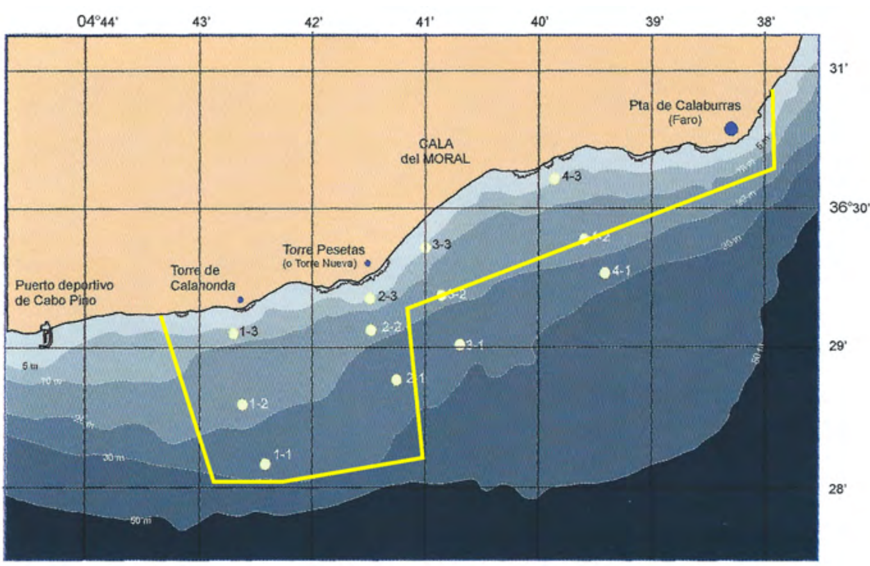

Figura 7. Localización y extensión (línea amarilla) de la ZEC Calahonda. (Modificado de García Raso *et al*. 2010).

Calaburras-Cabopino) y pequeños acantilados con estrechas playas (entre Vélez y Nerja). Sin embargo al este de Nerja, la sierra Almijara alcanza la línea de costa, debido a lo cual a partir de Maro el litoral presenta espectaculares acantilados con calas de difícil acceso (García Raso *et al.* 2010).

Estos afloramientos sirven de sustrato para una gran variedad de comunidades, lo que genera una gran diversidad biológica; de hecho el 70% de las especies marinas de nuestro entorno geográfico pueden encontrarse en estos tipos de hábitats (Templado *et al*. 2002, 2006, 2009). Aunque Maro ya presenta una figura de protección (Paraje Natural), el sector occidental (P. Calaburras-Cabopino) ha estado más desprotegido legalmente, viéndose amenazado por un urbanismo descontrolado (García Raso *et al.* 2010).

1.4.3 Oceanografía e Hidrología

Se puede decir, que en la cuenca del mar de Alborán es donde se concentra la maquinaría hidrológica mediterránea. Pues es en esta cuenca y a través del estrecho de Gibraltar, por donde se produce el intercambio de aguas y materiales que permiten la persistencia física del mar Mediterráneo (Rodríguez y Ruiz 2010). La elevada evaporación que sufre el Mediterráneo (~1,6 x 10^{12} m^3/ año; según García Lafuente y Criado 2001) hace que las aguas mediterráneas sean más densas (~38,4‰) que las atlánticas (<36.5‰), lo que produce un flujo negativo de flotabilidad que favorece la entrada de agua Atlántica superficial y la salida de agua mediterránea profunda (agua Levantina Intermedia entre los 200-600m y agua Mediterránea Profunda, más de 600m) (Parrilla y Kinder 1987). Esta masa de agua entrante se conoce como el “chorro de agua Atlántica” o “Atlantic Jet”, y es en realidad una mezcla de Agua Superficial Atlántica, Agua Central Noratlántica y Aguas Mediterráneas (Agua Levantina Intermedia y Agua Mediterránea profunda Occidental). Esta mezcla se produce en el estrecho de Gibraltar y favorece el enriquecimiento en nutrientes de las aguas superficiales que se adentran en el mar de Alborán (Macías *et al.* 2006,2007, 2008).

El chorro atlántico, tras pasar el estrecho de Gibraltar, sigue en dirección noreste por el talud continental hasta P. Calaburras, a partir de donde se separa

para formar el giro anticiclónico conocido como "Giro de Alborán Occidental" o "A1" (Figura 8). Este giro alimenta a su vez a otro giro denominado "Giro de Alborán Oriental" o "A2", menos estable y localizado entre las costas de Almería y el Cabo de las Tres Focas (Marruecos). La confluencia de las aguas del giro "A2" y aquellas procedentes del Mediterráneo, originan el "Frente Almería-Orán", el cual representa el límite entre aguas atlánticas y mediterráneas (Tintoré *et al.* 1988). Sin embargo la estabilidad y la posición de estos giros depende principalmente de la presión atmosférica y los vientos, pudiéndose llegar a producir la desaparición de algunos de estos giros o la generación de otros (Cano y García La Fuente 1991; Vargas-Yáñez *et al.* 2002; Macías *et al.* 2007).

En las zonas costeras las corrientes depende en cierta medida de la acción del viento (Arévalo y García 1983). No obstante se ha documentado una cierta influencia del "Atlantic Jet" sobre la hidrología costera comprendida entre Marbella

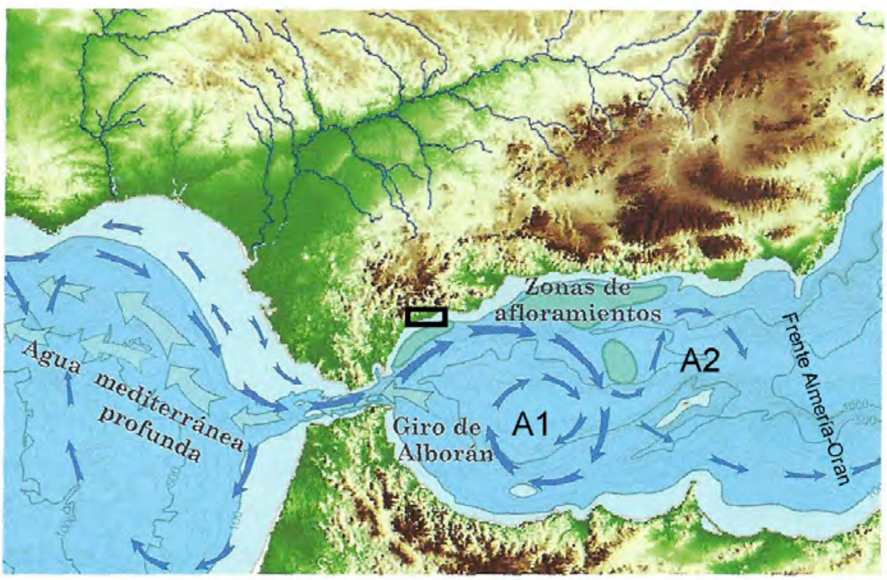

Figura 8. Esquema de las corrientes dominantes en la región Ibero-Marroquí. Las flechas azules representan las corrientes superficiales, en las que prevalece la entrada de agua atlántica y la formación del giro anticiclónico de Alborán. Este giro produce afloramientos en algunas partes del litoral malagueño, como es el caso de nuestra área de estudio (recuadro negro). Las flechas verdes indican la salida de agua profunda mediterránea, que siguen el talud continental ibérico hasta el cabo de San Vicente. Modificado de Templado y Luque 2004 (Dibujo de Gofas).

y P. Calaburras (Cano y García La Fuente 1991) (Figura 9). La presencia o no de vientos del este (levante), determina la posición del "Atlantic Jet" (Macías *et al*. 2007). En ausencia de levante dicho chorro tiende a desplazarse hacia el norte, acercándose más a las costas de Andalucía, esto tiene un efecto directo sobre dos ramales que se desprenden del "Atlantic Jet" los denominados "núcleo septentrional". Estos ramales se encuentran a unos 18Km de Marbella y discurren hacia P. Calaburras, alcanzando velocidades bastantes elevadas (40 m/s). El desplazamiento hacia el norte del "Atlantic Jet" provoca a su vez un acercamiento del "nucleo septentrional" a la costa andaluza, aumentando su velocidad e influencia sobre el tramo costero antes mencionado. Este fenómeno además se ve amplificado bajo condiciones meteorológicas en las que dominen los vientos de componente oeste (poniente) (Conde y Seoane 1982; Cano y García La Fuente 1991; Macías *et al*. 2007).

En el mar de Alboran son abundantes los afloramientos de aguas profundas ricas en nutrientes. Estos afloramientos se extienden por la zona de Estepona,

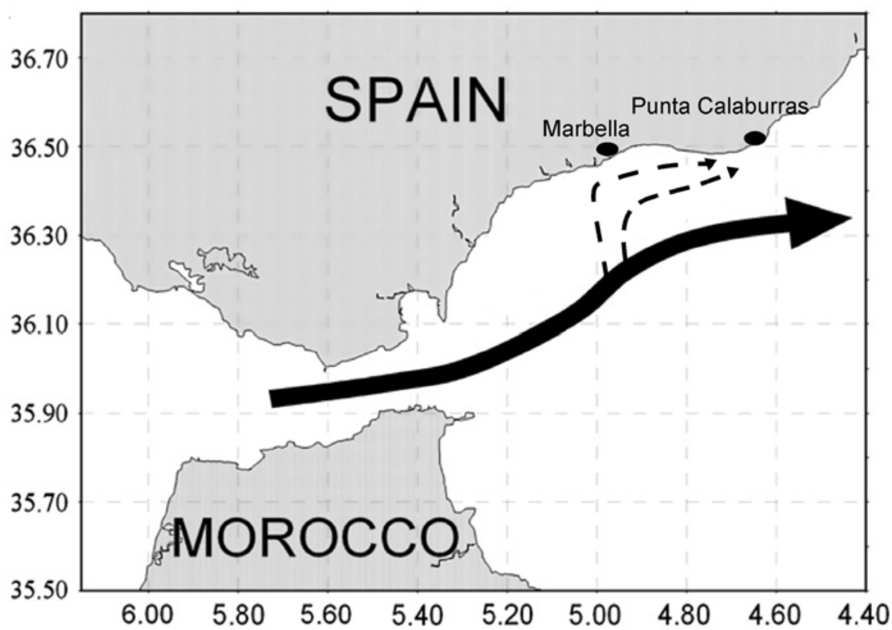

Figura 9. Esquema conceptual de la entrada del chorro atlántico (flecha negra) y los ramales que se desprenden de él "núcleo septentrional" (flechas negras discontinuas) (Modificado de Macías *et al*. 2008)

Marbella (cercanas a la zona de muestreo), Málaga, Motril y Almería, así como, en el frente "Almería-Orán" (Tintoré *et al.* 1988; Cano y García La Fuente 1991; Macías *et al.* 2007). Los orígenes de estos afloramientos son diversos y pueden estar producidos por diferentes fenómenos, como 1) la fricción generada entre las aguas del "chorro atlántico" y las aguas mediterráneas (lo que se ve favorecido por la ausencia de vientos de levante) (Tintoré *et al.* 1991; Macías *et al.* 2007), 2) oscilaciónes norte-sur del "chorro atlántico", 3) el transporte de Ekman en relación con los vientos de poniente (Sarhan *et al.* 2000) y 4) la topografía del fondo, debido a la presencia de isobatas curvadas y divergentes sobre la plataforma o cañones submarinos (Rodríguez *et al.* 2006).

En el litoral comprendido entre P. Calaburras y Calahonda las variables ambientales relacionadas con la columna de agua varían estacionalmente, alcanzando los valores más altos principalmente en verano (temperatura superficial del agua de mar (T): 27ºC; irradiancia solar (IS): ca. 4 log lm m^{-2}; concentración de clorofila a (Chl *a*): ca. 15 µg l^{-1}) y los más bajos en invierno (T: 13,5ºC; IS: ca. 3,5 log lm m^{-2}; Chl *a*: ca. 2 µg l^{-1}) (datos personales). Por su parte, la salinidad permanece más o menos constante a lo largo del año (en torno a 36,7‰), con valores algo menores que en el resto del Mediterráneo debido a la influencia del agua atlántica (http://www.ma.ieo.es/gcc/sistemas_observaciones.htm).

1.4.4 Biogeografía

En el litoral andaluz coinciden tres ecorregiones: el mar de Alborán, dentro de la provincia Mediterránea, la plataforma atlántica europea del Sur y los Afloramientos Saharauis, ambas dentro de la provincia Lusitánica (Spalding *et al.* 2007) (Figura 10).

Esta variabilidad biogeográfica hace que en el mar de Alborán podamos encontrar especies con diferentes afinidades. 1) Especies atlánticas, como el hidrozoo *Diphasia margareta* (Hassall, 1841), la gorgonia *Eunicella verrucosa* (Pallas, 1766), los moluscos gasterópodos *Rissoa guerinii* Récluz, 1843 y *Nassarius reticulatus* (Linnaeus, 1758), los bivalvos *Mytilus galloprovincialis* y *Cardita calyculata* (Linnaeus, 1758) o el crustáceo decápodo *Anapagurus hyndmanni*

(Bell, 1846), 2) especies mediterráneas, como el crinoideo *Antedon mediterranea* (Lamarck, 1816), la gorgonia *Eunicella singularis* (Esper, 1791), los gasterópodos *Alvania lineata* Risso, 1826 y *Euspira macilenta* (Philippi, 1844), el bivalvo *Pinna nobilis* Linnaeus, 1758 o el decápodo *Pagurus chevreuxi* (Bouvier, 1896), 3) especies subtropicales del norte de África, como las gorgonias *Ellisella paraplexauroides* (Stiasny, 1936), *Eunicella labiata* Thomson, 1927 y *Eunicella filiformis* (Studer, 1879) , los gasterópodos *Mathilda quadricarinata* (Brocchi, 1814) y *Cymbula safiana* (Lamarck, 1819), los bivalvos *Modiolus lulat* (Dautzenberg, 1891) y *Ungulina cuneata* (Spengler, 1798), los decápodos *Pagurus mbizi* (Forest, 1955) o *Cryptosoma cristatum* Brullé, 1837 o peces como la hurta (*Pagrus auriga* Valenciennes, 1843) o el poyo (*Scorpaena maderensis* Valenciennes, 1833) con poblaciones estables en Alborán. Por último mencionar aquellas especies cuyas poblaciones se concentran en el estrecho de Gibraltar y en sus proximidades, como los gasterópodos *Aclis verduini* van Aartsen, Menkhorst & Gittenberger, 1984, *Alvania vermaasi* van Aartsen, 1975 o *Jujubinus dispar* Curini-Galletti, 1982 (Pérès y Picard 1964; García Raso 1993; Gofas 1999; Rueda *et al.* 2010; Urra *et al.* 2013a,b; García Raso *et al.* 2013).

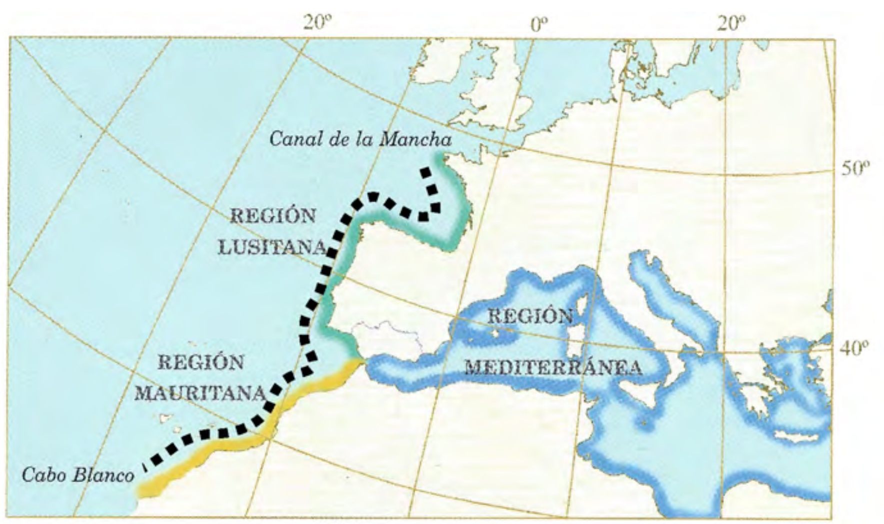

Figura 10. Mapa de las provincias biogeográficas según el tratado clásico de Ekman (1953). En los últimos trabajos la provincia Mauritánica se encuadra dentro de la provincia Lusitánica (línea punteada) (Spalding *et al.* 2007).

La influencia atlántica se hace notar también en las especies de macroalgas. Así en las cercanías de P. Calaburras especies atlánticas como *Cystoseira mauritanica* Sauvageau, *Fucus spiralis* Linnaeus, S*accorhiza polyschides* (Lightfoot) Batters o *Cystoseira usneoides* (Linnaeus) M. Roberts, encuentran aquí su límite de distribución dentro del Mediterráneo (Conde y Seoane 1982; Conde 1989; Flores-Moya *et al*. 1995; Barceló-Martí *et al*. 2000; Flores-Moya 2012). A medida que nos acercamos a la parte oriental del litoral malagueño (Torre del Mar y Nerja) la comunidad macrofitobentónica va cambiando, disminuyendo el porcentaje de especies atlánticas y aumentando la presencia de especies Mediterráneas endémicas como *Rissoella verruculosa* (Bertoloni) J.Agardh, o especies pan-tropicales como *Acetabularia acetabulum* (Linnaeus) P.C.Silva, , *Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux, o *Digenea simplex* (Wulfen) C.Agardh, que no se encuentran hasta el cabo de Gata (Conde y Seoane 1982; Conde 1989).

Esta diversidad de especies con diferentes afinidades hace que el mar de Alborán albergue la mayor diversidad biológica de todos los mares de Europa (Luque y Templado 2004; García Raso *et al*. 2010). Como ejemplo comentar, que solo dentro del ZEC de “Calahonda” y en un estudio preliminar ya se contabilizaron 355 especies de moluscos y 88 especies de decápodos, las cuales representan casi un 17 % y un 28 % del todas las especies de moluscos y decápodos presentes en todo el Mediterráneo y en el extremo occidental del mismo respectivamente (García Múñoz *et al*. 2008; Coll *et al*. 2010; Urra *et al*. 2011a,b; 2012a,b; 2013a,b; estudio presente).

1.5.1 Marco de la Tesis Doctoral

Hoy en día tanto las praderas de fanerógamas como los fondos de macroalgas están sufriendo una regresión a nivel mundial, que aunque puede deberse a causas naturales, está principalmente relacionada con actividades antrópicas (Walker y Kendrick 1998; Boudouresque *et al.* 2012). Actualmente, directivas como la Directiva Habitat, abogan por la protección y conservación de los hábitats y las poblaciones de las especies silvestres de la Unión Europea, mediante el establecimiento de una red ecológica, denominada Red Natura 2000, y de un régimen jurídico de protección de las especies. La Directiva Habitat, declara a las praderas de *Posidonia oceanica* como un hábitat prioritario para su conservación. La presencia de estas praderas en el ZEC ”Calahonda” fue primordial para la protección de esta zona. No obstante, la presencia de praderas de *Cymodocea nodosa* y de abundantes afloramientos rocosos (escasos en el litoral malagueño) cubiertos de macroalgas, así como de las especies asociadas a estos hábitats, ayudaron a la

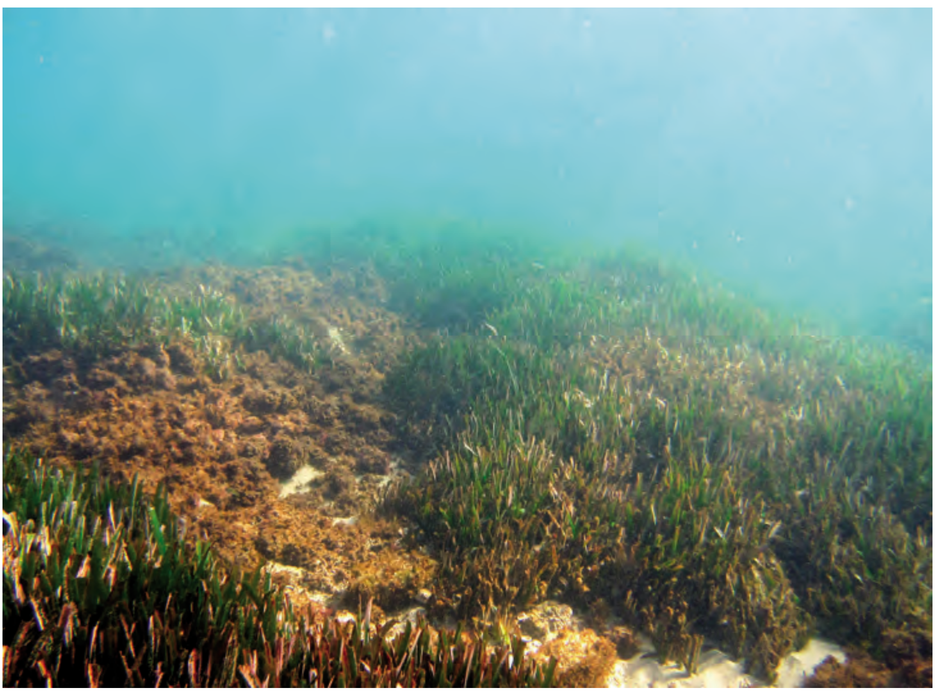

Figura 11. Visión general de los fondos mixtos formados por praderas fragmentadas de *Posidonia oceanica*, *Cymodocea nodosa* y fondos de macroalgas fotófilas dominados por *Halopteris scoparia*, presentes en el ZEC “Calahonda”.

designación de esta zona como Zona Especial de Conservación (BOJA 153 de 07/08/2015). La presente tesis surgió como parte de los estudios que se realizaron por parte del grupo de investigación RNM 0141 del departamento de Biología Animal de la Universidad de Málaga, a partir de los cuales se constataron la presencia de dichos hábitats y especies asociadas. El objetivo principal de esta tesis es el estudio de las asociaciones de decápodos ligadas a los hábitats vegetales presentes en el ZEC ”Calahonda”. De igual manera y aprovechando los datos fenológicos y de densidad de haces obtenidos tanto para *P. oceanica* como para *C. nodosa* durante el año de muestreo faunístico (julio 2007 - mayo 2008), se decidió continuar tomando datos hasta marzo de 2010, para así poder tener un período de tiempo suficiente parar analizar la dinámica estacional de estas fanerógamas, en esta zona de transición entre aguas atlánticas y mediterráneas.

1.5.2 Objetivos

En esta Tesis Docotoral se ha profundizado en el conocimiento de la fauna de decápodos presentes en la Zona Especial de Consevación (ZEC) “Calahonda” (Málaga). Los objetivos se han centrado en el estudio y análisis de la composición, estructura y dinámica temporal de las asociaciones de decápodos ligadas tanto a praderas de *Posidonia oceanica* y *Cymodocea nodosa* como a fondos de macroalgas fotófilas. Además de estudiar las relaciones existentes entre todas ellas.

Los objetivos específicos que se abordaron fueron:

1. Estudiar la influencia de las características oceanográficas del ZEC ”Calahonda” sobre la fenología y el estado de conservación de las praderas de *Posidonia oceanica* y *Cymodocea nodosa*, analizando tanto la dinámica estacional e interanual de sus parámetros fenológicos y número de haces, como su relación con las variables ambientales (capítulo 2).

2. Estudiar la composición y estructura de las asociaciones de crustáceos decápodos ligadas a praderas de *Cymodocea nodosa*, evaluando sus cambios estacionales y su relación con las variables ambientales, sedimentológicas, fenología de la planta y el tamaño de los “parches” estudiados (capítulo 3).

3. Caracterizar las asociaciones de crustáceos decápodos ligadas a praderas de *Posidonia oceanica*, y su dinámica temporal en relación tanto con las variables ambientales, hidrológicas y fenológicas (capítulo 4).

4. Analizar la estructura y composición de las asociaciones de crustáceos decápodos ligados a los fondos de macroalgas fotófilas dominadas principalmente por *Halopteris scoparia*, caracterizando tanto las diferencias entre los estratos (fronde-sedimento), como las diferencias estacionales y su relación con las variables ambientales, hidrológicas y los parámetros de las algas (altura, volumen, peso seco) (capítulo 5).

5. Estudiar la conectividad y flujo de especies entre los diferentes hábitats vegetales que constituyen los fondos del ZEC "Calahonda" y como esto influye en la diversidad global, estableciendo los hábitats preferentes para cada una de las especies dominantes y el uso de cada hábitat por parte de estas a lo largo del año de estudio. Además de analizar la diversidad taxonómica y trófica de cada una de las asociaciones de decápodos que están ligados a cada uno de estos hábitats (capítulo 6).

CAPÍTULO 2

Estructura y dinámica de las praderas de *Posidonia oceanica* y *Cymodocea nodosa* en el noroeste del mar de Alborán: una región de transición entre el Mediterráneo y el Atlántico

Este capítulo se basa/ This chapter is base on:

Structure and dynamic of *Posidonia oceanica* and *Cymodocea nodosa* meadows in the northwestern Alboran Sea: a Mediterranean–Atlantic transition region

Mateo-Ramírez A., Urra J., Marina P., Rueda J.L., García Raso J.E., In preparation.

Abstract

Structure of *Posidonia oceanica* and *Cymodocea nodosa* meadows and temporal dynamics of their phenological paramaters were studied from July 2007 to March 2010 in two sites of the northwestern Alboran Sea (Punta Calaburras and Calahonda). This area is remarkable for being one of the westernmost points in the distributional range of the Mediterranean seagrass *P. oceanica*. Both seagrass species present a shallow distribution (less than 5 m depth) with a configuration of small patches with different sizes and shapes, high shoot densities with low shoot heights. Plant parameters of both species presented temporal dynamics similar to other locations of their biogeographical distribution. Although *P. oceanica* seems to present a good health status (BIPo index ~0.6), with high shoot densities and flowering event, these meadows were larger in the past. *Cymodocea nodosa* meadows displayed acute and variable temporal changes and even disappearance in one site. Surprisingly, annual variability of *P. oceanica* meadows was similar or even less acute in this area close to the Atlantic Ocean in comparison to that observed in Mediterranean located meadows. On the other hand, *C. nodosa* showed transitional characteristics between Atlantic and Mediterranean meadows in relation to phenological parameters and annual variability. Probably these values of annual variability could be result of the constant input of cold Atlantic surficial waters, wave action and the low water transparency in the area. Temporal patterns of certain phenological parameters presented differences between the three sampled years in both seagrasses, stressing the importance of carrying out long term sampling for phenological studies.

Keywords: *Posidonia oceanica*, *Cymodocea nodosa*, Alboran Sea, local conditions, phenology.

Introduction

Posidonia oceanica and *Cymodocea nodosa* are the most abundant seagrass species in the Mediterranean Sea followed by both *Zostera noltei* and Z. *marina* (Luque and Templado 2004). The first is a Mediterranean endemism and in optimal conditions is considered to be the climax community of the Mediterranean infralittoral areas due to the highly diverse associated community supported by the high productivity, complexity and stability of this vascular plant (Mazzella *et al.* 1992).

Meadows of *P. oceanica* are the most extensive in the Mediterranean Sea covering ca. 2.5–4.5 millions of hectares that is close to 25 % of the Mediterranean basin shallower than 50 m (Pasqualini *et al.* 1998). On the other hand, *C. nodosa* is a species of subtropical affinity and it is typically considered a pioneer species that usually occurs in a wide variety of environments in open (from shallow waters down to 30–40 m, depending on the water transparency) or narrow bays, small harbours and coastal lagoons (Pérez-Lloréns *et al.* 2014). This species may sometimes form mono-specific and mixed meadows with the green alga *Caulerpa prolifera* and/or the seagrasses *Z. marina* and *Z. noltii* (Luque and Templado 2004).

Both *P. oceanica* and *C. nodosa* occur in areas with different environmental conditions, *C. nodosa* grows at temperatures ranging from 10 °C - 30 °C and it is also highly tolerant to salinity from 26 to 44 (Pérez-Lloréns *et al.* 2014). The optimum temperatures and salinity ranges of *P. oceanica* fluctuate between 10-28 °C and 36.5 in the Alborán Sea and 39.7 in the Cilician Sea (Pérez-Lloréns *et al.* 2014). These environmental requirements may influence the geographical distribution. *C. nodosa* is widely distributed throughout the Mediterranean Sea, the eastern Atlantic, from south Portugal to Senegal and around the Canary Islands (Luque and Templado 2004), but *P. oceanica* display its distribution limits in the western Alboran Sea (Estepona Bay, Sebkha-Bou-Areg, and Chaffarine islands) and in the Levantine Sea close to the Kizilliman Marine Protected Area (Turkish coast) and in Alexandria (Egypt) on the south shore (Celebi 2007; Pérez-Lloréns *et al.* 2014).

It is well known that the Alboran Sea displays transitional characteristics between the Atlantic Ocean and the Mediterranean Sea, with colder and low salinity water masses than other Mediterranean areas (Parilla and Kinder 1987). The entrance of surficial Atlantic waters through the Strait of Gibraltar generates an anticyclonic gyre due to the configuration of the Strait (more orientated to the northeast), the Coriolis effect, the topography of the Alboran basin and climatology (García Lafuente *et al.* 2000, Parrilla and Kinder 1987). These gyres produce upwellings of cold and nutrient enriched Mediterranean deep waters in the northwestern coasts of the Alboran Sea that support one of the highest biological productivity areas within the Mediterranean Sea (Sarhan *et al.* 2000; Rodríguez 1995) and this may also have some effects on the benthic vegetated assemblages (Fig. 1). In the Alboran Sea, *P. oceanica* forms extensive meadows in its easternmost sector, close to the Almeria-Oran Front, whereas in the central and western sector these are reduced from small meadows to patches, mainly living over hard substrata (Moreno and Guirado 2003; Luque and Templado 2004).

Posidonia oceanica and *C. nodosa* have been widely studied in the Mediterranean Sea, but most studies on *P. oceanica* focussed on seasonal and monthly variations (e.g. Bay 1984; Pergent and Pergent Martini 1988; Buia *et al.* 1992; Sánchez Lizaso 1993; Guidetti *et al.* 2002) and few studies considered inter-annual differences (Marbà and Duarte 1997; Gobert 2002; Peirano *et al.* 2011). The phenology of *C. nodosa* has been mainly studied during spring and summer months (Caye and Meinesz 1985; Pons Fabregas 2007; Zakhama-Sraieb *et al.* 2010) or within an annual cycle (Peduzzi and Vukovic 1990; Terrados and Ros 1992; Reyes *et al.* 1995; Cancemi *et al.* 2002; Cunha and Duarte 2007), but published data on inter-annual fluctuations are also very scarce.

Studies on phenological aspects of these two seagrasses are very scarce for the Alboran Sea so the main objectives of this study are: 1) to analyse the monthly and inter-annual variations in different seagrass parameters of *P. oceanica* and *C. nodosa* in this Mediterranean–Atlantic transition region and 2) to test if the environmental and hydrological characteristics of this area may have an influence over the status and the dynamic of these seagrasses in comparisson to other areas of their biogeographical distributions.

Material and methods

Study area

The study area is located within the marine Special Conservation Area called "Calahonda", included in the EU Natura 2000 network, in the Spanish coasts of the north-western Alboran Sea (Fig. 1). The area has a high biodiversity, with the coexistence of Atlantic and Mediterranean species (Urra *et al.* 2011a, 2013; Mateo-Ramírez and García Raso 2012). Phenological and environmental data were registered in two sampling sites, "Punta de Calaburras" (hereafter P. Calaburras; 36º 30.4´N - 04º 38.3´W) and "Calahonda" (36º 29.2´N - 04º 42.04´W), the latter located 7 km to the west and ca. 100 km to the Strait of Gibraltar. This stretch of coastline is characterized by rocky outcrops, intertidally and subtidally, representing one of the few natural rocky bottoms within this area of southern Spain.

In this area *P. oceanica* occurs as shallow fragmented meadows, formed by patches with areas ranging between 1 -130 m^2 (Urra *et al.* 2011b). The bathymetric range is very narrow, the patches appear between 1m – 6 m depth and usually fringing or growing over rocky outcrops in different locations between P. Calaburras and the small harbour of Cabopino. The high presence of dead rhizomes covered by macroalgae (*Halopteris scoparia* and *Asparagopsis armata*) interspaced with living seagrass meadows indicate that larger meadows were present in the past. *C. nodosa* can also be found in shallow infralitoral bottoms, forming fragmented meadows that generally occur in sheltered sites between rocky outcrops and sometimes mixed with *P. oceanica.*

The salinity in the study area is almost constant due to the absence of rivers or streams, ranging between 36.5 pss (autumn) and 36.8 pss (spring), with intermediate values in summer (36.7 pss) and winter (36.7 pss) which are typical of Atlantic water masses (http://www.ma.ieo.es/gcc/sistemas_observacion.htm). In fact the 42% of the seaweed species occurring in different bottom types of the studied area have an Atlantic origin (Flores-Moya 1989). Both sampling sites display maximum wave height values in autumn-winter (1-1.5 m) (data taken from http:// www.puertos.es) and due to their proximity to the Strait of Gibraltar, the frequent westerly and easterly winds, with velocities ranging between 3.6-5.7 m/s favour a constant wave action during the whole year in this part of the Alboran Sea (Fig. 1).

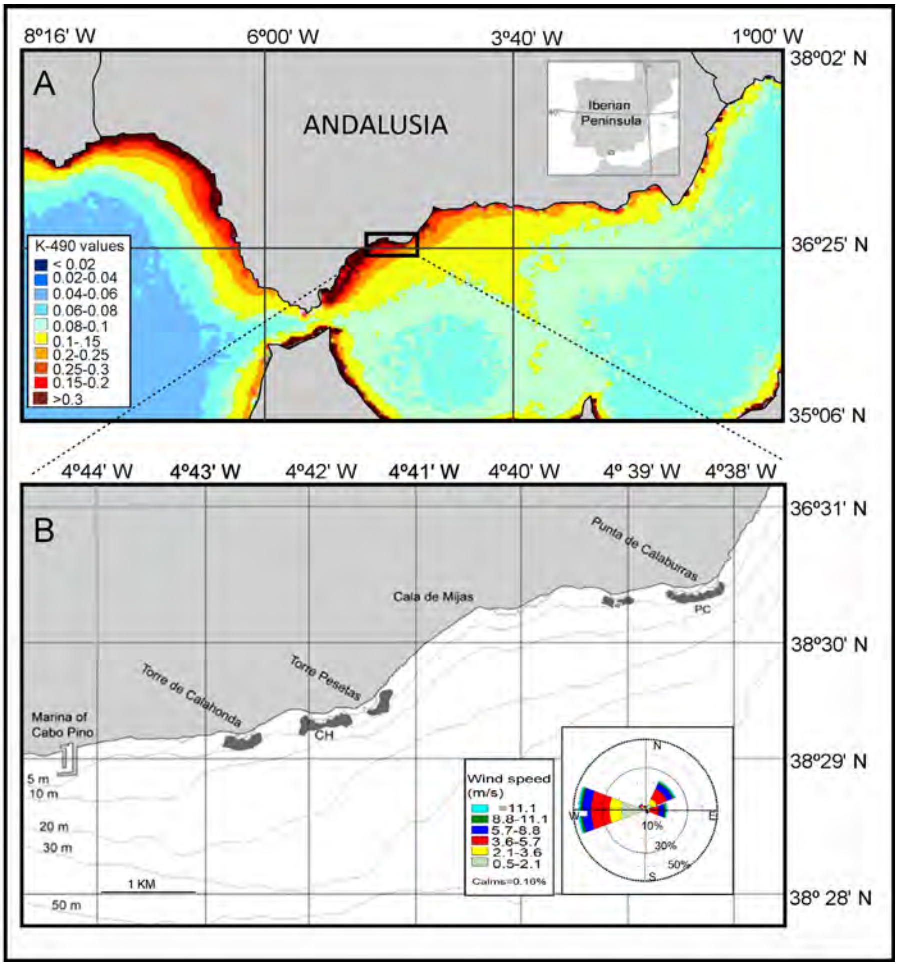

Figure 1. (A) Mean values of K 490 are related to turbidity (suspension material) and the concentration of chlorophyll *a*. (B) Map of the study area in the northwestern Alboran Sea. Grey areas indicate the location of the main seagrass meadows. P. Calaburras, PC; Calahonda, CH.

Collection of meadows density and leaf phenology data

Density and leaf related parameters as well as flowering data of *P. oceanica* and *C. nodosa* were recorded monthly from July 2007 to March 2010 in P. Calaburras and Calahonda. A non destructive technique was used for collecting phenological data at ca. 2 m depth (depth of maximum coverage) using scuba diving equipment. The line intercept method (eight 25m transects in each site) was used to estimate the coverage of both seagrasses. Shoot density (number of shoots per m^2) was estimated with the use of quadrants for *P. oceanica* (50 x 50cm) and *C. nodosa* (25 x 25 cm) in different seagrass patches across the study area, with a total of 5 or 10 replicates per month and site. This sampling area is similar to that used by other authors in previous studies on shallow Mediterranean seagrass beds (Buia *et al.* 1992; Guidetti *et al.* 2002; Amoutzopoulou and Haritonidis 2005; Kruzic 2008) and also suggested by Pergent Martini *et al.* (2005) for seagrass monitoring.

In order to estimate the leaf related parameters, ten shoots were randomly selected *in situ* within of each quadrant used for shoot density measurements, and, in each of them, the number of leaves per shoot (all leaves, undifferentiated between adult, intermediate and juvenile) was counted, and both the shoot height (from the basal part of the sheath to the blade tip) and the leaf width (at the mid-point between the sheath and the blade tip) of the highest leaf were measured to the nearest mm (n = 50 shoots per month and site), this methodology was used by Gobert (2002), who indicated its useful and its environmental friendly nature . When inflorescences were observed, the area of patches containing them was also measured and the density of shoots that contained inflorescences was taken.

Environmental variables

Seawater temperature measurements and water samples for analysing the concentration of chlorophyll *a* (Chl *a*) were taken during different days throughout each season (weeks before, during and after seagrass parameters data collection) at each site in order to study their relationship with the seagrass parameters. Surface water temperature was measured at midday (12:00) with an alcohol thermometer, and two replicates of 1 l of sea water (at the surface) were also collected per day and site and transported in darkness at low temperature to the laboratory for chlorophyll *a* determination. Pigment analyses were carried out by filtering through Whatman GF/C glass filters, extraction using 100% acetone for 12h in cool and dark conditions and measurements using a spectrophotometer at wavelengths of 630, 647, 664 and 750 nm. The chlorophyll *a* concentrations were obtained using the equation proposed by Jeffrey and Humphrey (1975).

Solar irradiance measurements during an annual cycle were obtained using HOBO Data Loggers that were deployed seasonally from winter 2009 to winter 2010. Each HOBO was placed daily close to the sampled seagrass meadows (at ca. 2 m depth) and set to record data with 10 min intervals between 10:00 and 14:00. Measurements were taken several days throughout each season (weeks before, during and after data collection) in both sites.

Samples of sediment were also taken seasonally within the sampled meadows (n = 5 replicates per season and site) in order to estimate the organic content in the sediment. This percentage was calculated by the weight loss of dry sediment (3 subsamples of 20 gr. per replicate) after ignition at 500ºC for 1h.

Statistical analyses

Difference in the shoot density, number of leaves, shoot height and leaf width of *P. oceanica* and *C. nodosa* between sites (P. Calaburras; Calahonda) or patch areas (1-25m^2; 25-50 m^2;>50m^2) were tested using a one-way PERMANOVAs, whereas two-way PERMANOVA design with months (M1;warm: July-September ; M2:temperate: November-December; M3;coldest: January-March and M4;cold: May-June) and years (A1: July 2007-May 2008; A2: September 2008-June 2009; A3: September2009-March 2010) as fixed factors was used to analysed temporal and annual differences. The same PERMANOVA design was utilized to test statistical differences of environmental variables between months along the three annual cycles. Analyses were based on Euclidean distances (Anderson 2001) and the significance of P values was determinate through 9999 permutations of row data and residuals under a reduced model for one or two-way analysis respectively. When the numbers of permutation were low, Monte-Carlo method was used to contrast the significance of P values. Two-way PERMANOVA pair-wise post hoc test ($P < 0.05$) was used for posterior multiple comparisons across months and years.

Seasonal trends and values of water temperature and chlorophyll *a* obtained in the present study matched practically with all those obtained by the NOAA (http://www.noaa.gov), and the former data set was then used for multiple regressions. When seagrass parameters and sediment and environments variables displayed a similar pattern, forward stepwise multiple linear regression analysis was used to investigate the corresponding relationships. However irradiance was analyzed apart because we only have data from March 2009 to March 2010. Prior to carrying out the regression analyses, potential significant relationships between the independent variables (phenology, sediment and environmental variables) were investigated using Pearson's correlation coefficient and variables that were significantly and highly correlated were eliminated from the analyses. Data used in the regression analyses were checked for normality using Kolmogorov and Smirnov test and transformed to ln when was necessary. These statistical procedures were performed using the software SPSS 20 and PRIMER 6.0 & PERMANOVA statistical package.

In order to know the magnitude of annual fluctuations in the different plants parameters of both segrasses species the coefficient of variation (CV %) was calculated with all collected data. Finally a BIPo index was calculated (López y Royo *et al.* 2010), in order to know the conservation status of *P. oceanica* meadows studied.

Results

Environmental variables

Mean seawater temperatures (T) showed a clear temporal trend throughout the 3 years in both sites, ranging from ca. 22 ºC in warm months (with exceptional values of 27 ºC in September 2009) to ca. 15 ºC in coldest moths (Fig. 2A, Table 1). Although Chl *a* showed higher values in Calahonda, both sites followed

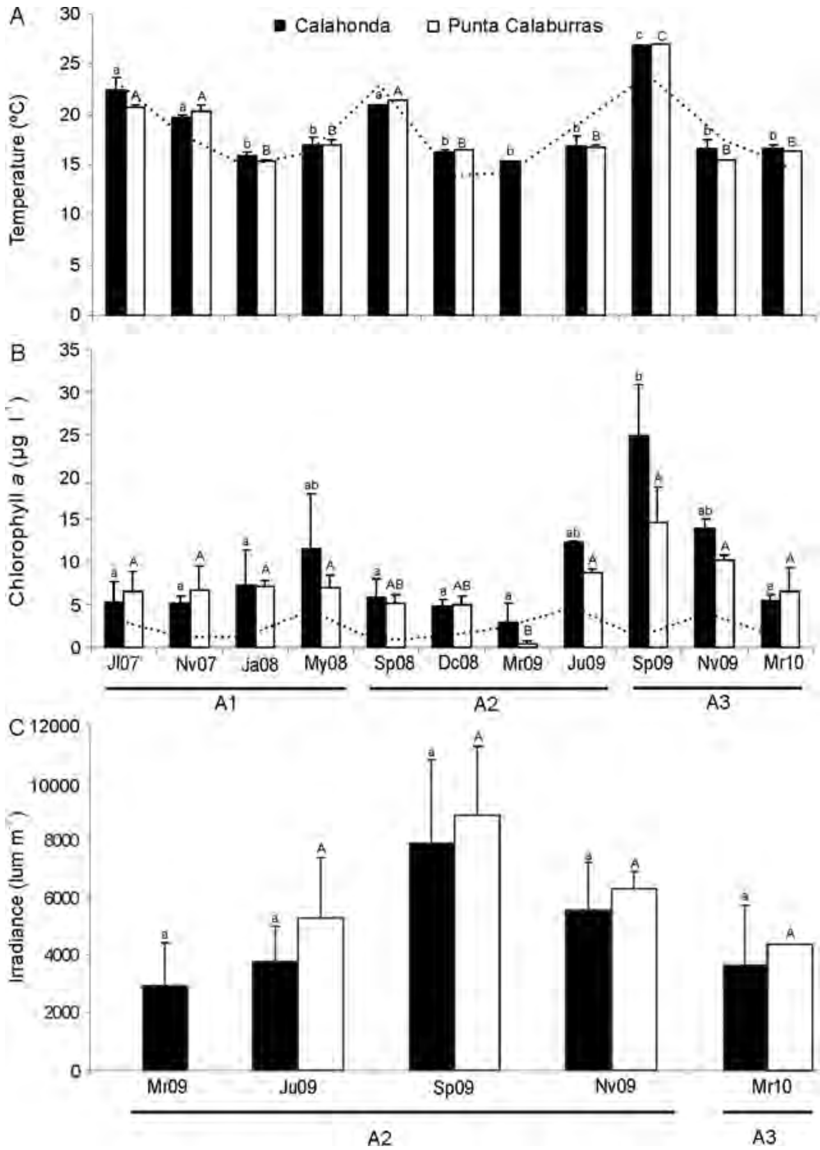

Figure 2. Environmental variables in P. Calaburras (empty bars) and Calahonda (solid bars): (A) Temperature, (B) concentration of chlorophyll *a* and (C) solar irradiance in different seasons. The discontinuous line shows the mean surface seawater temperature values from NOAA datasets collected in the study area. July, Jl; November, Nv; January,Ja; May, My; September, Sp; December, Dc; March, Mr; June, Ju. Mean ± standard error. Along the first (A1), second (A2) and third (A3) annual cycle. Letters above error bars display the results of PAIR-WISE test; different letters indicate signifcant differences at P< 0.05.

the same temporal trend with low values in coldest months and high in cold and warm months depend on the year (Fig. 2B; Table 1). Solar irradiance also displayed a temporal trend, with high values in warm months and low in coldest one, however these differences were not statistical different (Fig. 2C, Table 1). Percentage of organic matter (%OM) in *Posidonia oceanica* meadows showed the same seasonal trend in both sites, with high values in warm-cold months (ca. 1.6%) and low in temperate-coldest months (ca. 2.4%) (Table 1). In *Cymodocea nodosa* meadows, only in P. Calaburras % OM showed temporal differences. High values were recorded in warm-temperate months (maximum in July 07 with 4.09%) and minimum in March 10 (1.87%). In Calahonda the values were similar along the months and years (ca. 2%) (Table 1).

Structure and dynamics of **Posidonia oceanica** *meadows*

The coverage estimated for *P. oceanica* ranged between 14% in P. Calaburras and 20% in Calahonda. These meadows are composed by patches with different areas

Table 1. Results of one and two-way PERMANOVA testing differences in environmental variables analyzed in shallow seagrass meadows of the northwestern Alboran Sea, between sites, moths and years. . * Significant differences P<0.05; **P<0.01; *** P< 0.001; P-F, Pseudo-F.

Sites	Environmental variables	Seawater temperature	Solar irradiance	Chlorophyll *a*	Organic matter	
					P. oceanica	*C. nodosa*
Punta Calaburras	Seasonal	P-F=75.677; P<0.001***	P-F=2.075; P=0.164	P-F=5.324; P<0.01**	P-F=6.474; P<0.001***	P-F=10.81; P<0.001***
	Inter-annual	P-F=4.033; P<0.05*	--	P-F=2.896; P=0.068	P-F=0.898; P=0.414	P-F=21.07; P<0.001**
	Season*year	P-F=19.292; P<0.001***	--	P-F=4.971; P<0.01**	P-F=1.315; P=0.263	P-F=2.964; P<0.05*
Calahonda	Seasonal	P-F=8.872; P<0.01**	P-F=1.410; P=0.307	P-F=4.410; P<0.05*	P-F=10.323; P<0.001***	P-F=0.865; P=0.470
	Inter-annual	P-F=1.172; P=0.344	--	P-F=6.575; P<0.01**	P-F=1.822; P=0.171	P-F=2.571; P=0.079
	Season*year	P-F=0.646; P=0.639	--	P-F=3.947; P<0.05*	P-F=2.324; P<0.05*	P-F=4.03; P<0.01**
Among sites		P-F=0.195; P=0.657	P-F=3.410; P=0.078	P-F=7.136; P<0.01**	P-F=4.498; P<0.05*	P-F=108.7; P<0.001**

(ranging from 1 to over 130 m^2) which sometimes are interspaced with dead *P. oceanica* rhizome mattes. Shoot densities of *P. oceanica* were not significantly different between sites (one-way PERMANOVA; Pseudo-F= 0.031, P=0.862) when considering all measurements (849.93 ± 15.11 shoots m^{-2} in P. Calaburras; 845.48 ± 19.99 shoots m^{-2} in Calahonda; Mean ± SE) (Fig. 3A). Shoot densities in Calahonda displayed a temporal trend with high values in temperate months (maximum values observed in November 2007, ca.1055 shoots m^{-2}). On the other hand in P. Calaburras values were very similar throughout the year and did not present monthly differences (Fig. 3A; Table 2, Appendix 1). Shoot densities were similar between annual cycles in both sites (Table 2) and between patches with different areas (all measurement; one-way PERMANOVA; Pseudo-F=0.433, P=0. 0.651). Negative correlations between shoot densities with shoot height ($R_{Pearson}$=-0.268, P<0.01) and leaf number ($R_{Pearson}$= -0.387, P<0.01) were found.

Mature inflorescences were observed in March 2009 on orthotropic shoots of several patches with areas ranging 4-10 m^2 at ca. 2 m depth in P. Calaburras, and displaying a maximum of 28 inflorescences m^{-2}. A second and major flowering event was observed in nearly all patches in both P. Calaburras and Calahonda in November 2009. On this occasion, flowering densities were up to 144 inflorescences m^{-2} in P. Calaburras and up to 184 inflorescences m^{-2} in Calahonda (Urra *et al.* 2011b).

Shoot heights displayed similar values in both sites ranging between 26.60 ± 1.40 cm in P. Calaburras and 24.90 ± 1.18 cm, in Calahonda (one-way PERMANOVA ; Pseudo-F= 0.863, P= 0.357) (Fig. 3B). A very clear temporal trend was observed in both sites presented high values in cold months (maxima in May 2008 in both sites, ca. 39 cm) (Fig. 3B; Table 2; Appendix 1). Inter-annual differences were detected in both sites with mean annual values ranging between 22.46 ± 1.74 and 27.56 ± 2.51 cm (Fig. 3B; Table 2; Appendix 1). Shoot heights did not display significant differences between patches with different areas (one-way PERMANOVA; Pseudo-F= 2.196, P=0.113).

The mean leaf width displayed higher values in P. Calaburras (9.97 ± 0.03 mm) than in Calahonda (10.22 ± 0.03 mm) (one-way PERMANOVA; Pseudo-F= 14.486, P<0.001) (Fig. 3C, Table 2). Leaf width did not show a clear temporal trend, however

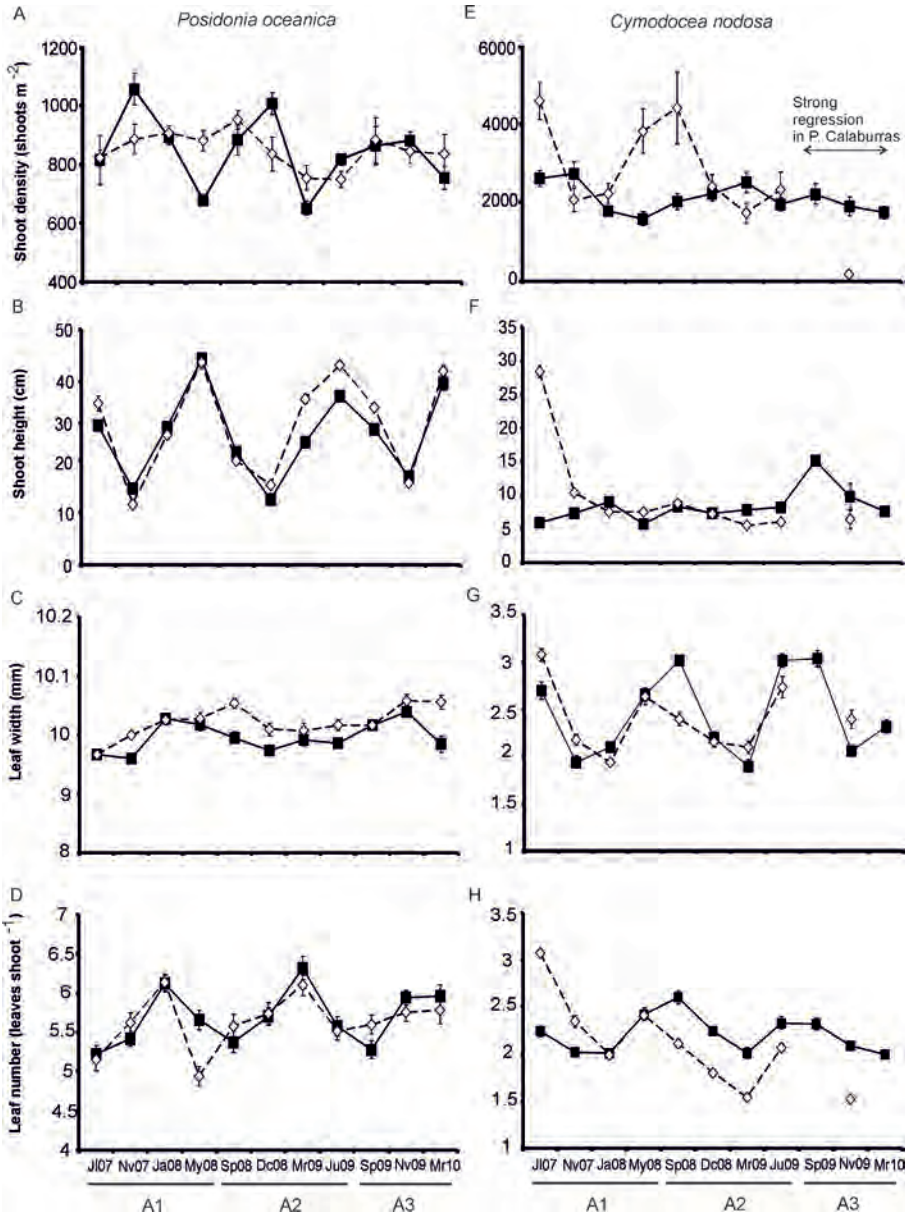

Figure 3. Phenological parameters of (A-D) *Posidonia oceanica* and (E-H) *Cymodocea nodosa* in P. Calaburras (dashed line) and Calahonda (solid line) Mean ± standard error. July, Jl; November, Nv; January, Ja; May, My; September, Sp; December, Dc; March, Mr; June, Ju. Mean±standard error. Along the first (A1), second (A2) and third (A3) annual cycles.

between patches (one-way PERMANOVA; Pseudo-F= 0.016, P=0.984).

Leaf width presented similar values (ca. 2 mm) in both sites (one-way PERMANOVA; Pseudo-F= 0.274, P=0.596) and in patches with different areas (one-way PERMANOVA; Pseudo-F= 0.9148, P=0.421) (Fig. 3G). Both sites displayed a similar temporal trend with high values in warm and cold months. Maxima were found in July 2007 and in September 2008 for P. Calaburras and Calahonda

Table 3. Results of two-way PERMANOVA testing for differences in the shoot density shoot height, leaf width and leaf number of *C. nodosa* between months, year and mixed factor year x month, which compares each months with the rest of the months sampled in each year. * Significant differences P<0.05; **P<0.01; *** P<0.001.

	Punta Calaburras				Calahonda			
Shoot density	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P
Year	2	41,999000	48.985	<0.001***	2	650910	2.949	0.060
Month	3	8,369000	9.761	<0.001***	3	987940	4.477	<0.01**
Year x Month	5	3,578600	4.174	<0.01**	5	710290	3.218	<0.05*
Residual	44	857390			44	220700		
Total	54				54			
Shoot height								
Year	2	608.95	139.05	<0.001***	2	55	11.785	<0.001***
Month	3	213.38	48.725	<0.001***	3	10.16	2.1769	0.090
Year x Month	5	217.2	49.597	<0.001***	5	31.31	6.7087	<0.001***
Resisdual	44	4.379			44	4.667		
Total	54				54			
Leaf width								
Year	2	14.453	721.02	<0.001***	2	0.088	1.6877	0.196
Month	3	1.5317	76.411	<0.001***	3	0.471	9.0816	<0.001***
Year x Month	5	1.6708	83.348	<0.001***	5	0.066	1.2694	0.296
Residual	44	0.0200			44	0.052		
Total	54				54			
Number of leaves								
Year	2	11.361	419.35	<0.001***	2	0.304	14.074	<0.001***
Month	3	2.4185	89.273	<0.001***	3	3.021	139.63	<0.001***
Year x Month	5	3.472	128.160	<0.001***	5	0.138	6.3748	<0.001***
Residual	44	0.0271			44	0.022		
Total	54				54			

The mean number of leaves per shoot was similar in both sites (ca.5.7 leaves shoot^{-1}) (one-way PERMANOVA; F= 0.422, P >0.519), displayed a temporal trend with high values in coldest month. Maxima values were observed in January 2008 for P. Calaburras, and in March 2009 for Calahonda (Fig. 3D; Table 2; Appendix 1). No differences of number of leaves in relation to annual cycles and patches area were found (Table 2) (one-way PERMANOVA; Pseudo-F= 1.185, P=0.315).

***Structure and dynamics of* Cymodocea nodosa**

The coverage estimated for *C. nodosa* was <5% in both sites, with patch dimensions ranging from 1 to over 60 m^2 that sometimes were mixed with patches of *P. oceanica*.

The mean shoot density of *C. nodosa* meadows was significantly higher (all measurements; one-way PERMANOVA; Pseudo-F= 14.920 P <0.001) in P. Calaburras (2640.71 ± 222.66 shoots m^{-2}; Mean ± SE) than in Calahonda (2122.76 ± 75.16 shoots m^{-2}) (Fig. 3E). In P. Calaburras shoot density displayed a temporal trend with high values in warm and cold months (maximum in July 2007, ca. 4592 shoots m^{-2}) (Fig. 3E; Table 3; Appendix 2). In summer 2009, no *C. nodosa* shoots were observed in this site, however some of them were spotted again in November 2009 but none were found in March 2010. A clear decline was observed between the first and third annual cycles (3180.80 ± 309.29, 2724.80 ± 341.23 and 144 ± 26.84 shoot m^{-2}) in P. Calaburras. On the other hand, in Calahonda shoot density displayed monthly and inter-annual changes, however were less acute than in P. Calaburras (maxima in July and November 2007) (Fig. 3E; Table 3; Appendix 2). Shoot densities were similar in patches with different area (one-way PERMANOVA; Pseudo-F= 1.217, P=0.309).

Shoot height was not significantly different between sites with values ca. 9 cm (one-way PERMANOVA; Pseudo-F= 2.581, P= 0.11) (Fig. 3F). Although shoot height did not follow a temporal trend, inter-annual changes were found in both sites ranging from 6.89 ± 0.44 to 13.45 ± 2.08 cm (Table 3). However, monthly differences were only observed in P. Calaburras showed maximum values in July 2007 (Fig. 3F; Table 3; Appendix 2). Shoot heights did not display differences between patches (one-way PERMANOVA; Pseudo-F= 0.016, P=0.984).

Leaf width presented similar values (ca. 2 mm) in both sites (one-way PERMANOVA; Pseudo-F= 0.274, P=0.596) and in patches with different areas (one-way PERMANOVA; Pseudo-F= 0.9148, P=0.421) (Fig. 3G). Both sites displayed a similar temporal trend with high values in warm and cold months. Maxima were found in July 2007 and in September 2008 for P. Calaburras and Calahonda

Table 3. Results of two-way PERMANOVA testing for differences in the shoot density shoot height, leaf width and leaf number of *C. nodosa* between months, year and mixed factor year x month, which compares each months with the rest of the months sampled in each year. * Significant differences P<0.05; **P<0.01; *** P<0.001.

	Punta Calaburras				Calahonda			
Shoot density	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P
Year	2	41,999000	48.985	<0.001***	2	650910	2.949	0.060
Month	3	8,369000	9.761	<0.001***	3	987940	4.477	<0.01**
Year x Month	5	3,578600	4.174	<0.01**	5	710290	3.218	<0.05*
Residual	44	857390			44	220700		
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Shoot height								
Year	2	608.95	139.05	<0.001***	2	55	11.785	<0.001***
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Year x Month	5	217.2	49.597	<0.001***	5	31.31	6.7087	<0.001***
Resisdual	44	4.379			44	4.667		
Total	54				54			
Leaf width								
Year	2	14.453	721.02	<0.001***	2	0.088	1.6877	0.196
Month	3	1.5317	76.411	<0.001***	3	0.471	9.0816	<0.001***
Year x Month	5	1.6708	83.348	<0.001***	5	0.066	1.2694	0.296
Residual	44	0.0200			44	0.052		
Total	54				54			
Number of leaves								
Year	2	11.361	419.35	<0.001***	2	0.304	14.074	<0.001***
Month	3	2.4185	89.273	<0.001***	3	3.021	139.63	<0.001***
Year x Month	5	3.472	128.160	<0.001***	5	0.138	6.3748	<0.001***
Residual	44	0.0271			44	0.022		
Total	54				54			

respectively. Leaf width showed differences between years in P. Calaburras, which presented a diminution from the first (2.46 ± 0.10 mm) to third annual cycle (1.63 ± 0.04 mm) (Fig. 3G; Table 3; Appendix 2).

Number of leaves per shoot was not significantly different between sites (ca. 2.4 leaves shoot^{-1}) (one-way PERMANOVA; Pseudo-F= 0.261, P=0.617) neither between patches with different area (one-way PERMANOVA; Pseudo-F= 1.975, P=0.157) (Fig. 3H). This variable present a similar temporal trend than leaf width and shoot density with maxima values in July 2007 and September 2008 for P. Calaburras and Calahonda respectively. Inter-annual changes were found in both sites with values ranging from 2.35 ± 0.08 to 2.52 ± 0.07 leaves shoot^{-1} (Fig. 3H; Table 3; Appendix 2).

Relationship between phenological, sediment and environmental variables

In *P. oceanica* the irradiance showed the highest values of R Square, explained 47.9% and 59.4% of the variability in relation to leaf number and shoot density respectively. In *C. nodosa* only sea water temperature showed a significant correlation with *C. nodosa* phenological variables, explained 24.4 % of shoot height variability (Table 4).

Table 4. Results of multiple forward stepwise regression analyses of *P. oceanica* and *C. nodosa* variables in relation to environmental and sediment variables. T, temperature, I, irradiance, Chl a, concentration of chlorophyll *a*, % OM, percentage of organic matter in the sediment. Only environmental variables accepted in each regression model (P <0.05) are listed.

	Coefficient	SE	F ratio	R^2	P
Posidonia oceanica					
Leaf number				0.186	<0.01
constant	6.308	0.311			
temperature	-0.037	0.17	4.573		
Leaf number				0.479	<0.05
constant	10.635	1.929			
irradiance	-1.319	0.52	6.424		
Shoot density				0.594	<0.05
constant	-571.8	431.4			
irradiance	372.4	116.3	10.255		
Cymodocea nodosa					
Shoot height				0.242	<0.05
constant	1.238	0.376			
temperature	0.051	0.021	5.753		

Discussion

The *Posidonia oceanica* meadows of P. Calaburras and Calahonda in spite of support a higher anthropogenic pressure (elevated urbanism), shows a good conservation status, with values of BIPo index ~0.6, similar to other meadows located in other areas with a lower population density (López y Royo *et al.* 2010). However the high presence of old death rhizome covered by macroalgae indicates that they were more abundant in the past suggesting that have been suffered a regression.

These meadows represent the westernmost ever studied and are located in one of the highest biological productivity areas within the Mediterranean Sea (Rodríguez 1995). This high productivity may influence low values of transparency; in fact the irradiance values obtained in this area at 5 m were similar to those found at 10 m depth by Kruzic (2008) in the eastern Adriatic Sea (Fig. 1, 2). Light and temperature are key factors which regulating abundance and productivity of seagrass (Sand-Jensen 1975; Marbà *et al.* 1996; Celebi 2007). However, light and seawater temperature explained a high percentage of variability of leaf number and shoot density of *P. oceanica* and shoot height of *Cymodoce nodosa* in P. Calaburras-Calahonda. In addition, the lower depth limit that presents these meadows (ca. 5 m) probably are related to the low water transparency, nevertheless, this variable marks the lower boundary of seagrasses (Ballesta *et al.* 2000; Boudouresque *et al.* 2006b). Moreover, the presence of coralligenous assemblages at 15 m, which are characteristic of the circalittoral biocenoses, also suggests a low water transparency of this area (Urra *et al.* 2012a). This narrow bathymetric distribution (ranging between 1-5m) exposes the meadows to a continuous hydrodynamism (mainly generated by the westerly winds, with values of wave height ranging between 0.3-0.7 m; values obtained from 1996-2011 data; http:// www.puertos.es), exposing them to high water activity. Patchy meadows of *P. oceanica, C. nodosa* as well as other seagrasses species has been reported in areas with these conditions, including *P. oceanica* meadows at northern distributional boundary (Adriatic Sea), where also presented a combination of shallow waters with low transparency and an open localization (Fonseca *et al.* 1983; Turk and Vukovic 1998; Reyes *et al.* 1995; Ballesta *et al.* 2000).

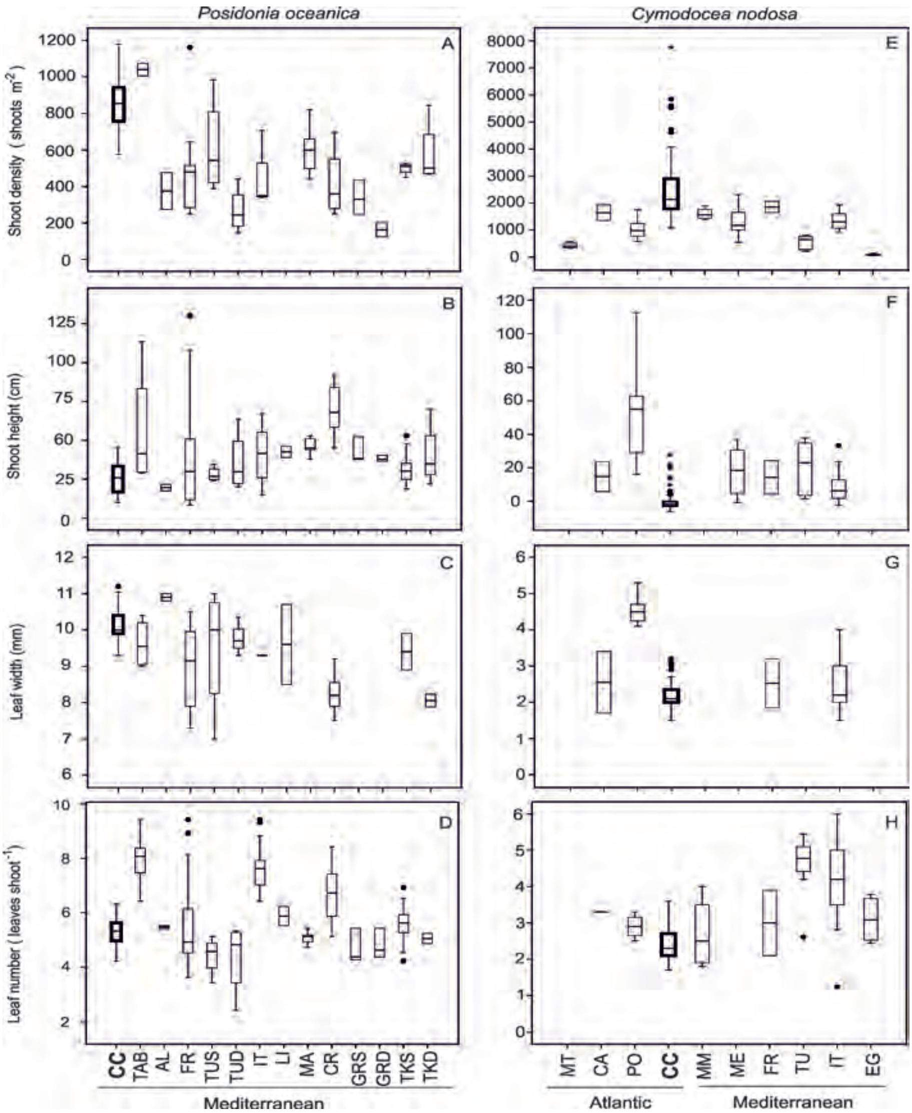

Figure 4. (box plot). Seagrass parameters of (A-D) *P. oceanica* and (E-H) *C. nodosa* in NW Alboran Sea (clustering the data from different months and years for P. Calaburras and Calahonda), as well as in other locations of the Mediterranean Sea and Atlantic Ocean. The line within the box represents the median; the upper and lower ends of the box are the third (Q_3) and first (Q_1) quartile, respectively; the ends of the lines extending vertically from the boxes (whiskers) are the minimum and maximum values; outliers are plotted as individual points. P. Calaburras-Calahonda, **CC**, (present study); Tabarca Island-E Spain, TAB, (Sánchez Lizaso 1993); Algeria, Al, (Semroud *et al.* 1990); France, FR, (Caye and Meinesz 1985; Pergent and Pergent-Martini 1988; Gobert 2002); Tunisian shallow (< 5m) and deep (> 5m) meadows, TUS and TUD, (Sghaier *et al.* 2006; Zakhama-Sraieb *et al.* 2010); Italy, IT, (Peduzzi and Vukovic 1990; Buia *et al.* 1992; Cancemi *et al.* 2002; Guidetti *et al.* 2002; Peirano *et al.* 2011); LI: Libya (Pergent *et al.* 2002); Malta, MA, (Borg *et al.* 2005); Croatia, CR; (Kruzic 2008); Greek shallow (< 5m) and deep (> 5m) meadows, GRS and GRD, (Amoutzopoulou and Haritonidis 2005); Turkish shallow (< 5m) and deep (> 5m) meadows respectively, TKS and TKD, (Celebi 2007); Mauritania, MT, (van Lent *et al.* 1991); Canary Islands, CA, (Reyes *et al.* 1995); Portugal, PO, (Cabaço *et al.* 2010; Cunha and Duarte 2007); Mar Menor-Murcia, MM, (Terrados and Ros 1992); Menorca-Balearic Islands, ME, (Pons Fabregas 2007); Tunisia, TU (Zakhama-Sraieb *et al.* 2010); Egypt, EG, (Mostafa *et al.* 2007).

In addition of the mosaic distribution of both seagrass species in P. Calaburras-Calahonda, these meadows are characterised by present an elevated number of shoot with short leaves. For example, shoot densities of *P. oceanica* meadows were higher (850-1000 shoots m^{-2}) than those located in other Mediterranean areas at similar depth, including the north Adriatic Sea (360-588 shoots m^{-2}; Turk and Vukovic 1998) and northeastern Levantine Sea (eastern distributional boundary; 528 shoots m^{-2}; Celebi 2007) (Fig. 4), but similar to other meadows of Tunisia that also grow over rocks (Mabrouk *et al.* 2009). However the values of shoot height were low, when compared to other Mediterranean and Atlantic meadows (Fig. 4). Meadows of *P. oceanica* with high shoot densities and low shoot height values also were found in other Alboran Sea locations (Marbá *et al.* 1996). In the same way other *C. nodosa* meadows with short leaves were also found in exposed locations (de lo Santos et al. 2013). Probably, the rock nature of the substrate over grows on *P. oceanica* and the exposed location of both seagrasses meadows to the hydrodynamism may play a key role structuring these meadows. In the case of *P. oceanica* could be a stress reduction strategy that involves increasing rhizome growth for anchorage as well as the shelf-shading effects, like showed the negative correlation between shoot densities, shoot height and number of leaves (Abbate *et al.* 2000; Gobert 2002; Giovannetti *et al.* 2008).

In relation to plant parameters, shoot height, leaf width and number of leaves in *P. oceanica* displayed a similar temporal trend than other european and north african meadows (Sánchez Lizaso 1993; Pergent and Pergent Martini 1988; Buia *et al.* 1992; Pergent *et al.* 2008; Sghaier *et al.* 2006; Peirano *et al.* 2011). On the other hand, there are few studies that show a temporal variability of *P. oceanica* shoot densities, but in all of them maximum match with our results (Mabrouk *et al.* 2009; Dural 2010; Periano *et al.* 2011). All parameters of *C. nodosa* meadows showed a temporal trend agree with general dynamic of this specie and with other Mediterranean and Atlantic meadows (Terrados and Ros 1992; Reyes *et al.* 1995; Guidetti *et al.* 2002; Cancemi *et al.* 2002; Luque and Templado 2004; Mostafa *et al.* 2007; Pérez-Lloréns *et al.* 2014).

Cymodocea nodosa presented a higher annual variability than in *P. oceanica* (Table 5); since the former is a species with a higher plasticity (Marbà *et al.* 1996;

Table 5. Magnitud of intra-annual fluctuations (coefficient of variation %) in the different seagrass parameters for *P. oceanica* and *C. nodosa* meadows in P. Calaburras and Calahonda (NW Alboran Sea), as well as in other locations of the Mediterranean Sea and the Atlantic Ocean.

Site	Country	Reference	*Posidonia oceanica*			
			Shoot density	Shoot height	Leaf width	Leaf number
Punta Calaburras	Spain	Present study	13.1	38.7	3.5	8.5
Calahonda	Spain	Present study	17.4	34.7	7.6	8.3
Tabarca	Spain	Sánchez Lizaso 1993		58.4		10.7
Banyuls sur mer	France	Pergent and Pergent-Martini (1988)		23.5		6.7
Port cros	France			39.6		19.4
La Revellata Bay (Corsica)	France	Gobert (2002)	20.6	30.0	8.2	18.4
Monterosso al Mare	Italy	Peirano *et al.* 2011	42.4	43.7	7.5	20.6
Lacco Ameno (Ischia Island)	Italy	Buia *et al.* 1992		32.3		10.4
Otranto (Apulia)	Italy	Guidetti 2002	41.2	34.5		3.6
			Cymodocea nodosa			
Punta Calaburras	Spain	Present study	49.3	73.1	21.1	16.7
Calahonda	Spain	Present study	26.3	37.1	12.7	18.5
Canary Islands	Spain	Reyes *et al.* 1995	21.1	17.9	43.0	11.4
Ria Formosa	Portugal	Cunha and Duarte 2007		37.5		
Mar Menor	Spain	Terrados and Ros 1992	19.9			37.5
Punta San Pietro Bay (Ischia Island)	Italy	Cancemi *et al.* (2002)	23.2	48.5	22.7	18.3
Bay of Piran (Gulf of Trieste)	Italy	Peduzzi and Vukovic (1990)	54.3	69.2	64.3	33.9
Alexandria	Egypt	Mostafa *et al.* (2007)	40.2			22.7

Guidetti *et al.* 2002). On the other hand, shoot density and leaf number of *P. oceanica* showed a lower annual variability compared with other Mediterranean meadows (Table 5). While all phenological parameters of *C. nodosa* showed intermediate (between Atlantic and Mediterranean meadows) values of variability, with the exception of P. Calaburras, where presented higher values like results to its declined during 2009 (Table 5). Probably, the special characteristic of the study area, low water transparency, constant hydrodynamism and the lower intra-annual temperature changes (15.3-22.5 ºC) in comparison to other Mediterranean areas, such as the Adriatic (9-24 ºC), Tunisian coasts (14- 31 ºC) or southern Italian coasts (11.8-24.8 ºC) (Peduzzi and Vukovic 1990; Guidetti *et al.* 2002; Sghaier *et al.* 2006) could be related to these values of annual variability.

The present study shows that the majority of plant parameters of both species in the studied area were constant between sites and patches, while displayed higher differences between years. In fact, a decrease of all the phenological variables of *C. nodosa* meadows was detected in P. Calaburras during the sampling period. This reduction was probably reflecting a stressful condition which resulted in the disappearance of this meadow (Marbà and Duarte 1994; Cabaço *et al.* 2010). However, there are low numbers of inter-annual studies, especially for *C. nodosa*, but all of these also show that plants parameters present an inter-annual variability, highlighting the need for performing long-term phenological studies (Marbà *et al.* 1996; Gobert 2002; Pons Fabregas 2007; Cunha and Duarte 2007; Zakhama-Sraieb *et al.* 2010; Peirano *et al.* 2011).

Shoots with inflorescences followed by fruit development have been observed in consecutive years (2008-2009), indicating that sexual reproduction of *P. oceanica* may potentially occur in meadows at the western distributional limit (Urra *et al.* 2011b). Unlike *P. oceanica*, no inflorescences were observed in *C. nodosa* meadows. These and other *C. nodosa* meadows of the southern Iberian Peninsula (e.g. Calahonda, Ria Formosa) display low genotypic richness, suggesting a predominant clonal propagation and a high affinity to Atlantic populations (i.e. Atlantic influence) (Cunha and Duarte 2007; Alberto *et al.* 2008; OSPAR 2010).

Conclusion

In conclusion, meadows of *P. oceanica* and *C. nodosa* of the NW Alboran Sea displayed species-specific seasonal dynamics throughout three consecutive years and similarities to those recorded in other areas of their biogeographical distribution. Nevertheless, differences in some of the parameters (e.g. shoot density and height), the meadows configuration (patches) and the lower annual variability than other Mediterranean meadows could be the result of the peculiar local environmental conditions of this area close to the Strait of Gibraltar (e.g. cold Atlantic waters, shallow depth, upwellings, constant wave action, low water transparency). The inter-annual studies provide essential information for testing the status of these seagrasses meadows and their sensitivity to environmental changes (Pergent-Martini *et al.* 2005).

This study represents the first one of its kind for both seagrasses in the Alboran Sea; an area within the Mediterranean-Atlantic transition region and it may provide a baseline for further long term studies of the westernmost meadows of *P. oceanica* (a priority habitat included in the Habitat Directive 92/43/CEE). This coastal area of southern Spain are exposed to different anthropogenic impacts (e.g. coastal infrastructures; elevated urbanism), however and although they present a certain regression, *P. oceanica* meadows of SCA "Calahonda" have a good conservation status, support one of the most biodiverse and complex faunistic assemblages for seagrass species within the Mediterranean Sea (Urra *et al.* 2013).

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Appendixes

Appendix 1. Two-way PERMANOVA pair-wise analysis of *P. oceanica* parameters among months and years using t-statistic. Values of significance were calculated used Monte Carlos (MC) method. M1, July, September; M2, November, December; M3 January, March; M4, May, June; A1, July 2007-May 2008; A2, September 2008-June 2009; A3, September 2009-March 2010.* Significant differences P<0.05; **P<0.01; *** P< 0.001. Only appears the values of the phenological parameters that presented differences in the mixed factor year x month.

Punta Calaburras	groups	shoot density		shoot height		leaf weight		number of leaf	
		t	P(MC)	t	P(MC)	t	P(MC)	t	P(MC)
Month M1	A1 vs A2			2.536	<0.05*	6.036	<0.01**		
	A1 vs A3			0.182	0.854	3.754	<0.01**		
	A2 vs A3			5.121	<0.01**	2.859	<0.01**		
Month M2	A1 vs A2			5.223	<0.01**	0.953	0.371		
	A1 vs A3			5.034	<0.01**	4.545	<0.01**		
	A2 vs A3			0.849	0.423	2.936	<0.01**		
Month M3	A1 vs A2			2.838	<0.05*	0.949	0.377		
	A1 vs A3			4.416	<0.01**	1.147	0.278		
	A2 vs A3			2.501	<0.05*	1.727	0.121		
Month M4	A1 vs A2			0.181	0.867	0.745	0.477		
Year A1	M1 vs M2			4.558	<0.01**	3.59	<0.01**		
	M1 vs M3			1.231	0.257	3.65	<0.01**		
	M1 vs M4			1.482	0.186	3.202	<0.05*		
	M2 vs M3			6.139	<0.001***	2.230	0.059		
	M2 vs M4			9.196	<0.001***	1.914	0.095		
	M3 vs M4			3.876	<0.01**	0.107	0.916		
Year A2	M1 vs M2			5.422	<0.001***	3.066	<0.05*		
	M1 vs M3			8.143	<0.001***	2.572	<0.05*		
	M1 vs M4			14.158	<0.001***	3.7	<0.05*		
	M2 vs M3			13.824	<0.001***	0.109	0.915		
	M2 vs M4			23.049	<0.001***	0.656	0.528		
	M3 vs M4			4.238	<0.01**	0.596	0.564		
Year A3	M1 vs M2			7.804	<0.001***	2.711	<0.05*		
	M1 vs M3			2.805	<0.05*	1.566	0.150		
	M2 vs M3			11.511	<0.001***	0.112	0.913		

Calahonda	groups	shoot density		shoot height		leaf weight		number of leaf	
		t	P(MC)	t	P(MC)	t	P(MC)	t	P(MC)
Month M1	A1 vs A2	0.713	0.507	2.619	<0.05*	1.530	0.172		
	A1 vs A3	0.461	0.660	0.406	0.687	3.981	<0.01**		
	A2 vs A3	0.232	0.819	3.489	<0.01**	1.296	0.233		
Month M2	A1 vs A2	0.745	0.474	2.051	0.076	0.843	0.432		
	A1 vs A3	2.829	<0.05*	2.840	<0.05*	5.622	<0.001***		
	A2 vs A3	2.635	<0.05*	6.738	<0.001***	5.242	<0.01**		
Month M3	A1 vs A2	7.193	<0.001***	1.205	0.265	2.496	<0.05*		
	A1 vs A3	2.918	<0.05*	3.038	<0.05*	2.389	<0.05*		
	A2 vs A3	2.202	0.060	3.638	<0.01**	0.448	0.659		
Month M4	A1 vs A2	6.328	<0.001***	2.922	<0.05*	1.329	0.220		
Year A1	M1 vs M2	2.493	<0.05*	6.607	<0.001***	0.442	0.668		
	M1 vs M3	0.963	0.370	0.118	0.908	3.702	<0.01**		
	M1 vs M4	1.814	0.109	5.221	<0.01**	2.499	<0.05*		
	M2 vs M3	2.784	<0.05*	7.503	<0.001***	3.9	<0.01**		
	M2 vs M4	6.863	<0.001***	13.818	<0.001***	2.851	<0.05*		
	M3 vs M4	8.288	<0.001***	6.124	<0.001***	0.501	0.632		
Year A2	M1 vs M2	1.956	0.088	8.261	<0.001***	1.226	0.259		
	M1 vs M3	4.09	<0.01**	0.860	0.420	0.243	0.807		
	M1 vs M4	1.195	0.268	5.169	<0.001***	0.434	0.668		
	M2 vs M3	8.076	<0.001***	5.326	<0.001***	1.342	0.218		
	M2 vs M4	4.526	<0.01**	10.228	<0.001***	0.571	0.582		
	M3 vs M4	5.423	<0.001***	3.254	<0.05*	0.304	0.771		
Year A3	M1 vs M2	0.235	0.816	10.679	<0.001***	2.312	0.052		
	M1 vs M3	1.424	0.191	3.511	<0.01**	2.081	0.067		
	M2 vs M3	2.480	<0.05*	7.412	<0.001***	3.687	<0.01**		

Appendix 2. Two-way PERMANOVA pair-wise analysis of *C. nodosa* parameters among months and years using t-statistic. Values of significance were calculated used Monte Carlos (MC) method. M1,July, September; M2, November, December; M3 January, March; M4, May, June; A1, July 2007-May 2008; A2, September 2008-June 2009; A3, September 2009-March 2010.* Significant differences P<0.05; **P<0.01; *** P< 0.001. Only appears the values of the phenological parameters that presented differences in the mixed factor year x month.

Punta Calaburras	groups	shoot density		shoot height		leaf weight		number of leaf	
		t	P(MC)	t	P(MC)	t	P(MC)	t	P(MC)
Month M1	A1 vs. A2	0.179	0.863	9.096	<0.001***	0.179	0.863	4.543	<0.01**
	A1 vs. A3	9.879	<0.001***	13.586	<0.001***	9.879	<0.001***	22.113	<0.001***
	A2 vs. A3	4.819	<0.001**	16.665	<0.001***	4.819	<0.01**	43.818	<0.001***
Month M2	A1 vs. A2	0.826	0.428	2.535	<0.05*	0.826	0.428	0.283	0.781
	A1 vs. A3	6.539	<0.001***	2.009	0.084	6.539	<0.001***	2.910	<0.05*
	A2 vs. A3	7.359	<0.001***	0.065	0.952	7.359	<0.001***	2.741	<0.05*
Month M3	A1 vs. A2	1.366	0.214	1.52	0.172	1.366	0.214	3.138	<0.05*
	A1 vs. A3	8.554	<0.001***	19.136	<0.001***	8.554	<0.001***	48.5	<0.001***
	A2 vs. A3	6.745	<0.001***	4.473	<0.01**	6.745	<0.001***	66.408	<0.001***
Month M4	A1 vs. A2	2.062	0.070	1.622	0.137	2.062	0.070	0.643	0.539
Year A1	M1 vs. M2	4.6	<0.01**	7.475	<0.001***	4.6	<0.01**	6.24	<0.001***
	M1 vs. M3	4.42	<0.01**	9.83	<0.001***	4.42	<0.01**	7.867	<0.001***
	M1 vs. M4	1.052	0.323	9.305	<0.001***	1.052	0.323	2.54	<0.05*
	M2 vs. M3	0.418	0.680	2.245	0.055	0.418	0.680	4.382	<0.01**
	M2 vs. M4	2.767	<0.05*	1.928	0.087	2.767	<0.05*	4.199	<0.01**
	M3 vs. M4	2.56	<0.05*	0.053	0.959	2.56	<0.05*	6.338	<0.001***
Year A2	M1 vs. M2	2.063	0.071	2.675	<0.05*	2.063	0.071	2.954	<0.05*
	M1 vs. M3	2.814	<0.05*	2.431	<0.05*	2.814	<0.05*	4.743	<0.01**
	M1 vs. M4	2.031	0.082	3.882	<0.01**	2.031	0.082	2.639	<0.05*
	M2 vs. M3	1.718	0.124	1.332	0.222	1.718	0.124	0.885	0.398
	M2 vs. M4	0.15	0.882	2.164	0.062	0.15	0.882	4.423	<0.01**
	M3 vs. M4	1.164	0.274	0.369	0.723	1.164	0.274	5.297	<0.001***
Year A3	M1 vs. M2	2.683	<0.05*	7.741	<0.001***	2.683	<0.05*	32.932	<0.001***
	M1 vs. M3								
	M2 vs. M3	2.683	<0.05*	7.741	<0.001***	2.683	<0.05*	32.932	<0.001***

Calahonda	groups	shoot density		shoot height		leaf weight		number of leaf	
		t	P(MC)	t	P(MC)	t	P(MC)	t	P(MC)
Month M1	A1 vs. A2	2.101	0.071	2.756	<0.05*			8.552	<0.001***
	A1 vs. A3	1.215	0.262	4.519	<0.01**			3.157	<0.05*
	A2 vs. A3	0.581	0.576	3.473	<0.01**			0.191	0.855
Month M2	A1 vs. A2	0.237	0.219	0.038	0.972			3.200	<0.05*
	A1 vs. A3	0.066	0.073	1.111	0.299			3.464	<0.05*
	A2 vs. A3	0.33	0.318	1.124	0.293			1.723	0.124
Month M3	A1 vs. A2	2.894	<0.05*	1.775	0.114			2.108	0.068
	A1 vs. A3	0.215	0.835	2.084	0.069			2.557	<0.05*
	A2 vs. A3	2.633	<0.05*	0.71	0.501			3.772	<0.01**
Month M4	A1 vs. A2	1.504	0.179	3.805	<0.01**			3.043	<0.05*
Year A1	M1 vs. M2	0.297	0.775	1.49	0.184			19	<0.001***
	M1 vs. M3	3.971	<0.01**	3.268	<0.01**			10.954	<0.001***
	M1 vs. M4	3.824	<0.01**	0.255	0.805			0.535	0.602
	M2 vs. M3	2.996	<0.05*	2.074	0.074			3.138	<0.05*
	M2 vs. M4	3.185	<0.05*	2.059	0.073			9.985	<0.001***
	M3 vs. M4	1.046	0.323	4.061	<0.01**			6.893	<0.001***
Year A2	M1 vs. M2	0.746	0.471	1.71	0.122			10.25	<0.001***
	M1 vs. M3	1.561	0.159	0.861	0.419			13.02	<0.001***
	M1 vs. M4	0.274	0.789	0.059	0.957				
	M2 vs. M3	0.901	0.390	1.383	0.197			2.631	<0.05*
	M2 vs. M4	1.077	0.314	1.797	0.115			6.608	<0.001***
	M3 vs. M4	1.89	0.095	0.877	0.410			8.746	<0.001***
Year A3	M1 vs. M2	0.877	0.397	1.871	0.098			9.26	<0.001***
	M1 vs. M3	1.534	0.165	3.918	<0.01**			5.692	<0.01**
	M2 vs. M3	0.573	0.585	1.002	0.336			3.357	<0.05*

CAPÍTULO 3

Cambios estacionales en la estructura de las asociaciones de crustáceos decápodos asociados a praderas de *Cymodocea nodosa* en el Mar de Alborán (Mediterráneo occidental)

Este capítulo se basa/ This chapter is based on:

Temporal changes in the structure of the crustacean decapod assemblages associated with *Cymodocea nodosa* meadows from the Alboran Sea (Western Mediterranean Sea)

Mateo-Ramírez A., García Raso J.E.

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Abstract

The decapod assemblages associated with two shallow meadows of *Cymodocea nodosa*, located in the same geographical area (southern Spain) but on different substrates and with different patch size, have been analyzed. They display similar structure (diversity indices not significantly different), without a clear relation of richness and abundances to patch size, and with the same dominant species (the family Hippolytidae and, in particular, *Hippolyte leptocerus* are characteristic of this habitat). Composition of both crustacean assemblages is influenced by species that are common in neighbouring habitats. Therefore the connectivity among them is an important factor in the qualitative and quantitative structure of these decapod communities. Species richness appears to be higher than in *Cymodocea* meadows elsewhere in the Mediterranean and Atlantic at a similar depth, perhaps as consequence of the biogeographical location and the high diversity and connectivity with surrounding biotopes. High evenness values are the result of the structure and location of these meadows, which are fragmented and interspersed with other biotopes (sandy and rocky bottoms), resulting in an "ecotone effect". On the other hand, the structures of the decapod assemblages differ significantly according to season. The abundance and species richness are both related to plant phenology and the dominant species present a positive correlation with the number of leaves per shoot. The maximum abundance of many species is coincident with the greatest seagrass development (spring – summer), which provide more resources (surface, biomass, protection, food). Therefore, seasonality is linked to plant life cycle, but also to the interrelationships and biology of the species, which are adapted and specialized to the environmental features of these shallow habitats.

Keywords: *Cymodocea nodosa*, decapods, space - time variations, diversity, patch sizes, Western Mediterranean Sea.

Introduction

Marine seagrass meadows are essential elements in the biological structure and physical-chemical process of the coastal areas (Duarte and Sand-Jensen, 1990). They fulfil many important and varied functions such as the construction of new microhabitats with different ecological conditions, therefore enhancing biodiversity and biological interactions (Bellan-Santini *et al.* 1994; Pedersen *et al.* 1997; Orth *et al.* 1984; Phillips and Meriez 1988). Several studies deal with specific zoological groups associated with *Cymodocea nodosa* or with the total macrofauna in general (Ledoyer 1966, 1968; Scipione *et al.* 1996; Sánchez-Jerez *et al.* 1999; Guidetti and Bussotti 2000; Koutsoubas et al. 2000; Corbera *et al.* 2002; Barbera-Cebrián *et al.* 2002; Riera *et al.* 2003; Vizzini and Mazzolla 2004; Brito *et al.* 2005; Tuya *et al.* 2006, González *et al.* 2007; Como *et al.* 2008) but a few of them are focussed on the crustacean decapod community in the Atlantic Ocean (Schaffmeister *et al.* 2006) or the Mediterranean Sea (Ledoyer 1966, 1968; Števčić 1991; Reed and Manning 2000; García Raso *et al.* 2006a). On the other hand, the results found in these studies have shown quantitative and qualitative differences which could be attributed to different factors, such as the geographic area, sampling period, seagrass structural complexity, depth, substrata, sampling methodology, predation, among others. Some of these relationships have been analyzed in different geographical areas, such as Europe (Borg and Schembri 2000; Attrill *et al.* 2000; Hirst and Attrill 2008), North America (Lewis and Stoner 1983), Australia (Bell and Westoby 1986, Worthington *et al.* 1992, Kwak and Klumpp 2004), Indonesia (Unsworth *et al.* 2007) and seagrass species (*Zostera marina*, *Z. capricorni*, *Posidonia oceanica*, *Posidonia australis*, *Cymodocea serratula*, *C. rotundata*, Halodule spp., *Halophilla ovalis*, *Thalassia testudinum*, etc), sometimes with apparently contradictory results (e.g., the densities of the shrimp *Hippolyte* in two different studies (Lewis and Stoner 1983)). However, difficulties in macrofaunal estimates and in the interpretations should be taken into account, mainly when the species or groups under study prefer a specific microhabitat and/or a particular food resource (for example, within decapods, the caridean shrimps and the penaeids; Mellors and Marsh 1993). Other factors to consider in the interpretations are the sampling methodology (Borg and Schembri 2000), the life cycles and larval settlement (Bell and Westoby 1986), the species adaptation and the predatory pressures (Unsworth *et al.* 2007).

The aim of this study is to help to clarify, as far as possible, some of these situations, but focussing specifically on the seagrass *Cymodocea nodosa* and its decapod fauna. For this purpose, we compare two decapod assemblages from two very shallow meadows in the same geographic area. They are located only 7 kilometers apart, but on bottoms with different exposure level, substrata and surrounding habitats. Nevertheless there are no appreciable differences in depth, sea water temperature or plant phenology, and considering that the biogeographical setting is the same. Assemblage structures (values of diversity indices, richness, abundances, species composition) were analyzed spatially and temporally and, also in relation to the plant phenology. In addition, the existence of small patches of different sizes in one of the studied zones allowed us to evaluate the possible effect of fragmentation of habitat and species/area relationship. There are some studies dealing with those topics (Attrill *et al.* 2000, Bell *et al.* 2001; Barbera-Cebrián *et al.* 2002; Tanner 2005; Hirst and Attrill 2008; Macreadie *et al.* 2009) but they have never been carried out on the small seagrass *Cymodocea nodosa* and specifically on decapods.

The study area

The sampling area is located off the coast of Mijas (Málaga, southern Spain, western Mediterranean Sea) (Figure 1), within the marine Site of Community Importance (SCI) known as Calahonda (code ES6170030) in the Natura 2000 Network. It is one of the very few natural rocky outcrops existing on the shores of Malaga province and a "hotspot" for European biodiversity (García Raso *et al.* 2010) due to its high species richness with the presence of endangered and unique species and to the coexistence of species from different biogeographic origins (Atlantic Mediterranean, African-European), mainly studied for molluscs (Urra *et al.* 2011; Gofas, personal communication). This is a consequence of its geographical location (near the Straits of Gibraltar) and its oceanographic, physical-chemical and upwelling features (see Ekman 1953; Briggs 1974; Conde and Seoane 1982; Parrilla and Kinder 1987; Tintoré *et al.* 1991; Gofas 1999).

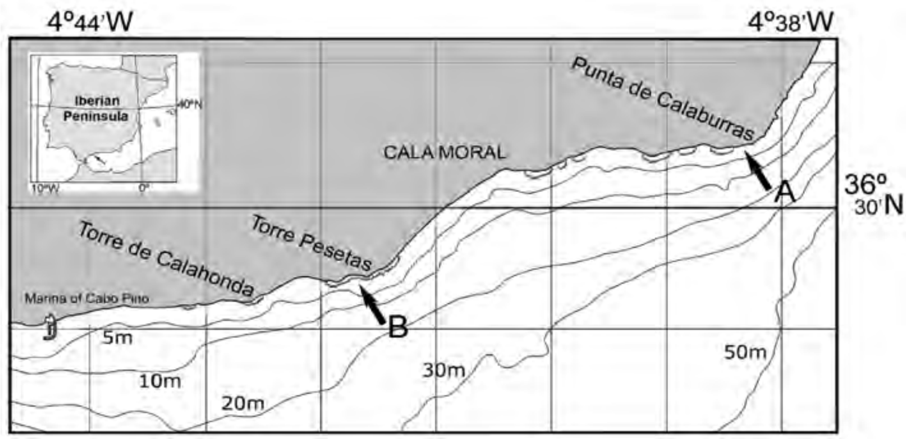

Fig. 1. Study area. Punta de Calaburras (A), Calahonda (B) (Southern Spain).

In the study area, small patches (1-10 m long) of *Cymodocea nodosa* can be found between 1 and 5 m depth, mixed with rocks, sand, seaweed and *Posidonia oceanica* (which is close to its westernmost biogeographical distribution limit). Two shallow sites were selected, "Punta de Calaburras" (PC) 36º30'23" N - 04º38'41"W and Calahonda (CH) 36º29'21"N - 04º41'55"W. In Punta de Calaburras, the patch is of about 27 m^2 at 0.6 - 1m, subjected to wave action (which determines the abundance of pebbles). Calahonda is a more sheltered site, and the meadow studied is composed of patches between 0.62 and 10.34 m^2 (mean: 5 m^2) at 1.5 - 2 m depth and protected by large rocks.

Material and Methods

Sampling methodology

The samples were taken seasonally from July 2007 to May 2008 (July - summer "s"; November - autumn "a"; January or February - winter "w" and May - spring "p"); by two SCUBA divers during day. The specimens were collected with a manual airlift pump connected to an air tank, with a 0.5 mm mesh bag to prevent the loss of small specimens. The sampling methodology is friendly with the environment, and this represents a basic requirement in a protected area where the *Cymodocea* meadows are adjacent to fragile *Posidonia* meadows (the westernmost known site). In addition, this sampling gear is more effective than the hand net (Borg and Schembri 2000), because it collects the species living in all strata and therefore, the assemblages are better characterized. Random samples in areas with different densities could modify the results (Lewis and Stones 1983). For such a reason five 50x50 cm (total area 1.25 m^2) quadrants or replicates were pumped at each site and sampling date in order to study spatial and temporal variability. In text and tables, the replicates are indicated with a number (1 to 5) after seasonal codes (e,g. w5). A similar methodology was indicated by Short and Coles (2001) and applied by Como *et al.* (2008). When compared with previous studies, the total area sampled at each sampling date is slightly higher to the one mentioned by García Raso (1990), Como *et al.* (2008) on *Posidonia* and *Cymodocea* faunal assemblages, but slightly smaller to the one mentioned by Barbera-Cebrián *et al.* (2002) and Sánchez *et al.* (1999). However, their sampling methods were different.

The studied patches of *Cymodocea* were measured. In the phenological part of this study, *Cymodocea* patches were randomly selected with a quadrant of 50 x 50 cm, subdivided (25x25 cm) in order to obtain shoot density. In each quadrant, ten randomly-selected shoots were analysed in situ for leaf length (from base to apex) and maximum width, as well as number of leaves per shoot.

Sediment granulometry was analysed with a column of standard sieves (Buchanan 1984) and Trask index was calculated (Trask 1950). Organic matter in the sediment was measured by ignition at 500 ºC, for 1 h, of 5 replicates per site and season collected in the same area where fauna and seagrass phenological parameters where taken.

Data on shallow water temperature were provided by the "Grupo Mediterráneo de Cambio Climático del Instituto Español de Oceanografía de Málaga" (http://www.ma.ieo.es/gcc/sistemas_observacion.htm), obtained from a meteorological station in Fuengirola, close to the studied area. In addition, water temperatures were measured on site at the time of sampling with thermometers with 0.1ºC precision and with an automatic temperature recorder (HOBO). Occasionally, complementary measurements were taken 24 h before and after sampling in order to improve the data set.

Data analysis

Several studies carried out in the Atlantic (African and European) and Mediterranean Sea have been used for the identification of the decapods species, including the classic and basic study of Zariquiey (1968) as well as recent revisions and checklists (such as, Ng *et al.* 2008).

Data sets of the seagrass phenological variables were checked for normality (Kolmogorov-Smirnof test) and significance (ANOVA and U of Mann-Whitney) using the SPSS software package.

The correlations between species richness and patch area, number of shoots per square meter, number of leaves per shoot, leaf length and width, total number of individuals and abundance of the three dominant species in each replicate were determined by Pearson or Spearman coefficients. The correlation between number of individuals / species richness and patch size were only analysed in Calahonda. Correlation between assemblage structure and seasonal / spatial variations were analysed with the PRIMER software package (Clarke and Warwick 1994), using a fourth root transformation of quantitative data without standardisation.

Possible significant differences between sampling stations and annual seasons were assessed with the ANOSIM routine (non-parametric permutation procedure applied to the similarity matrix) routine. To determine the relations between assemblages a similarity matrix (Bray-Curtis index) was used to construct CLUSTER and bivariate MDS plots (MDS routine). Furthermore, the diversity values of the Shannon index (Shannon and Weaver, 1963), Simpson index (Simpson 1949) and evenness values (Pielou, 1969) were determined (DIVERSE routine). ANOVA and U of Mann-Whitney were used to compare the diversity index and phenological variables in each zone. Finally, the relative abundance or dominance (Di, %), the frequency of occurrence (Fi, %) and the contribution of species to average within-group similarity (SIMPER routine), were calculated.

Results

Abiotic factors (sediment, temperature)

Granulometric analyses show that surface sediments from two sites are distinct. In Calahonda, the mean size of particle (Q_{50}) was between 0.25 and 0.50 mm. The mud and organic matter content were 1.7%, and 1.8 ± 0.4% respectively. The Trask index value was 0.667. Therefore, the Calahonda sediments are considered well-sorted fine sandy bottoms. In Punta de Calaburras the sediment characteristics (4 mm < Q_{50} < 63 mm, mud content: 3.3%, organic content: 3.1 ± 0.8%, Trask index: 1.364) are indicative of mixed sediments, with mud and stones, moderately selected. These differences are mainly a consequence of the different hydrodynamic conditions - exposure level. The fine sands in Calahonda are related to a more sheltered area due to large rocks that attenuate wave action, while Punta de Calaburras contains many pebbles and is a little more exposed and slightly shallower site.

In 2007 and 2008, the annual mean temperature of seawater was the highest of the decade. Monthly means at Fuengirola station (calculated from a 23-years series) and monthly anomalies at both sites in 2007 and 2008 (difference between monthly mean at each site and a monthly mean from 23-years series) are shown in Table 1. During the sampling period, the mean values were 18.57 ºC ± 2.42 ºC in Punta de Calaburras and 18.68 ºC ± 2.74 ºC in Calahonda. Seasonal changes of temperature are also shown in Table 1. Strong westerly winds led to decreased water temperature in spring 2008.

Phenology of **Cymodocea nodosa**

A complete study on the phenology of the seagrass meadows (2007 - 2010) in this area is under development. Hence, Table 2 only shows the seasonal mean values (with standard deviation) observed during this study (summer 2007 to spring 2008).

The phenological parameters of *Cymodocea nodosa* present a seasonal trend with high values of number of leaves per shoot and leaf width in summer - spring

Table 1. A, Temperature of sea water from a station in Fuengirola, close to the studied area (general monthly means and (standard deviation) obtained from a series of 23 years, 1985 to 2007 and the monthly anomalies found in the years 2007 and 2008; data from IEO Fuengirola). B, Mean temperatures and (standard deviation) observed during sampling in shallow waters of the studied areas, Punta de Calaburras and Calahonda.

	(A)			(B)		
Month	Means values ºC (SD) Fuengirola	Anomaly 2007	Anomaly 2008		Punta de Calaburras	Calahonda
January	14.46 (0.79)	0.38	0.77	Winter 08	15.33 (0 29)	15.88 (0.63)
February	14.41 (1 26)	-0.17	1.23			
March	14.99 (0.83)	-0.45	0.22			
April	15.29 (0.74)	0.03	-0.14	Spring 08	17.00 (0.91)	17.00 (1.41)
May	16.36 (1.08)	-0.35	-0.75			
June	18.10 (0.97)	-1.88	0.45			
July	20.22 (0.85)	0.30	0.70	Summer 07	20.50 (0.50)	22.50 (2.0)
August	20.77 (0.72)	1.17	2.13			
September	20.14 (1.41)	2.56	0.66			
October	18.36 (1.13)	2.21	1.21	Autumn 07	20.38 (1 25)	19.75 (0.50)
November	16.69 (0.83)	1.72	-0.39			
December	15.28 (0.56)	0.55	-1.05			
Average		+ 0.51	+ 0.42			

Table 2. Phenology of *Cymodocea nodosa* in the study areas Calahonda (CH) and Punta de Calaburras (PC). Mean values ± standard deviation.

	Shoot density m^{-2}	Leaf number per shoot.	Leaf length (cm)	Leaf width (cm)
Summer 07CH	2620.80 ± 454.72	2.70 ± 0.65	5.97 ± 1.90	0.22 ± 0.04
PC	4592.00 ± 1039.38	3.08 ± 0.49	28.40 ± 6.24	0.31 ± 0.02
Autumn 07 CH	2731.20 ± 695.42	1.94 ± 0.47	7.28 ± 1.78	0.20 ± 0.02
PC	2072.00 ± 648.32	2.18 ± 0.39	10.35 ± 3.01	0.24 ± 0.04.
Winter 08 CH	1785.60 ± 120.19	2.10 ± 0.36	9.02 ± 2.26	0.20 ± 0.03
PC	2235.20 ± 584.29	1.94 ± 0.24	7.50 ± 2.12	0.21 ± 0.04
Spring 08 CH	1593.60 ± 392.55	2.66 ± 0.48	5.76 ± 2.09	0.24 ± 0.05
PC	3824.00 ± 1258.82	2.64 ± 0.60	7.54 ± 3.50	0.24 ± 0.04
Mean values CH	2182.80 ± 576.63	2.35 ± 0.39	7.01 ± 1.50	0.22 ± 0.02
PC	3180.80 ± 1228.66	2.46 ± 0.51	13.45 ± 10.06	0.25 ± 0.04

and minimum values in autumn - winter. The shoot density displayed a similar trend in both sites but in Calahonda the minimum values was obtained in spring. Finally although the leaf length showed in Punta de Calaburras the same seasonal trend, in Calahonda this trend is different, showing high values in winter and minimum in spring.

The crustacean decapod community

A total of 932 specimens belonging to 34 species were captured. Table 3 shows the relative abundance (Di, %) and frequency of occurrence (Fi, %) of these species at both stations.

The best represented families in this biotope are: Hippolytidae with 5 species (*Hippolyte leptocerus*, *Hippolyte inermis*, *Hippolyte varians*, *Hippolyte niezabitowskii*, *Eualus cranchi*), Majidae with 4 species (*Pisa carinimana*, *Acanthonyx lunulatus*, *Achaeus gracilis* and *Achaeus cranchii*), Paguridae with 3 species (*Pagurus anachoretus*, *Cestopagurus timidus* and *Anapagurus hyndmanni*) and Xanthidae with 3 species (*Xantho pilipes*, *Xantho hydrophilus granulicarpus* and *Xantho poressa*).

The species with a high contribution to average within-group similarity from Punta de Calaburras and from Calahonda were listed in Table 4 (see also groups 1 and 2, 3 and 5 respectively, in Figure 4).

At both sites, the species that displayed a frequency of occurrence below 5% can be classified as accidental and related to adjacent habitats: in Calahonda, *Galathea squamifera* (Di = 0.32%, a sciaphilic species mainly living in cavities), *Parthenopoides massena* (Di = 0.32, common on detritic bottoms deeper than 15 m), *Philocheras trispinosus* (Di = 0.32, typical species of the well-sorted fine sands community), *Xantho poressa* (Di = 0.32, from pebbled shallow bottoms) and *Achaeus cranchii* (Di = 0.32, common in deeper water) as well as *Pinnotheres pisum* (Di = 0.64%, Fi = 10%, bivalve commensal living within *Pinna rudis*); in Punta Calaburras, *Palaemon serratus* (Di = 0.32, from photophilic algae and rocky bottoms), *Hippolyte varians* and *H. niezabitowskii* (Di = 0.16, both unusual species in the studied area and associated with photophilic environments, specially seaweeds and *Zostera* respectively) and, finally, *Achaeus cranchii* (Di = 0.16, more

Table 3. Checklist of the species collected in the study areas Calahonda and Punta de Calaburras with their relative abundance or dominance (Di, %) and frequency of occurrence (Fi, %).

	Calahonda		P. Calaburras		Total Di
	Di	Fi	Di	Fi	
PENAEIDEA Family Sicyoniidae					
Sicyonia carinata (Brünnich, 1768)	2.23	20	0.32	10	0.97
CARIDEA Family Palaemonidae					
Palaemon serratus (Pennant, 1777)	0	0	0.32	5	0.22
Family Hippolytidae					
Hippolyte leptocerus (Heller, 1863)	20.06	65	14.94	80	16.67
Hippolyte inermis Leach, 1815	3.82	25	10.71	50	8.39
Hippolyte varians Leach, 1814	0	0	0.16	5	0.11
Hippolyte niezabitowskii D'Udekem d'Acoz, 1996	0	0	0.16	5	0.11
Eualus cranchii (Leach, 1817)	0.96	10	1.95	25	1.61
Family Alpheidae					
Athanas nitescens (Leach, 1814)	0	0	7.95	45	5.27
Alpheus dentipes Guérin-Méneville, 1832	0	0	0.32	10	0.22
Family Processidae					
Processa edulis edulis (Risso, 1816)	8.92	35	0.49	15	3.33
Processa robusta Nouvel & Holthuis, 1957	4.14	20	0.49	15	1.72
Family Crangonidae					
Philocheras trispinosus (Hailstone, 1835)	0.32	5	0	0	0.11
Philocheras fasciatus (Risso, 1816)	17.52	65	2.76	45	7.74
ANOMURA Family Diogenidae					
Clibanarius erythropus (Latreille, 1818)	1.27	10	11.85	60	8.28
Calcinus tubularis (Linnaeus, 1767)	0.96	10	13.47	90	9.25
Family Paguridae					
Pagurus anachoretus Risso, 1827	0.64	10	1.14	30	0.97
Cestopagurus timidus (Roux, 1830)	0.64	10	5.19	65	3.66
Anapagurus hyndmanni (Bell, 1845)	7.64	65	11.2	60	10.00
Family Galatheidae					
Galathea squamifera Leach, 1814	0.32	5	0	0	0.11
Family Porcellanidae					
Pisidia longicornis (Linnaeus, 1767) for. *longimana*	0.64	10	0.97	10	0.86
BRACHYURA Family Leucosiidae					
Ebalia edwardsii Costa, 1838	0	0	1.14	25	0.75
Family Pirimelidae					
Pirimela denticulata (Montagu, 1808)	7.64	50	0.32	10	2.80
Sirpus zariquieyi Gordon, 1953	4.46	30	1.30	25	2.37
Family Portunidae					
Liocarcinus navigator (Herbst, 1794)	2.23	35	2.92	50	2.69
Family Pilumnidae					
Pilumnus hirtellus (Linnaeus, 1761)	7.96	25	1.95	35	3.98
Family Xanthidae					
Xantho pilipes A. Milne-Edwards, 1867	0	0	0.32	10	0.22
Xantho hydrophilus granulicarpus (Forest, 1953)	0	0	0.49	15	0.32
Xantho poressa (Olivi, 1792)	0.32	5	4.06	35	2.80
Family Pinnotheridae					
Pinnotheres pisum (Linnaeus, 1767)	0.64	10	0	0	0.22
Family Parthenopidae					
Parthenopoides massena (Roux, 1830)	0.32	5	0	0	0.11
Family Majidae					
Pisa carinimana Miers, 1879	1.27	20	0	0	0.43
Acanthonyx lunulatus (Risso, 1816)	1.27	20	1.79	30	1.61
Achaeus gracilis O.G. Costa, 1839	3.50	35	1.14	25	1.94
Achaeus cranchii Leach, 1817	0.32	5	0.16	5	0.22

frequent in deeper bottoms).

The number of individuals (N) and species richness (S) throughout the year followed a similar trend: with peaks in spring and summer and minimal values in winter (Figure 2 A and B). Values were slightly higher in Punta de Calaburras than in Calahonda. Species richness ranged between 3 (PC w4) and 17 (PC s2) in Punta de Calaburras, and between 1 (CH w3) and 12 (CH p4) in Calahonda. Abundances (number of individuals) fluctuated between 4 (PC w4) and 121 ind. (PC s2) in Punta de Calaburras, and between 1 (CH w3) and 59 ind. (CH p4) in

Table 4. SIMPER analyses. Species ranked according to their average within-group similarity at Punta de Calaburras (PC) and Calahonda (CH) (groups 1 and 2, 3, 5 in figure 4), through seasonality. Av.Abund: average abundance, Av.Sim: average similarity, Sim/SD: similarity/standard deviation, Contrib.%: average contribution to similarity, Cum.%: cumulative percentage of similarity.

Species	Av.Abund	Av.Sim	Sim/SD	Contrib.%	Cum.%
Punta Calaburras (PC)					
Calcinus tubularis	1.79	8.58	1.54	19.84	19.84
Hippolyte leptocerus	1.68	6.29	1.1	14.54	34.38
Clibanarius erythropus	1.24	6.18	0.8	14.29	48.67
Anapagurus hyndmanni	1.30	5.09	0.74	11.76	60.42
Cestopagurus timidus	0.97	4.11	1.00	9.50	69.93
Hippolyte inermis	1.08	2.97	0.60	6.86	76.79
Athanas nitescens	0.90	2.28	0.61	5.28	82.07
Philocheras fasciatus	0.56	1.52	0.34	3.51	85.57
Polybius navigator	0.63	1.35	0.47	3.12	88.69
Xantho poressa	0.63	1.03	0.31	2.39	91.08
Calahonda (CH)					
Philocheras fasciatus	1.29	7.41	0.75	19.31	19.31
Hippolyte leptocerus	1.34	7.29	0.89	18.98	38.29
Anapagurus hyndmanni	0.89	6.02	0.75	15.67	53.96
Pirimela denticulata	0.78	5.64	0.98	14.69	68.65
Polybius navigator	0.37	2.10	0.36	5.47	74.12
Sycionia carinata	0.28	1.87	0.29	4.88	79.00
Hippolyte inermis	0.39	1.80	0.42	4.69	83.69
Processa edulis edulis	0.63	1.30	0.47	3.39	87.08
Sirpus zariquieyi	0.47	1.14	0.33	2.96	90.04

Calahonda. The mean values found in each site (considering all replicates) were: S = 8.90 ± 3.78 species and N = 30.80 ± 26.12 ind. for Punta de Calaburras and S = 6.37 ± 3.35 species and N = 16.53 ± 15.96 ind. for Calahonda.

Abundance and species richness of decapod assemblages were related to seagrass phenological variables. The number of leaves per shoot and number of shoot per square meter are similar at both sites (Mann-Whitney U test Z = - 0.627 P = 0.531 and Z= -1.921, P = 0.055). In the whole studied area, the number of leaves per shoot is positively correlated to abundance and species richness ($R_{Pearson}$

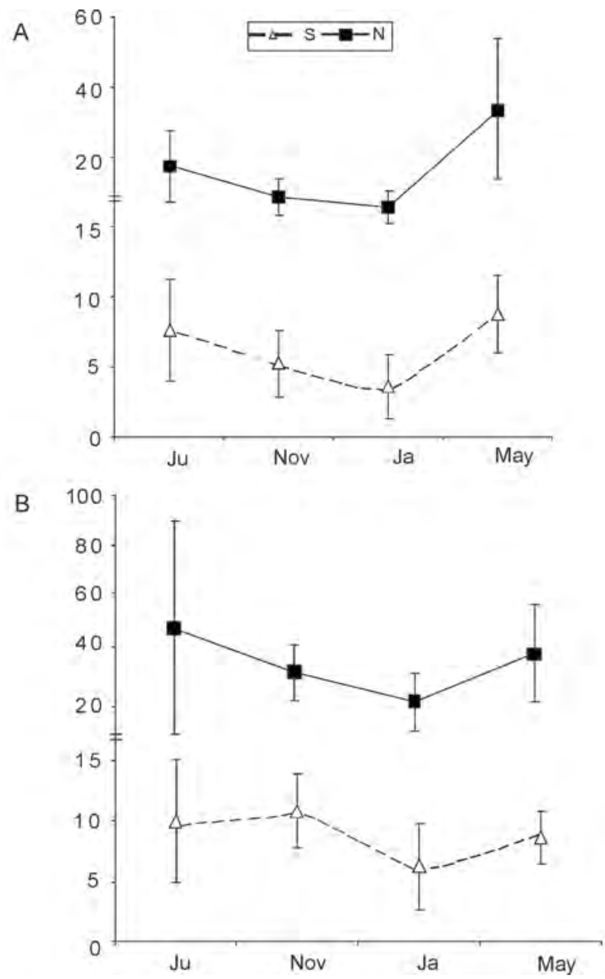

Fig. 2. Seasonal evolution (mean ± SD) of species richness (S) and number of individuals (N) at Calahonda (A) and Punta de Calaburras (B) sites (Ju = July, Nov = November, Ja = January, May = May).

= 0.621, P = 0.000025 and $R_{Pearson}$ = 0.486, P = 0.002 respectively). Considering each site separately, the number of leaves per shoot is also positively correlated to the abundance and richness in Calahonda ($R_{Pearson}$ = 0.623, P = 0.004 and $R_{Pearson}$ = 0.620, P = 0.005 respectively). Nevertheless, a correlation with the number of individuals ($R_{Pearson}$ = 0.635, P = 0.003) was only observed in Punta de Calaburras. Similarly, the abundance of the dominant species *Hippolyte letocerus* and *Hippolyte inermis* displayed a positive correlation with the number of leaves per shoot ($R_{Spearman}$= 0.346, P = 0.029 and $R_{Spearman}$=0.498, P = 0.001) and the abundance of *Anapagurus hyndmanni* is also positively correlated with the number of leaves per shoot but also with the number of shoots per square meter ($R_{Spearman}$= 0.477, P = 0.001; $R_{Spearman}$= 0.418, P = 0.007).

Abundance and species richness did not display any correlation with the patch size (in Calahonda) ($R_{Sperman}$ = -0.052, P = 0.827 and $R_{Sperman}$ = -0.212, P = 0.370). This could be a consequence of the non-significant correlations between the patch area and the abundance of the three species before mentioned, *Hippolyte letocerus*, *Hippolyte inermis* and *Anapagurus hyndmanni* ($R_{Spearman}$= 0.003, P = 0.989; $R_{Spearman}$= -0.241, P = 0.306 and $R_{Spearman}$= -0.334, P = 0.15 respectively).

The results for the Calahonda assemblage (Figure 3A) displayed low-middle values in diversity indices and high evenness (H'= 1.00 ± 0.68 winter, 1.77 ± 0.23 spring; 1-λ = 0.82 ± 0.03 spring, 0.893 ± 0.082 winter; J'= 0.83 ± 0.054 spring, 0.95 ± 0.04 winter). The mean values were H'= 1.49 ± 0.59, J' = 0.90 ± 0.06 and 1-λ = 0.85 ± 0.09. On the other hand, the assemblage in Punta de Calaburras shows higher values in diversity indexes and lower evenness (Figure 3B) (H'= 1.42 ± 0.66 winter, 2.04 ± 0.26 autumn; 1-λ = 0.72 ± 0.29 summer, 0.87 ± 0.05 autumn; J'= 0.76 ± 0.22 summer, 0.87 ± 0.05 autumn). The mean values were H'= 1. 74 ± 0.54; 1-λ = 0.79 ± 0.20 and J'= 0.82 ± 0.16. Only slight differences were observed between the values from both areas, but they are not significantly different (H': F_{ANOVA} = 2.204 with P = 0.146; J' and 1-λ: Mann-Whitney U test Z = 131, P = 0.097 and Z = 184, P = 0.866, respectively).

Significant difference was observed between seasonal samples of the global

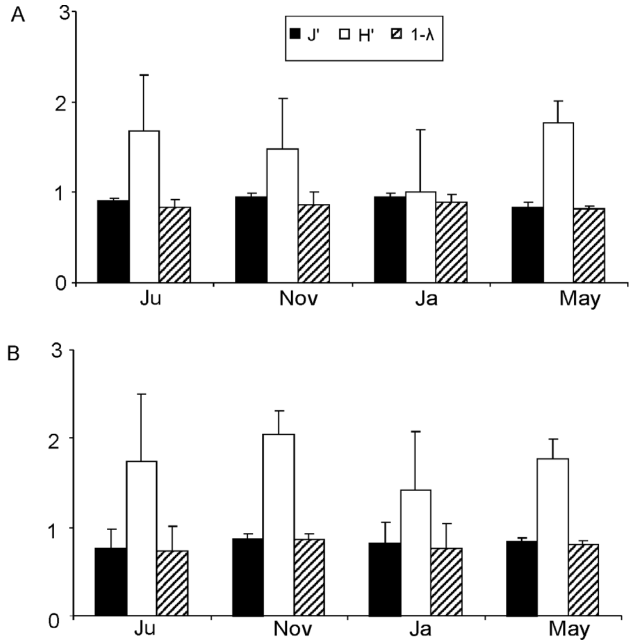

Fig. 3. Mean values and standard deviation of Pielou (J'), Shannon (H') and Simpson (1-λ) diversity indexes at Calahonda (A) and Punta de Calaburras (B) sites (Ju = July, Nov = November, Ja = January, May = May).

decapod community (Punta de Calaburras + Calahonda), but with a low R value (R_{ANOSIM} = 0.225, P = 0.001) (the same occurs when the temperature is considered, R_{ANOSIM} = 0.466, P = 0.001). Difference was more significant when assemblages of Punta de Calaburras and Calahonda are considered separately across the seasonal groups (R_{ANOSIM} = 0.612, P = 0.001).

Within sites (Table 5), seasonality was noted in Calahonda (R_{ANOSIM} = 0.425, P = 0.001): most seasonal groups show significant differences except autumn and winter. The species with highest contribution to the dissimilarity or characterization of summer assemblage were *Anapagurus hyndmanni*, *Pirimela denticulada*, *Philocheras fasciatus*, *Hippolyte inermis* and *Sirpus zariquieyi* (94.51% of cumulate contribution), and the autumn assemblage was mainly characterized by *Syciona carinata*, *Polybius navigator*, *Anapagurus hyndmanni* and *Hippolyte leptocerus* (with a 95.03%). Significant seasonality was also observed in Punta de Calaburras (R_{ANOSIM} = 0.390, P = 0.001). Summer and winter showed the highest differences, while the most similar were summer and autumn. In summer, *Calcinus tubularis*, *Hippolyte inermis*, *Athanas nitescens*, *Hippolyte leptocerus*, *Cestopagurus timidus*, *Anapagurus hyndmanni* and *Sirpus zariquieyi* represent a cumulated contribution of 91.39% and, in winter, *Clibanarius erythropus*, *Philocheras fasciatus*, *Calcinus tubularis*, *Hippolyte leptocerus* and *Polybius navigator* represent 92.44%.

Table 5. ANOSIM pairwise test comparing seasonal groups at Calahonda (CH) and Punta de Calaburras (PC) sites.

	Calahonda (CH)		Punta de Calaburras (PC)	
Groups	R	P	R	P
Ju,Nov	0.706	0.016*	0.208	0.056 ns
Ju,Ja	0.326	0.024*	0.684	0.008**
Ju, May	0.468	0.008**	0.268	0.056 ns
Nov, Ja	0.125	0.214 ns	0.256	0.063 ns
Nov, May	0.656	0.008**	0.628	0.008**
Ja, May	0.366	0.024*	0.600	0.008**

P = significance level; $^*P < 0.05$, $^{**}P < 0.01$; n.s. = non significant; R = rank of similarities between samples; Ju = July; Nov = November; Ja = January; May = May.

These two assemblages, 7 kilometers apart from each other and within the same habitat, are significantly different ($R_{ANOSIM} = 0.362$, $P = 0.001$). These differences and similarities are shown in the quantitative analyses of aggregation CLUSTER (Figure 4A) and ordination MDS (Figure 4B). Punta de Calaburras (PC) samples and replicates form a single group (only the replicates PCw3 and PCw4 are not included) organized into two seasonal subgroups: summer-autumn and winter-spring; in contrast, broader differences are observed in Calahonda (CH), because in spite of having the same similarity (28.62%), Calahonda replicates are organized into three groups with different seasonality (spring-summer: group 2, autumn: group 3 and winter: group 4).

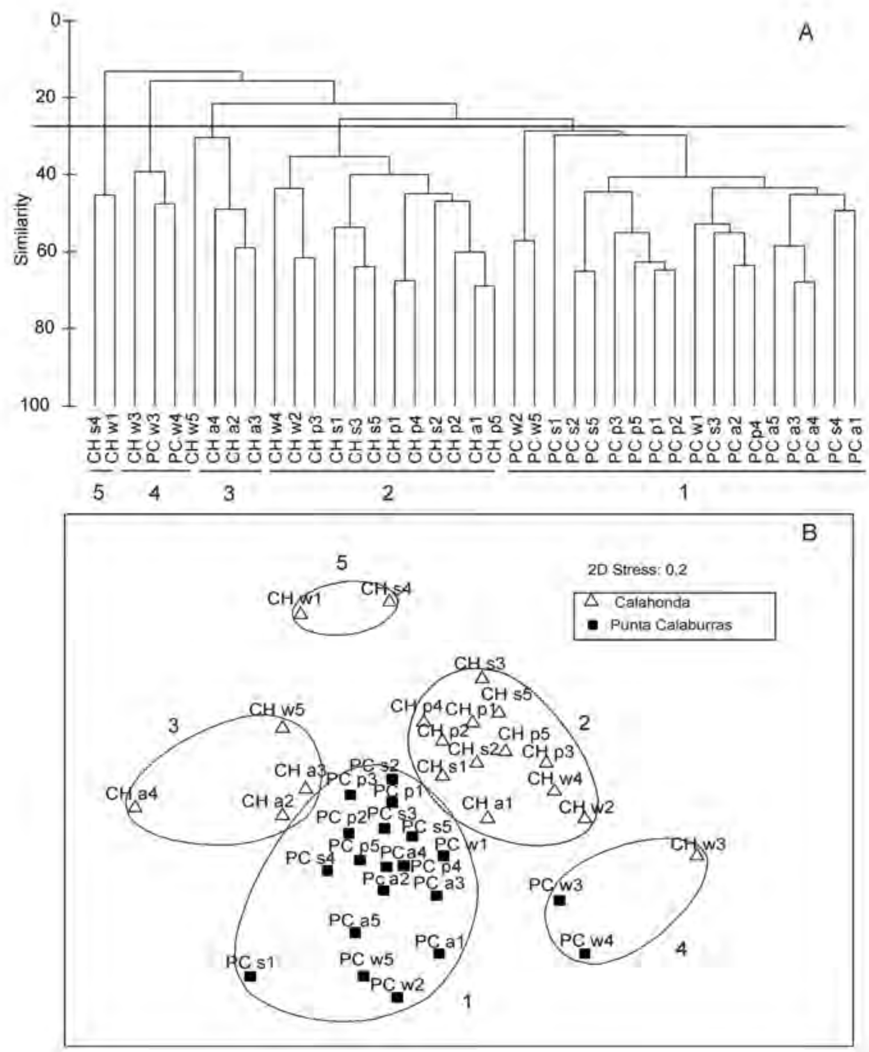

Fig. 4. Quantitative aggregation (Cluster) (A) and ordination (MDS) (B) analyses. Groups 1–5 discriminated at a similarity level of 28%. CH = Calahonda; PC = Punta de Calaburras; Ju = July; No = November; Ja = January; Ma = May. Numbers after month codes are replicate ranks.

Discussion

The *Cymodocea nodosa* meadows from Calahonda and Punta de Calaburras, in Southern Spain, show seasonal structural dynamics, with higher number of shoots m^{-2} than observed in other areas such as Ischia (Italy) (Cancemi *et al.*, 2002), Mar Menor (Terrados and Ros 1992), Canary Islands (Reyes *et al.* 1995) and the Mauritanian Arguin Bank (van Lent *et al.* 1991), but with a lower number of leaves per shoot than that found in Tenerife or in the Adriatic Sea (Reyes *et al.* 1995, Guidetti *et al.* 2002). According to Terrados and Ros (1992) *Cymodocea nodosa* has a stable, genetically controlled leaf development model and differences may be attributed to variable nutrient availability affecting plant size. In fact, differences were observed in our data among patches located in two shallow sites characterized by slightly different environmental conditions. A comprehensive study on the phenology of this meadow from 2007 to 2010 is currently in preparation.

As a general feature, the studied decapod community associated with shallow *Cymodocea nodosa* patches shows high species richness, with 34 species recorded. This richness is higher than that found in meadows at similar depths in the Adriatic Sea (1.5-3 m, 30 species, Števčič 1991) or Ischia (3 m, 18 species, Scipione *et al.* 1996) and lower than in Cabo de Gata (Almeria, SE Spain) when combining day and night samplings (48 species), but similar when only considering daytime samplings (34 species, García Raso et al. 2006). Nevertheless, it must be pointed out that the Cabo de Gata meadow is located at 10-14 m depth, therefore deeper and less influenced by the heavy stress caused by waves at shallower stations, which undoubtedly favours meadow habitability and diversity. In a study of decapod assemblages of *Posidonia oceanica* from Malta the diversity values were increased with increasing depth (maximum at 16 m) (Borg and Schembri 2000).

The incidence of depth on species richness was noted nearby on soft-bottoms transects (García Muñoz *et al.* 2008), where 18 species of decapods were identified at 5 m (shallow sandy bottoms) and 29, 30 and 38 species at 15 m (in fine-sand, coarse-sand and coralligenous bottoms respectively). A similar influence of depth on faunal assemblages was observed in other groups such as molluscs (Rueda *et al.* 2000, Koulouri *et al.* 2006, Urra *et al.* 2011a).

The dominant decapod species at both sites was *Hippolyte leptocerus*, linked to the leaf stratum, as in daytime samples of *Cymodocea nodosa* from Almeria and other seagrass assemblages from French, Italian and Tunisian coasts (Ledoyer 1968, 1984; Scipione *et al.* 1996; Reed and Manning 2000; García Raso *et al.* 2006a). In addition, this confirms the dominance of the family Hippolytidae in these biotopes (Ledoyer 1966, 1968, 1969, 1984; Kikuchi and Pérès 1997; Templado 1984, Scipione *et al.* 1996), as it also occurs in the decapods assemblage of the seaweed *Caulerpa prolifera* (Lopez de la Rosa *et al.* 2006). This family in general and the genus *Hippolyte* in particular, are perfectly adapted to these environments and strata (leaves) by their shape, colour and behaviour, thus reducing their vulnerability to predation by visual hunters (Main 1987). Another dominant species at both sites was the hermit crab *Anapagurus hyndmanni*; but curiously, this species was absent on adjacent shallow sandy bottoms (5 m) and markedly abundant at deeper (15-25 m) detritic bottoms in the studied area (García Muñoz et al. 2008).

Few others species show a total abundance of more than 5%, partly as a result of the environmental conditions and ecotone effect. Moreover, they also vary according to sites. *Philocheras fasciatus*, *Processa edulis*, *Pilumnus hirtellus* and *Pirimela denticulata* (the latter with a number of specimens similar to that of *A. hyndmanni*) are abundant in Calahonda, while *Calcinus tubularis*, *Clibanarius erythropus*, *A. hyndmanni*, *Hippolyte inermis* and *Atanas nitescens* are dominant in Punta de Calaburras. These differences are related to substrate composition, different sediment granulometry (as consequence of hydrodynamic conditions), and/or interaction with adjacent biotopes (see below). Spatial variations in seagrass faunal assemblages are common and have been attributed to the impact of nearby habitats (Skilleter et al. 2005) and physical factors. For example, Bowden *et al.* (2001) highlight a relation between the number of species and sediment variations due to tidal currents and waves. In our study, adjacent habitats determine the presence and relative abundance of specific species in these small meadows, since they are interspersed with *Posidonia*, sands, rocks/pebbles and seaweeds. Nevertheless *H. leptocerus* is always the dominant species and the diversity indices of the assemblages show similar values.

The Calahonda meadow is located in a sheltered area protected by large rocks, which allows the settlement of well-sorted fine sands with little mud. The influence of sandy substratum is proven by species such as *P. fasciatus*, which lives buried in sediment and is a characteristic species of "SFBC" well-sorted fine sandy bottoms (Pérès and Picard 1964, Massé 1972, etc). *Processa edulis* is a typical species of seagrass leaf stratum (Ledoyer 1966, 1968; Harmelin 1964) and *Caulerpa* (López de la Rosa *et al.* 2006), but was also found in adjacent sandy bottoms, hiding during daytime in the sediment and eating during nighttime in the meadow, since it is a predator of other invertebrates (Ledoyer 1966, Chessa *et al.* 1989). *Polybius navigator* and *Sycionia carinata*, although less abundant, also contribute to the characterization of Calahonda *Cymodocea* patches but are found in adjacent algae bottoms, hidden in the sandy substrate (García Raso *et al*. 2006, Lopez de la Rosa *et al.* 2006, Števčić 1991).

The meadow of Punta de Calaburras is not protected by large rocks and contains many pebbles. The dominance of the hermit crab *Clibanarius erythropus* in this shallow meadow is related to the presence and abundance of pebbles (Zariquiey 1968, Gherardi 1990, 1991). Other species, which also contribute to the characterization of this assemblage but with lower abundances, such as *Calcinus tubularis*, *Athanas nitescens* and *Hippolyte inermis*, characterize *Posidonia oceanica* seagrass; the latter in the leaf stratum (Ledoyer 1966) and the two former in the rhizome stratum (together with another hermit crab *Cestopagurus timidus*) (García Raso 1990). *Calcinus tubularis* and *Athanas nitescens* also live on shallow rocky bottoms; in fact, the rhizome stratum of *Posidonia oceanica* is considered to be comparable to a hard bottom (Bellan-Santini *et al.* 1994). These differences and similarities between stations are reflected in the aggregation and ordination analyses.

Furthermore, decapods are mobile animals. Therefore, with some exceptions, their presence cannot be "exclusively" associated with a single biotope, unlike other groups such as molluscs, with reduced mobility or higher dependence on a specific sediment or biotope (Hemminga and Duarte 2000; Luque and Templado 2004). Actually, the dissimilarity and characterization of analogous decapod assemblages (among "hard bottoms", or "soft bottoms") at similar depths relies heavily on quantitative values (García Raso *et al.* 1996, García Muñoz *et al.* 2008) and this holds true also for some other groups (Nakaoka *et al.* 2001). Analyzing the effect of habitat fragmentation on the macroinvertebrate communities associated with *Zostera marina,* Frost *et al.* (1999) mention: "differences were represented by subtle shifts in the relative abundance of a few common species rather than by larger shifts or wholesale species replacement".

The decapod abundance (mean = 18.4 ind m^{-2}) is low when compared to that of *Posidonia oceanica* meadows (more complex habitat, with more strata and ecological niches, García Raso 1990) but higher than that found in Mediterranean *Cymodocea* meadows (García Raso *et al.* 2006, Števčić 1991).

Middle to low values in the diversity indexes were observed, but higher than those found in *Cymodocea* assemblages from Almeria (only daytime samples, García Raso *et al.* 2006) and some seaweed assemblages of *Caulerpa prolifera* in Cadiz (López de la Rosa *et al.* 2002, 2006). This is the result of a more equitable distribution (highest evenness values), probably related to an ecotone effect, since the studied *Cymodocea* meadow is structured into patches interspersed with other habitats representing different ecological niches and including different associated species and dominances. Moreover, as already mentioned, mobility enables decapods easier access to new resources, thus resulting in a mixed and more equitable community. Hence, crustaceans (such as palaemonid shrimps and some peracarids) inhabiting fragmented *Zostera* seagrass meadows showed increased abundance at the boundary between sand and seagrass (Tanner 2005). In any case, the values found are well below those of *Posidonia oceanica* meadows (García Raso 1990).

The positive correlation observed between specimen numbers, species richness, and seagrass phenology (with seasonal differences in the number of leaves per shoot) points out a direct (through their cycles) or indirect (through associated resources) relation between plant and animal communities. However, other factors (e.g, temperature, photoperiod) could be influencing both variables. Hence, high abundances of most species coincide with maximum seagrass development (spring-summer), this is the case of *Hippolyte inermis* and *H. leptocerus*, linked to the leaf stratum. Other species may respond to additional factors. For example, the high abundances of *Polybius navigator*, *Pirimela denticulata*, *Athanas nitescens*, *Anapagurus hyndmanni* and *Philocheras fasciatus* observed in this period are, in part, related to recruitments. Nevertheless, the maximum of *Calcinus tubularis* (spring-summer) corresponds to adult specimens, since juveniles mainly occur in autumn (Manjón-Cabeza and García Raso 1995). *Clibanarius erythropus*, an important species in Calaburras, has thermal requirements and prefers cool temperatures (12-17 ºC), and its activity increaseds up to 22-23 °C and decreases upwards (Warburg and Shuchman 1984). Ovigerous females of *C. erythropus* occur in Málaga mainly in summer (García Raso 1982). Both circumstances may explain their low abundance in warm-season samples, while autumn-winter maximum coincides with the presence of a high number of juveniles, since recruitment may have taken place in autumn.

Seasonal changes in the abundance of decapods and fishes in tropical seagrass beds (Kwak and Klumpp 2004) corresponded to those of seagrass biomass and availability of food organisms. Nevertheless, although broad-scale relationships between flora and fauna do exist, the species show a different ecological specialization and response to the characteristics and availability of a habitat as well as different abilities to compete for resources, including predator-prey interactions (Bell and Westoby 1986, Futuyuma and Moreno 1988, Worthingon *et al.* 1992, Kwak and Klumpp 2004, Unsworth *et al.* 2007).

The significant seasonal pattern is not a general feature of all benthic assemblages (slightly higher in Calahonda than in Punta de Calaburras). No seasonality was reported for the deeper decapod community from Almeria (Garcia Raso *et al.* 2006); the contrary was observed for *Caulerpa prolifera* shallow bottoms in the internal inlet of the Bay of Cadiz (Lopez de la Rosa *et al.* 2006). This seasonality is reflected in the abundances of dominant species (see previous comments), which allows to discriminate annual periods and stations. The different responses of each animal, in each habitat/substrate, also conditioned by the assemblages (composition and interrelations), lead to differences in seasonal patterns. Nakaoka *et al.* (2001) found that pattern of seasonal change in abundance differs between substrates. Also, seasonality must be more pronounced in shallower habitats since temperature (and hydrodynamic conditions) are more fluctuating and show significant seasonal differences. Seasonality is also common in other groups associated with these habitats such as mollusc assemblages in *Caulerpa prolifera* (Rueda and Salas 2003) and *Zostera marina* meadows (Rueda and Salas 2008).

On the other hand, we must point out that the size of the *Cymodocea nodosa* patches in Calahonda, within the analyzed size range (between 5 and 10.3 m^2) and years under study, are not reflected on species richness, or on the density of individuals. This is in agreement with faunal studies on *Zostera marina* seagrass (Bell *et al.* 2001, Hirst and Attrill 2008) and with observed response to experimental fragmentation of seagrass habitats (Macreadie *et al.* 2009). This may be the result of the compensation between the positive edge effect and the negative area loss effect. Consequently, in this area and the years under study, *Cymodocea nodosa* patches maintain the structure of the decapod assemblages regardless of their size. Attrill et al (2000), in a spatial study carried out within a sub-tidal *Zostera marina* seagrass bed, suggest that there is no evidence that structural complexity of seagrass (biomass/surface area) directly influences the composition of the associated macroinvertebrate fauna and the possible relationships with macroinvertebrate diversity is a sampling artefact, a simple species-area relationship (more of the rare species are captured as the size of sample increases).

In any case, the seagrass biomass - plant life cycle - is considered a key organizing factor in macrophyte-associated crustaceans assemblages (Stoner 1980, Lewis and Stoner 1983, Lewis 1984), and the presence and abundance of some species are determinate directly, by the habitat complexity including microhabitats (biomass - protection), or indirectly (food resources - epiphytes), but also by the species adaptation, their life cycles, the larval settlement and the predatory pressures (Unsworth *et al.* 2007, Bell and Westoby 1986).

As a general conclusion, the decapod assemblages of *Cymodocea nodosa* from both sites display a more or less similar structure (diversity indexes not significantly different), without a clear relation of richness and abundances to patch size. These assemblages have similar dominant species than other Mediterranean *Cymodocea* assemblages, but draw a large part of their crustacean fauna (qualitative but also quantitative composition) from neighbouring habitats. This is an important factor, because the connectivity between habitats for mobile fauna (movements after larval recruitment, between juvenile and adult habitats; between no breeding and breeding habitats, and in general among different habitats) is partially known but poorly studied (García Raso *et al.* 1996, García Muñoz et al 2008, Gillanders *et al.* 2003). Thus, the coexistence of different habitats in the studied sites, in a small area, creates a constant species flow that supports the results found (high values of species richness and the partially different faunal composition). The differences found are significantly related to sampling period, which is linked to plant life cycle (biomass-protection-food), but also to the biology of the associated species and their interrelationships.

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CAPÍTULO 4

Asociaciones de decápodos ligados a praderas fragmentadas de *Posidonia oceanica* en el mar de Alborán (Mediterráneo occidental): composición, dinámica temporal e influencia de la estructura de la pradera

Este capítulo se basa en/This chapter is based on:

Crustacean decapod assemblages associated with fragmented *Posidonia oceanica* meadows in the Alboran Sea (Western Mediterranean Sea): composition, temporal dynamics and influence of meadow structure

Mateo-Ramírez A., Urra J., Marina P., Rueda J.L., García Raso J.E.

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Abstract

The decapod assemblage associated with a *Posidonia oceanica* meadow located near its western limit of biogeographic distribution was studied over an annual cycle. Fauna samples were taken seasonally over a year (five replicates per season) in two sites located 7 km apart, using a non-destructive sampling method (airlift sampler) for the seagrass. The dominant species of the assemblage, *Pisidia longimana*, *Pilumnus hirtellus* and *Athanas nitescens*, were associated with the protective rhizome stratum, which is mainly used as a nursery. The correlations between decapod assemblage structure and some phenological parameters of the seagrass shoots and wave height were negative or null, which reflects that species associated with the rhizome had a higher importance than those associated with the leaf stratum. The abundance and composition of the decapods assemblage as well as the ecological indexes displayed a seasonality trend with maximum values in summer-autumn and minimum in winter-spring, which were related to the seawater temperature and the recruitment periods of the dominant species. The spatial differences found in the structure and dynamics of the assemblages may be due to variations in the recruitment of the dominant species, probably as a result of the influence of local factors (e.g. temperature, currents) and the high dispersal ability of decapods, together with the patchy configuration and the surrounding habitats. The studied meadows are fragmented and are integrated within a mosaic of habitats (*Cymodocea nodosa* patches, algal meadows, rocky and sandy bottoms), which promotes the movement of individuals and species among them, maintaining a high species richness and evenness.

Keywords: Alboran Sea, decapod assemblages, fragmented, *Posidonia oceanica*, temporal dynamics.

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Introduction

Posidonia oceanica (Linnaeus) Delile is the most abundant of the four indigenous Mediterranean seagrasses and forms the most extensive beds, with a total area in the Mediterranean Sea ranging between 25,000 and 45,000 km^2 (Luque and Templado 2004). The architecture of *P. oceanica* beds, with different strata and microhabitats (leaves, rhizomes and interspersed soft sediments), supports different biotic assemblages (Pérès and Picard 1964; Kikuchi and Pérès 1977; Kikuchi 1980) and, in addition, offers shelter and acts as a nursery area for many animals, including some species of commercial importance (Gillanders 2006). Mixed photophilous and sciaphilic assemblages, including crustacean decapods, coexist (Luque and Templado 2004; García Raso *et al.* 2006a). Grazer species such as those belonging to the genus *Hyppolite* are associated with the upper, well-lit strata leaves), while the lower strata (rhizomes) acts as 'hard and dark strata', providing refuge and protection for many sciaphilic species. The high faunistic diversity results in a large number of inter- and intra-specific strategies and movements, which are further governed by intrinsic and extrinsic factors such as seasonal periods, food resources (e.g. epiphytes), depth, predation and the exchange of species from adjoining biotopes (García Raso *et al.* 1996; Borg *et al.* 2010). The latter can be favored by the seagrass meadows fragmentation because it produces a patchy configuration that may be interspersed with other habitats (other seagrass species, macroalgae, hard or soft bottoms) (Barberá-Cebrián *et al.* 2002; Jackson *et al.* 2006; Mateo-Ramírez and García Raso 2012; Urra *et al.* 2013a).

In the Alboran Sea, *Posidonia oceanica* forms extensive meadows in its easternmost sector, close to the Almeria–Oran Front, whereas in the central and western sectors these are reduced from small meadows to patches, mainly existing over hard substrata (Luque and Templado 2004;Junta de Andalucía 2011). The westernmost distributional limit for *P. oceanica* is located between Cádiz and Málaga provinces (Southern Spain) in the Northern Alboran Sea, and in Sebkha-bou-Areg and the Chafarines Islands in the Southern Alboran Sea (Pérez-Lloréns *et al.* 2014). In general, seagrass beds exhibit a natural fragmentation due to seasonal growth, die-off, storm events or hydrodynamic action (Duarte and Sand-Jensen 1990; Fonseca 1992; Abbate *et al.* 2000). The influence of Atlantic waters with lower salinities likely plays a role in the fragmentation of meadows in the Alboran Sea (Luque and Templado 2004). However, anthropogenic impacts, such as coastal constructions (Ruíz and Romero 2003), illegal bottom trawling (González-Correa *et al.* 2005; Rueda *et al.* 2009), beach replenishment (González Correa *et al.* 2008) and organic pollution due to fish cultures (Ruíz *et al.* 2001), may also result in extensive fragmentation, which in turn may promote changes in the structure of the associated animal community. This alteration may have both positive and negative effects on the associated faunal assemblages (Eggleston *et al.* 1998; Urra *et al.* 2013a).

Many studies have been carried out on the fauna associated with *P. oceanica* beds (e.g. Templado 1984; Gambi *et al.* 1992; Sánchez-Jerez *et al.* 1999, 2000; Barberá-Cebrián *et al.* 2002; Dimech *et al.* 2002; Ateş *et al.* 2005,2006; Como *et al.* 2008; Borg *et al.* 2010; Urra *et al.* 2013)a, but few of them have focused on the structure of the decapod assemblages (García Raso 1990a; Borg and Schembri 2000). Besides, there is no information about this topic for the westernmost distribution area of *P. oceanica* (close to the Strait of Gibraltar), where there is a high influence of Atlantic waters, and *P. oceanica* only forms small patches on rocky bottoms.

The present study analysed the crustacean decapods assemblage associated with *P. oceanica* fragmented meadows inhabiting the Atlantic–Mediterranean transition area (close to the Strait of Gibraltar). The main goals were to determine if the geographic location, configuration of the meadows (i.e. patchiness), and phenological and environmental parameters play a role in the composition and structure of the associated decapod populations.

Material and Methods

Study area

The study was carried out within the site of community importance (SCI) known as 'Calahonda' (code ES6170030), which is included in the Natura 2000 network and located off the Mijas coast (Málaga, Southern Spain; Fig. 1). Two sites were sampled: Punta de Calaburras (PC; 36º30´23´´ N, 04º38410´´ W) and

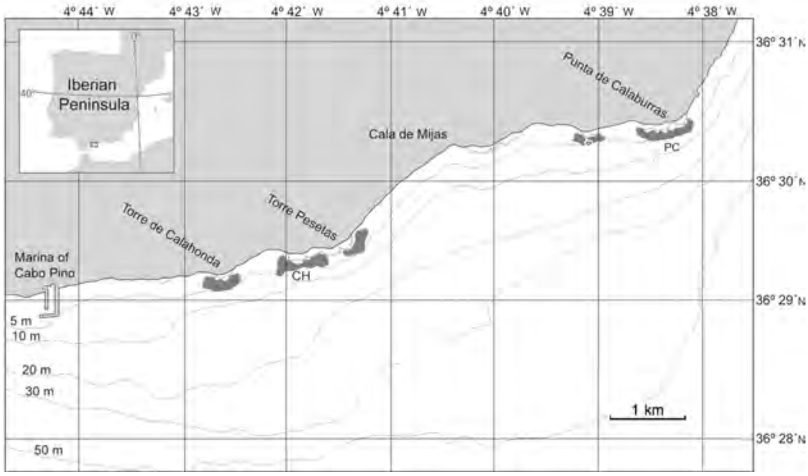

Fig. 1. Study area showing the location of sampling sites in the NW Alboran Sea. PC, Punta Calaburras; CH, Calahonda.

Calahonda (CH; 36º29´21´´ N, 04º41´55´´ W). PC is subjected to more wave action, resulting in a higher occurrence of pebbles than at CH, which is a more sheltered site with large rocks surrounded by soft sediments. The meadows studied are located close to the westernmost distributional limit of *Posidonia oceanica* (Luque and Templado 2004) and display a fragmented configuration formed by patches with diameters ranging between 1 and 130 m^2, with a coverage of *c*. 14% (Urra *et al.* 2011b). In addition, it grows preferentially on hard substrata (rocks) and in areas that are sheltered by shallow rocky outcrops (2–5 m in depth).

The presence of dead rhizomes covered by algae (i.e. *Halopteris scoparia* and *Asparagopsis armata*) interspersed with living seagrass meadows indicates that the *P. oceanica* meadows occupied a larger area in the past. Extensive macroalgae forests down to 5–7 m and patches of the small seagrass *Cymodocea nodosa* (coverage <5%), which frequently forms mixed meadows with *P. oceanica*, are also found in the area.

Salinity remains almost constant throughout the year due to the low freshwater input in the area, ranging between 36.5 in fall and 36.8 in spring (salinity data given in practical salinity scale; and taken from Instituto Español de Oceanografía: http://www.ma.ieo.es/gcc/sistemas_ observacion.htm). Solar irradiance at 2 m depth at the sampling sites displays a seasonal pattern with high values in summer (3.95 ± 0.1 log lm·m^{-2}), intermediate in spring and fall and low values in winter (3.47 ± 0.15log lm·m^{-2}) (Á. Mateo-Ramírez, unpublished data).

Sample collection and sampling methodology

Samples were collected by SCUBA divers at a depth of 2 m in seagrass patches of different sizes: small (1–10 m^2 area), medium (10–30 m2) and large (>30 m^2). Sampling took place during daytime (in the morning) and seasonally in July (summer), November 2007 (fall), January (winter) and April 2008 (spring). In total, 40 faunistic samples (five replicates per site and season) were taken using a quadrat measuring 50 × 50 cm and an air-lift sampler (Borg and Schembri 2000; Mateo-Ramírez and García Raso 2012). The suction time was the same for each sample collected (3 min). This sampling methodology is environmentally friendly for seagrass and is a basic requirement in studies carried out in marine protected areas, such as this SCI, and is similar to the methodology practiced by Mateo-Ramírez and García Raso (2012) and Urra *et al.* (2013a) in this SCI. In addition, it is more effective than the use of hand nets (Borg and Schembri 2000) because it collects the species living in all strata (leaves and rhizome) and therefore the assemblage can be better characterized. In the laboratory, every faunistic sample was sieved over mesh sizes down to 0.5 mm, storing each size fraction in 70% ethanol. Each species was identified and the numbers of individuals were counted. The abundance of decapods is expressed as the number of individuals per sample. The sizes of the dominant species were analysed in order to distinguish two groups: juveniles (small size) and adults (large size). The minimum size of adults was determined from the literature (Zariquiey Álvarez 1968; Manjón-Cabeza and García Raso 1994) and our personal data (collected samples).

To determine the shoot density (shoots·m^{-2}) in each season, five replicates of a quadrat measuring 50 × 50 cm were used in both sites (PC and CH) in the same patches where fauna was collected. In addition, 10 randomly chosen shoots in each quadrat were analysed in situ (n = 50 shoots per site and season) in order to determine the shoot parameters. Number of leaves per shoot (leaves·shoot^{-1}), the leaf height (from the basal part of the sheath to the blade tip) and the leaf width (at the mid-point between the sheath and the blade tip) of the largest leaf were measured.

Seawater temperatures (T) and water samples for analysis of the concentration of chlorophyll *a* (Chl *a*) were measured on different days throughout each season (weeks before, during and after data collection). Two 1-l replicates of seawater (at the surface) were collected in each site and transported in darkness at low temperature to the laboratory for Chl *a* determination. Pigment analyses were carried out by filtering through Whatman GF/C glass filters. The pigments of the retained cells were then extracted using 100% acetone for 12 h in cool and dark conditions. The solution was measured using a spectrophotometer at wavelengths of 630, 647, 664 and 750 nm. The Chl *a* concentrations were obtained using the equation proposed by Jeffrey and Humphrey (1975). Samples of sediment were also taken on each sampling occasion (five replicates per season and site) in order to estimate the percentage of organic matter (%OM) within the sampled *P. oceanica* patches. This percentage was calculated by the weight loss of dry sediment (three subsamples of 20 g per replicate) after ignition at 500°C for 1 h. Wave height (m) information obtained with the High Resolution Limited Area Model and Wave Model numeric models was taken from the Instituto Nacional de Meteorologia (Spain).

Statistical analyses

The composition, structure and seasonal changes of the decapod assemblages were analysed from the values of abundance [N, total number; NJ, number of juveniles (small size); NA, number of adults (large size)], frequency index (Fi; percentage of samples in which a particular species is present), dominance index (Di; percentage of individuals of a particular species within the sample), species richness (S) and the ecological indexes of Shannon–Wiener diversity (H') and evenness (J'). The ecological indices were obtained using the PRIMER v. 6 software (Clarke and Gorley 2006).

Two-way permutational multivariate analysis of variance (PERMANOVA) were used to test for differences in the environmental variables, the seagrass parameters and the ecological indexes between sites (PC, CH) and months/seasons July 2007 (summer), November 2007 (fall), January 2008 (winter) and April 2008 (spring). One-way PERMANOVA were used to test for differences between seagrass patch areas and to analyse the seasonality in the abundance of the main species. Analyses were based on Euclidean distances. The significance of P values was determined through 9999 permutations of residuals under a reduced model or of the raw data, for two- or one-way analysis, respectively (PERMANOVA + for PRIMER, Anderson *et al.* 2008). The analysis of similarity (ANOSIM) procedure was carried out for multivariate statistical comparisons of groups of samples according to the different factors considered (sites, months/seasons and patch areas) and the similarity percentages analysis (SIMPER) was used to identify those species that contributed to the similarity and dissimilarity among these groups. The similarity matrix used for ANOSIM analysis was calculated using Bray-Curtis index. The data were double square transformed. Both analyses were executed using the PRIMER v.6 software (Clarke and Gorley 2006). Correlations between ecological values (S, N, NJ, NA, H' and J') with seagrass parameters (shoot density, number of leaves per shoot, leaf height and width, patch area) and environmental variables (T, Chl *a*, %OM and wave height) were calculated by Pearson co-efficients. Finally, canonical correspondence analysis (using the software CANOCO) was performed to study the relationships among the seagrass parameters, environmental variables and the abundances of the top dominant decapod species.

Results

Environmental variables

None of the analysed environmental variables displayed significant differences between sites (Table 1). Seawater temperature showed a significant temporal trend with maximum values in summer (20–24.5 °C) and minimum ones in winter (15–16.5 °C) at both sites (PC, Pseudo-F = 22.525, $P < 0.01$; CH, Pseudo-F = 4.478, $P < 0.05$). The Chl *a* concentration displayed a significant temporal pattern at CH (Pseudo-F = 2.836, $P < 0.05$), with values ranging from 24.34 $\mu g \cdot l^{-1}$ in spring to 3.22 $\mu g \cdot l^{-1}$ in summer, whereas at PC the temporal changes were non-significant (Pseudo-F = 0.079, P = 0.969) and the highest values were detected in fall (12.31 $\mu g \cdot l^{-1}$). The %OM displayed a significant temporal trend at CH (Pseudo-F = 5.310, $P < 0.01$), with maximum values in summer (1.61–2.84%) and minimum ones in winter (0.99–2.11%), whereas at PC temporal changes were non-significant (Pseudo-F = 2.245, P = 0.097) and the highest value was observed in winter (1.44–2.65%). Wave height showed non-significant temporal differences at both sites (PC, Pseudo-F = 1.183, P = 0.334; CH, Pseudo-F = 2.852, P = 0.055), with maximum values (*c.* 2 m wave height) in fall for PC and in spring for CH, and minimum values in spring for PC (0.7 m) and in fall for CH (0.6 m).

Phenology of **Posidonia oceanica**

All phenological parameters of *Posidonia oceanica* displayed significant differences among seasons, but not between sites (Table 1). Shoot density showed a significant temporal trend at CH with maximum values in fall (856–1180 $shoots \cdot m^{-2}$; Pseudo-F = 10.871, $P < 0.001$), while at PC the maximum values occurred in winter (840–980 $shoots \cdot m^{-2}$), but without temporal significant differences (Pseudo-F = 0.926, P = 0.44) (Fig. 2A). Leaf number displayed significant temporal changes at CH (Pseudo-F = 7.681, $P < 0.01$) and PC (Pseudo-F = 33.518, $P < 0.001$), with maximum values in winter (6 $leaves \cdot shoot^{-1}$; Fig. 2B).

Leaf height showed a significant temporal trend with maximum values in spring at both CH (29–46 cm, Pseudo-F = 56.863, $P < 0.001$) and PC (35–45 cm, Pseudo-F = 18.513, $P < 0.001$) (Fig. 2C). Leaf width displayed a significant temporal trend at both sites (CH, Pseudo-F = 7.410, $P < 0.01$; PC, Pseudo-F = 6.340, $P < 0.01$), with maximum values in winter (10–10.6 mm; Fig. 2D). The last two seagrass parameters presented non-significant differences between different patch areas (Table 1).

Table 1. Results of the two-way Permutational Multivariate Analysis of Variance to test the significance of the seagrass parameters (shoot density,leaf height and width in cm, number of leaves) and environmental variables (wave height, temperature, Chl *a* concentration and % organic matter) between sites and among seasons and areas of seagrass patches.

Factors	n	Site	Season	Season*Site
Environmental factors				
Wave heigth	54	P-F=0.228; P=0.644	P-F=2.189; P=0.103	P-F=1.081; P=0 369
Temperature	27	P-F=0.153; P=0.694	P-F=9.401; P<0.01**	P-F=1.938; P=0.163
Chlorophyll *a*	60	P-F=0.200; P=0.654	P-F=2 216; P=0.089	P-F=1.885; P=0.143
% Organic matter	106	P-F=6.641E-4; P=0.98	P-F=3.145; P<0.05*	P-F=4.842; P<0.01**
Phenological factors				
Shoot density	38	P-F=0.210; P=0.650	P-F=8.150; P<0.001***	P-F=6.651; P<0.01**
Leaf height	38	P-F=9.420E-2; P=0.762	P-F=50441; P<0.001***	P-F=1.021; P=0.400
Leaf width	38	P-F=1.412; P=0 245	P-F=12.721; P<0.001***	P-F=1.585; P=0 208
Number of leaves	38	P-F=3.799; P=0.064	P-F=25.119; P<0.001***	P-F=5.425; P<0.01**
Phenological factors	n	Patch area		Patch area*Site
Shoot density	19	P-F=0.278; P=0.753		P-F=0.555; P=0.586
Leaf height	19	P-F=2.240; P=0.138		P-F=0.130; P=0.883
Leaf width	19	P-F=2.629; P=0.105		P-F=0.218; P=0.797
Number of leaves	19	P-F=1.066; P=0.369		P-F=1.196; P=0 336

P-F, Pseudo-F values.

*Significant differences at $P < 0.05$; ** at $P < 0.01$ and *** at $P < 0.001$.

Composition and structure of the decapod assemblage

A total of 1185 individuals were collected, belonging to 34 species and 18 families (Table 2). The family Inachidae (four spp.) was the best represented among decapods, followed by Hippolytidae, Alpheidae, Paguridae and Epialtidae (with three spp. each). The family Porcellanidae was the most abundant one [227 individuals (ind.)], followed by Alpheidae (184 ind.), Pilumnidae (183 ind.) and Paguridae (160 ind.). The assemblage displayed 16 species with dominance values higher than 1%, with *Pisidia longimana* and *Pilumnus hirtellus* as the top dominant species (18.7% and 15.4% Di, respectively), followed by *Athanas nitescens*, *Cestopagurus timidus*, *Calcinus tubularis* and *Achaeus gracilis* (>5% Di in all cases). Most of these species were also recorded as the most frequent species (Table 2).

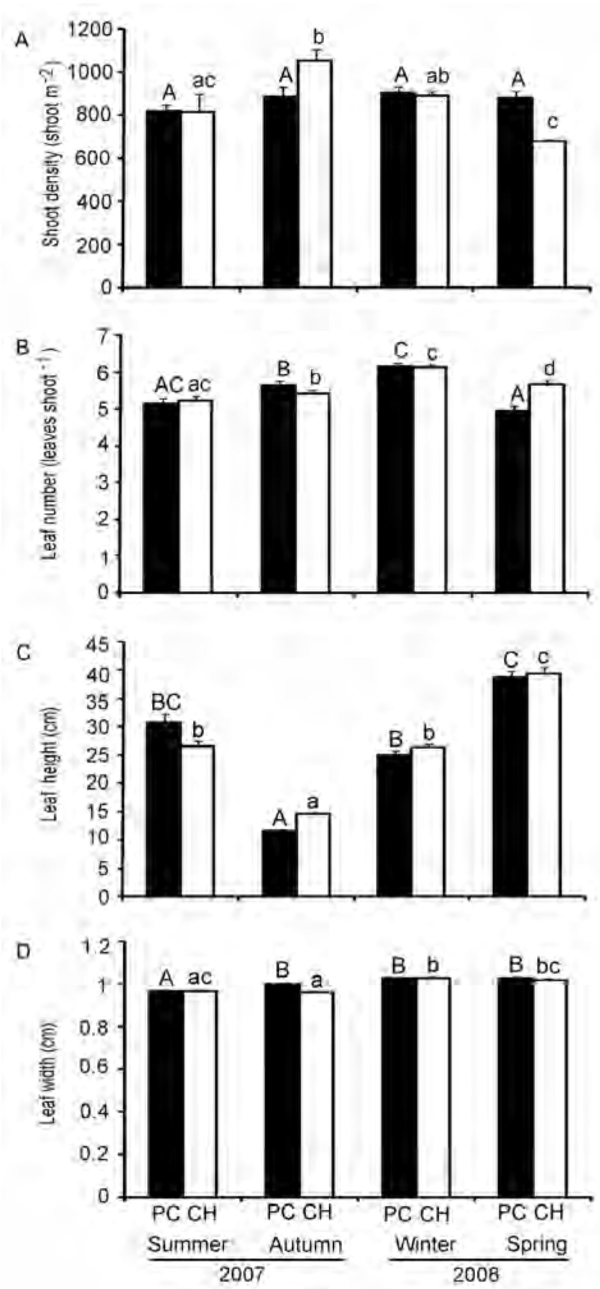

Fig. 2. Seasonal trends of parameters of *Posidonia oceanica*. (A) Shoot density (shoots·m^{-2}), (B) number of leaves (leaves·shoot^{-1}), (C) leaf height (cm) and (D) leaf width (cm) at Punta Calaburras (PC, solid bars) and Calahonda (CH, empty bars). Mean + SE. Letters above error bars display the results of PAR-WISE tests; different letters indicate significantly different means at P < 0.05. Capital letters refer to PC comparisons and lower-case letters to CH comparisons.

Table 2. Checklist of the species collected at Punta Calaburras and Calahonda with their relative dominance (Di, %) and frequency of occurrence (Fi, %).

	P. Calaburras		Calahonda		Total
	Di	Fi	Di	Fi	Di
Family Sicyoniidae					
Sicyonia carinata (Brünnich, 1768)	0.26	5	1	15	0.51
Family Palaemonidae					
Palaemon xiphias Risso, 1816	0.13	5	1	5	0.42
Palaemon elegans Rathke 1837	0.13	5	0.5	10	0.25
Family Hippolytidae					
Hippolyte leptocerus (Heller, 1863)	0.77	15	2.24	30	0.84
Hippolyte inermis Leach, 1816	0.38	15	2	35	1.27
Eualus cranchii (Leach, 1817 [in Leach, 1815-1875])	3.59	40	3.24	40	3.54
Family Alpheidae					
Athanas nitescens (Leach, 1813 [in Leach, 1813-1814])	18.85	70	5.24	35	13.42
Alpheus macrocheles (Hailstone, 1835)	0.13	5	0.25	5	0.08
Alpheus dentipes Guérin-Méneville, 1832	1.79	15	0.25	5	2.03
Family Processidae					
Processa edulis edulis (Risso, 1816)	0.13	5	0.75	15	0.42
Processa robusta Nouvel & Holthuis, 1957	2.18	40	8.23	50	4.3
Family Crangonidae					
Philocheras fasciatus (Risso, 1816)	0.51	10	1.75	15	0.84
Family Diogenidae					
Calcinus tubularis (Linnaeus, 1767)	8.72	65	4.49	45	7.26
Family Paguridae					
Pagurus anachoretus Risso, 1827	1.54	40	1.75	30	1.6
Cestopagurus timidus (Roux, 1830)	6.92	70	8.98	55	7.59
Anapagurus hyndmanni (Bell, 1846)	5.9	55	1.25	20	4.3
Family Galatheidae					
Galathea squamifera Leach, 1814	0.13	5	0	0	0.08
Family Porcellanidae					
Porcellana platycheles (Penna, 1777)	0.64	25	0	0	0.42
**Pisidia longimana* (Risso, 1816)	15.77	80	24.69	75	18.73
Family Leucosiidae					
Ebalia edwardsii Costa, 1838	2.44	45	0.5	10	1.77
Family Pirimelidae					
Pirimela denticulata (Montagu, 1808)	0	0	0.25	5	0.08
Sirpus zariquieyi Gordon, 1953	1.92	50	0.25	5	1.35
Family Polybiidae					
Liocarcinus navigator (Herbst, 1794)	0	5	1	20	0.34
Family Pilumnidae					
Pilumnus hirtellus (Linnaeus, 1761)	15.26	75	15.96	70	15.44
Family Xanthidae					
Xantho poressa (Olivi, 1792)	1.28	10	0	0	0.84
Xantho hydrophilus (Herbst, 1790)	3.85	65	3.99	35	3.88
Family Pinnotheridae					
Pinnotheres pisum (Linnaeus, 1767)	0	0	0.25	5	0.08
Family Epialtidae					
Pisa carinimana Miers, 1879	0.64	15	1.5	25	0.93
Pisa tetraodon (Pennant, 1777)	0.13	5	0.25	5	0.17
Acanthonyx lunulatus (Risso, 1816)	1.15	20	1	15	1.43
Family Inachidae					
Achaeus gracilis (Costa, 1839)	4.62	50	7.98	60	5.4
Inachus phalangium (Fabricius, 1775)	0	0	0.25	5	0.08
Macropodia rostrata (Linnaeus, 1761)	0.26	10	0	0	0.17
Macropodia czernjawskii (Brandt, 1880)	0	0	0.25	5	0.08

*See García Raso (1987)

Twenty-nine species were identified at PC, with *A. nitescens*, *P. longimana* and *P. hirtellus* showing the highest dominance values. Four species were collected exclusively in this site, *Galathea squamifera*, *Macropodia rostrata*, *Porcellana platycheles* and *Xantho poressa*; however, they represented a low number of individuals and displayed low frequency values (Table 2). Thirty species were identified at CH, with *P. longimana*, *P. hirtellus* and *C. timidus* as the top dominant species, and four exclusive ones, *Pirimela denticulata*, *Pinnotheres pisum*, *Inachus phalangium* and *Macropodia czernjawskii*.

Between sites, *A. nitescens* and *C. tubularis* displayed higher dominance values at PC than at CH, while *Hyppolite leptocerus* and *Hyppolite inermis* (species linked to seagrass leaves) were more abundant at CH than at PC (Table 2).

Species richness (S) presented significant differences between sites and among seasons (Table 3). Maximum values were observed at PC and CH in fall (14.20 ± 0.66 and 11.6 ± 1.29 spp.·sample^{-1}; mean ± SE) and the minimum values in summer at PC (7.40 ± 1.03 spp.·sample^{-1}) and in winter at CH (3.60 ± 1.15 spp.·sample^{-1}) (Fig. 3A).

Total abundance (N) also showed significant differences between sites and among seasons (Table 3). At PC, maximum abundances were observed in fall (86.60 ± 19.79 ind.·sample^{-1}) and minimum values in winter (17 ± 6.28

Table 3. Results of the one- and two-way Permutational Multivariate Analysis of Variance testing the significance of the species richness (S), total abundance (N), adult abundance (NA), juvenile (small size) abundance (NJ), evenness (J') and Shannon–Wiener diversity (H') between sites and among seasons and areas of patches.

Index	n	Site	Season	Season*Site	n	Patch area
S	39	P-F=5.150; P<0.05*	P-F=22.095; P<0.001***	P-F=4.035; P<0.05*	18	P-F=1.663; P=0 201
N	39	P-F=8.154; P<0.01**	P-F=9.692; P<0.001***	P-F=4.814; P<0.01**	18	P-F=2.572; P=0.097
NA	39	P-F=6.831; P<0.05*	P-F=2.507; P=0.075	P-F=1.933; P=0.14	18	P-F=0.367; P=0.727
NJ	37	P-F=4.550; P<0.05*	P-F=15.689; P<0.001***	P-F=6.800; P<0.01**	16	P-F=0.239; P=0.826
J´	39	P-F=0.200; P=0.67	P-F=4 303; P<0.05*	P-F=1 367; P=0 277	18	P-F=0.886; P=0.437
H´	39	P-F=4.681; P<0.05*	P-F=10.706; P<0.001***	P-F=3.068; P<0.05*	18	P-F=0.871; P=0.466

P-F, Pseudo-F values.

*Significant differences at P < 0.05; ** at P < 0.01 and *** at P < 0.001.

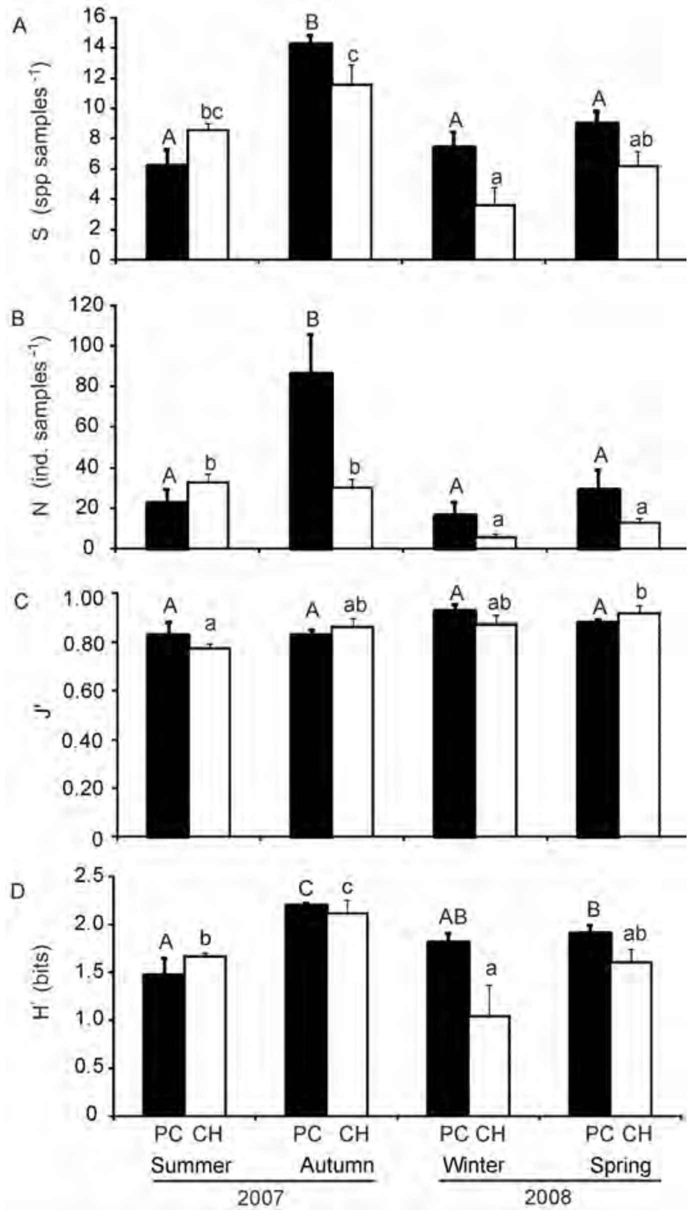

Fig. 3. Seasonal trends of values of the ecological indexes. (A) Species richness (S, number of species, spp.·sample $^{-1}$), (B) abundance (N, number of individuals, ind.·sample^{-1}), (C) evenness (J') and (D) Shannon–Wiener diversity (H', bits) at Punta Calaburras (PC, solid bars) and Calahonda (CH, empty bars). Mean + SE. Letters above error bars display the results of PAR-WISE tests; different letters indicate significantly different means at $P < 0.05$. Capital letters refer to PC comparisons and lower-case letters to CH comparisons.

ind.·sample^{-1}) (Fig. 3B). Maximum abundances were due to the high number of individuals, mainly juveniles (small sizes), of *A. nitescens* (Di =26.79%; 116 ind.), *P. longimana* (Di = 12.70%; 55 ind.) and *P. hirtellus* (Di = 17.55%; 76 ind.), which accounted for 98.57% juveniles (small sizes) and 57.4% of the total fall abundance (Table 3). In this assemblage, *P. longimana* was the most abundant species in summer (Di = 28.07%; 32 ind.) and in winter (Di = 18.82%; 16 ind.), whereas *Anapagurus hyndmanni* was in spring (Di = 20.27%; 30 ind.). The species *A. nitescens* (Pseudo-F = 8.143; P < 0.01) and *A. hyndmanni* (Pseudo-F = 7.180; P < 0.01) displayed significant temporal changes in their abundances throughout the study period. At CH, the abundances were at their maximum in summer (32.6 ± 4.8 ind.·sample^{-1}) and at their minimum in winter (5.80 ± 1.82 ind.·sample^{-1}) (Fig. 3B). The maximum value observed in summer was related to an increase in the number of individuals, mainly juveniles (small-sized individuals), of *P. longimana* (Di = 31.74%; 55 ind.), *P. hirtellus* (Di = 23.31%; 38 ind.) and *C. timidus* (Di = 16.56%; 27 ind.), representing 73.61% of the total summer abundance. The species *P. longimana* (Pseudo-F = 3.655; P < 0.05) and *Processa robusta* (Pseudo-F = 9.023; P < 0.01) were the only dominant species displaying significant seasonal changes, the latter as the top dominant in fall [(Di = 16%, 24 ind., 62.5% juveniles (small sizes)]. Abundances of both adult and juvenile (small-sized) individuals were significantly different between sites (Table 3). The abundances of juvenile (small-sized) individuals presented significant temporal differences, with maximum values in summer–fall and minimum values in winter–spring (Pseudo-F = 15.689; P < 0.001), while the abundances of adults were higher in winter–spring but with non-significant differences. The percentages of adult and juvenile (small-sized) individuals varied throughout the year in different ways depending upon the species. Among the dominant species, the juvenile (small-sized) individuals of *P. hirtellus* were more abundant than adults throughout the entire year, with the maximum abundance values registered in fall (Fig. 4B). For *P. longimana*, juvenile (small-sized) individuals were more abundant than adults in warm months (summer and spring), showing the highest percentages in spring. Contrary to this, *A. nitescens* presented a higher percentage of adults throughout the year, with some recruitment during summer–fall.

Evenness values (J') were not significantly different between sites (Table 3). Nevertheless, significant temporal differences in evenness were found at CH, with maximum values in spring (0.92 ± 0.04) and minimum values in summer (0.83 ± 0.05) (Fig. 3C). Values of the Shannon–Wiener diversity index showed significant temporal and inter-site differences (Table 3). The maximum values were observed at PC and CH in fall (>2 bits) and the minimum values

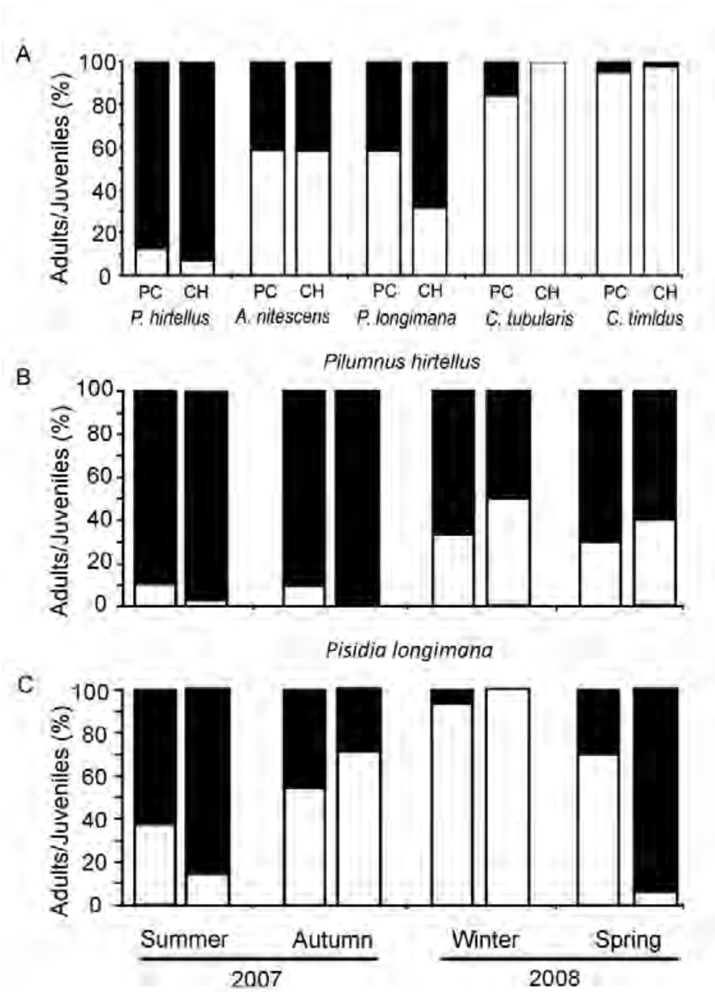

Fig. 4. Ratio of juvenile (small-sized) individuals and adults. (A) Total ratios of the top five dominant species; (B and C) seasonal ratio trends of the top two dominant species, *Pilumnus hirtellus* and *Pisidia longimana*, at Punta Calaburras (PC) and Calahonda (CH). Solid segments of the bars represent juvenile (small-sized) individuals and empty segments represent adult (large-sized) individuals.

in summer (1.48 ± 0.17 bits) and in winter (1.04 ± 0.33 bits) for PC and CH, respectively (Fig. 3D).

Similarity of the decapod assemblages between sites and among seasons and patch areas

The composition and structure of the decapod assemblages presented differences among seasons (R_{ANOSIM} = 0.305; P < 0.05) but not among patch areas (R_{ANOSIM} = 0.158; P = 0.043) or sites (R_{ANOSIM} = 0.07; P < 0.05; very low R values). The temporal differences were due to changes in the abundance values and the presence of certain species collected exclusively in some months (Table 4). The differences between summer and fall (R_{ANOSIM} = 0.388; P < 0.05; SIMPER average dissimilarity 63.01%) were mainly due to higher abundances of some of the top dominant species of the assemblage, such as *Athanas nitescens* and *Processa robusta* in fall and *Pisidia longimana* in summer (Table 4). The summer– winter differences (R_{ANOSIM} = 0.349; P < 0.05; SIMPER average dissimilarity 71.84%) were mainly related to the higher abundance of *P. robusta* and *Xantho hydrophilus* in winter and of *Pagurus anachoretus* in summer (Table 4). A decrease in the abundance of *A. nitescens* and *Pilumnus hirtellus* in winter and the presence of *Pisa carinimana* in fall marked differences between these seasons (R_{ANOSIM} = 0.323; P < 0.05; SIMPER average dissimilarity 69.38%) (Table 4). Finally, the differences between fall and spring (R_{ANOSIM} = 0.468; P < 0.05; SIMPER average dissimilarity 61.52%) were mainly related to lower abundances of *A. nitescens* and higher ones of *Anapagurus hyndmanni* in spring than in fall (Table 4).

Relationships among the environmental variables, the seagrass parameters and the decapod assemblages

Species richness and abundance [total and juvenile (small-sized) individuals] were positively correlated to seawater temperature and the former negatively to Chl *a* concentration (Table 5). The seagrass parameters and the ecological indexes showed few significant correlations but species richness was positively correlated to shoot density and negatively correlated to leaf height and width. Total, adult and juvenile (small-sized individuals) abundances were negatively correlated with

Table 4. Results of similarity percentages analyses. Species ranked according to their average within-group similarity within seasons (Punta de Calaburras and Calahonda).

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Summer					
P. hirtellus	1.54	14.72	5.94	30.17	30.17
P. longimana	1.55	13.24	1.74	27.13	57.30
C. timidus	0.95	4.83	0.91	9.90	67.20
C.tubularis	0.81	4.32	0.69	8.85	76.04
A. gracilis	0.73	3.68	0.68	7.54	83.58
P. anacharetus	0.52	2.31	0.52	4.74	88.32
Autumn					
A. nitescens	1.69	8.32	4.85	15.62	15.62
P. hirtellus	1.51	6.53	1.84	12.26	27.87
P. longimana	1.45	6.27	1.80	11.77	39.65
P. robusta	1.17	5.87	1.66	11.02	50.67
A. gracilis	1.12	4.32	1.24	8.10	58.77
H. leptocerus	0.79	3.40	0.92	6.38	65.15
X. hydrophilus	0.91	3.04	0.89	5.70	70.85
E. cranchii	0.91	2.96	0.90	5.55	76.40
C. tubularis	0.82	1.99	0.69	3.74	80.15
P. carinimana	0.65	1.99	0.68	3.73	83.87
C. timidus	0.74	1.89	0.70	3.55	87.43
E. edwardsii	0.57	1.38	0.53	2.59	90.02
Winter					
P. longimana	0.96	8.96	1.10	26.87	26.87
P. robusta	0.81	6.77	0.78	20.31	47.18
X. hydrophilus	0.67	5.96	0.78	17.87	65.05
P. hirtellus	0.47	2.22	0.42	6.67	71.72
A. nitescens	0.53	1.96	0.43	5.88	77.60
A. gracilis	0.35	1.29	0.30	3.86	81.46
E. cranchii	0.39	1.27	0.29	3.81	85.27
C. tubularis	0.50	1.05	0.29	3.16	88.44
E. edwardsii	0.35	1.03	0.29	3.10	91.53
Spring					
C. timidus	1.13	9.46	1.70	21.55	21.55
A. hyndmanni	1.10	8.55	1.20	19.47	41.02
P. hirtellus	0.82	5.35	0.89	12.18	53.20
P. longimana	0.89	4.45	0.68	10.13	63.34
C. tubularis	0.73	4.14	0.66	9.43	72.76
P. anacharetus	0.65	3.21	0.68	7.31	80.07
A. gracilis	0.60	2.79	0.52	6.36	86.43
X. hydrophilus	0.62	2.33	0.52	5.32	91.74

Av. abund., average abundance; ave sim., average similarity; sim./SD, similarity/standard deviation; contrib.%, average percentage contribution to similarity; cum.%, cumulative percentage similarity.

leaf height. No relationships were found between the ecological indexes and patch area or wave height (Table 5).

Table 5. Relationships (Pearson correlation) between the species richness (S), total abundance (N), adult abundance (NA), juvenile (small size) abundance (NJ) evenness (J') and Shannon–Wiener diversity (H') with the seagrass parameters (shoot density, number of leaves, leaf height and width), patch area and the environmental variables [wave height, temperature, Chl *a* concentration and % organic matter (%OM)].

Index	T	Chl a	%O.M.	Wave height	Shoot density	Number of leaves	Leaf height	Leaf width	Patch area
S	R=0.377; P<0.05*	R=-0.360; P<0.05*	R=0.102; P=0.535	R=0.070; P=0.673	R=0.345; P<0.05*	R=-0.158; P=0.336	R=-0.581; P<0.01**	R=-0.353; P<0.05*	R=-0.198; P=0.416
N	R=0.393; P<0.05*	R=-0.247; P=0.130	R=0.003; P=0.987	R=0.154; P=0.350	R=0.072; P=0.663	R=-0.145; P=0.378	R=-0.506; P<0.01**	R=-0.205; P=0.211	R=-0.218; P=0.370
NA	R=0.187; P=0.254	R=-0.163; P=0.322	R=0.039; P=0.812	R=0.266; P=0.102	R=0.112; P=0.499	R=-0.134; P=0.417	R=-0.337; P<0.05*	R= -0.101; P=0.542	R=-0.151; P=0.424
NJ	R=0.512; P<0.01**	R=-0.283; P=0.080	R=-0.290; P=0.862	R=0.038; P=0.820	R=0.029; P=0.863	R=-0.134; P=0.414	R=-0.578; P<0.01**	R=-0.264; P=0.104	R=-0.296; P=0.112
J	R=-0.548; P<0.01**	R=0.363; P<0.05*	R=-0.270; P=0.871	R=0.248; P=0.127	R=0.085; P=0.609	R=0.372; P<0.05*	R=0.147; P=0.370	R=0.411; P<0.01**	R=0.065; P=0.793
H	R=0.150; P=0.362	R=-0.245; P=0.132	R=0.166; P=0.313	R=0.138; P=0.401	R=0.393; P<0.05*	R=-0.760; P=0.645	R=-0.438; P<0.01**	R= -0.231; P=0.157	R=-0.089; P=0.718

*Significant differences at $P < 0.05$ and ** at $P < 0.01$.

Canonical correspondence analysis indicated that the first two axes accounted for 75.2% of the total variance in the species-environment relationships and 24.3% of the species variance. Leaf height (0.502), percentage of organic matter (0.423), leaf number (-0.428) and shoot density (-0.348) showed the highest correlations with axis I, whereas seawater temperature (0.686), leaf width (-0.614) and wave height (-0.591) presented the highest correlations with axis II. Forward selection indicated that leaf height ($F = 4.03$; $P < 0.01$) and seawater temperature ($F = 3.56$; $P < 0.01$) could explain most of the variance in the species data. The scatter diagram showed an ordination of the samples in relation to seasons of the year. The samples scattered along axis II following an increase in seawater temperature from the positive to the negative part of the axis (Fig. 5). The majority of the species is near the origin of axes (showing a poorly differentiated profile distribution). Nevertheless, some species appeared more separated in relation to axis I, indicating a possible relationship with the phenological parameters (such as *Processa robusta*; Fig. 5).

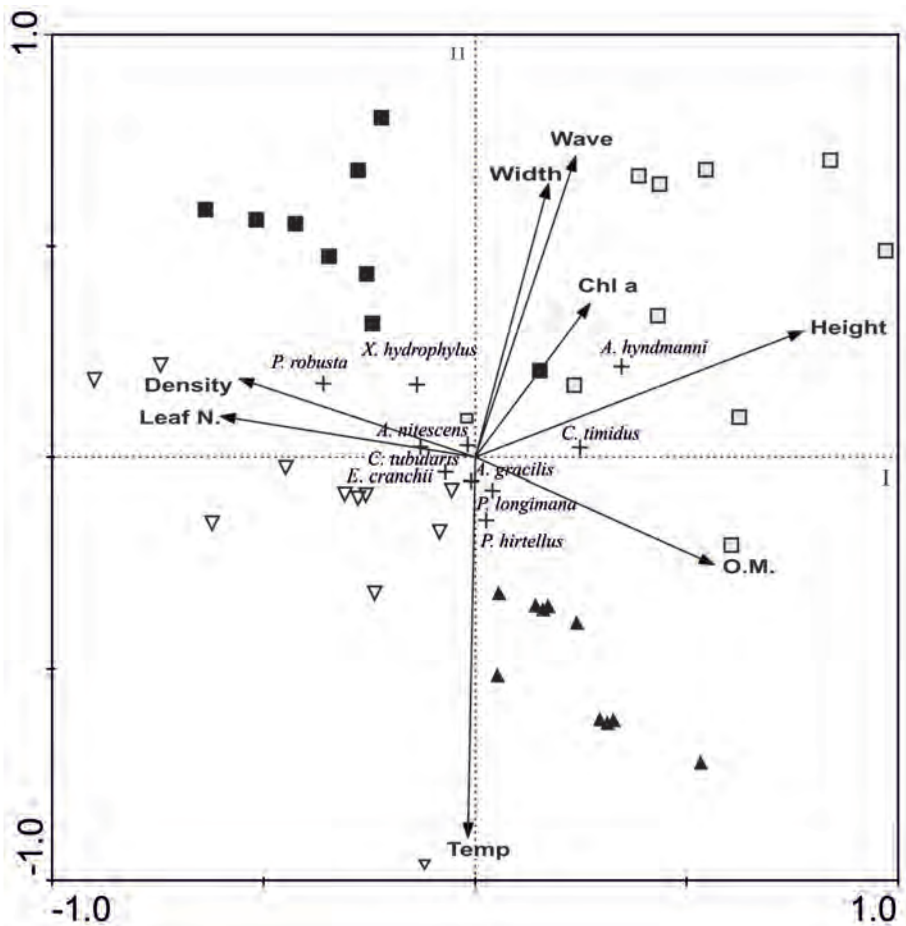

Fig. 5. Plot from the canonical correspondence analysis of environmental variables, seagrass parameters and top dominant species in relation to axes I and II (eigenvalues: 0.118 and 0.085, respectively). Temp, seawater temperature; O.M., percentage of organic matter; Chl a, chlorophyll a concentration; Wave, wave height; Density, shoot density; Leaf N, leaf number; Height, leaf height and Width, leaf width. ▲ summer; △ fall; ■ winter; ■ spring.

Discussion

Phenology of **Posidonia oceanica**

The temporal trend observed for *Posidonia oceanica* meadows of PC and CH (Northwestern Alboran Sea) is similar to that reported for other Mediterranean meadows of this species (Eastern Spain: Sánchez Lizaso 1993; Italy: Guidetti *et al.* 2002). The meadows studied here were characterized by a patchy structure, showing higher shoot density and lower leaf height values in comparison to those from meadows located at similar depths in other Mediterranean areas (Northeast Spain: Marbà *et al.* 1996; Italy: Buia *et al.* 1992; Greece: Amoutzpoulou-Schina and Haritonidis 2005). However, Marbà *et al.* (1996) studied *P. oceanica* meadows in the Northeastern Alboran Sea (close to the Almería–Oran Front) and observed similar phenological characteristics (i.e. high shoot densities and low leaf heights) to those of this study (Northwestern Alboran), suggesting that local factors may play a key role in controlling the growth of *P. oceanica*. These factors and probably the shallow location of the studied meadows (high wave exposure) at PC and CH may have important effects upon the phenological parameters of *P. oceanica*.

Composition and structure of the decapod assemblages

The decapod assemblages inhabiting the *Posidonia oceanica* meadows of PC and CH were dominated by species mainly associated with the rhizome stratum, such as *Pisidia longimana*, *Pilumnus hirtellus*, *Athanas nitescens*, *Calcinus tubularis* and *Cestopagurus timidus*. This faunistic composition showed similarities with those reported for other *P. oceanica* meadows (García Raso 1990a; Borg and Schembri 2000; Sánchez-Jerez *et al.* 2000; Box Centeno 2008). García Raso (1990a) observed that abundances of the hermit crabs *C. timidus* and *C. tubularis* (dominant species in *P. oceanica* meadows in South-eastern Spain and abundant in the present study area) depended upon the bathymetry (e.g. *C. tubularis* prefers deeper bottoms) as well as local factors such as environmental quality, surface currents and shell availability (Zupo *et al.* 1989; García Raso 1990a; Belci *et al.* 2010). By contrast, the geographic location of the Alboran Sea, with the acute Atlantic influence, marks some differences such as the absence of some

Mediterranean species commonly found in *P. oceanica* meadows located eastward of the Almería–Oran Front, and the presence of typical Atlantic species that do not extend towards the Mediterranean Sea. This is the case for the hermit crab *Pagurus chevreuxi*, found in areas of the Central and Western Mediterranean Sea (Zariquiey Álvarez 1968; Templado 1984; Borg and Schembri 2000) but absent from the present study area, and *Anapagurus hyndmanni*, an Atlantic species that occurs in the Alboran Sea (García Raso 1982; García-Gómez 1994; García Muñoz *et al.* 2008) but is absent eastward of the Almería–Oran Front. A similar patron had been observed for mollusks (Urra *et al.* 2013a).

The methodology used in this study (air-lift sampler) allowed the collection of species linked to the foliar stratum, such as the shrimp *Hyppolite inermis* and the hermit crab *C. timidus*, both cited as dominant species in other *P. oceanica* meadows (Ledoyer 1966; Borg and Schembri 2000; Belci *et al.* 2011). The hippolytid *H. inermis* is a characteristic species of this stratum, whereas *C. timidus* makes vertical movements towards the apical part of the shoots or along them in daytime to feed (Ledoyer 1966; Borg and Schembri 2000; Mateo-Ramírez and García Raso 2012). However, the species associated with the rhizome stratum generally make a greater contribution to the faunistic richness of *P. oceanica* meadows, with a higher diversity of decapods than the leaf stratum (Templado 1984; Borg and Schembri 2000). This was also observed in PC and CH, where the majority of the dominant decapods are sciaphilic species associated with hard substrata (i.e. the rhizomes), which provide ideal conditions for adults and shelter for juveniles of different species. This is the case for *P. hirtellus*, a common crab species in infralittoral rocky bottoms that also uses the *P. oceanica* rhizomes and associated calcareous algae concretions as nursery areas, as observed in this and other studies (Vadon 1981; García Raso and Fernández Muñoz 1987; GarcíaRaso 1988). The high dispersal ability of decapods, together with the patchy configuration of the studied meadows and the presence of different habitats, rocky outcrops and algal stands interspersed among them, may explain why the most common species in this assemblage also occur in adjacent habitats. In this context, the species *Achaeus gracilis*, *Achantonyx lunulatus*, *Sirpus zariquieyi* and *Eualus cranchii* were collected in the surrounding photophilous algae meadows (Mateo-Ramírez A., Urra J., Marina P., Rueda J.L., García Raso J.E. unpublished data). The latter is an opportunistic species that can occur in biotopes with cavities and on photophilic seaweed (García Raso 1990b), as well as in the leaf stratum of *P. oceanica* (Borg and Schembri 2000). The species *Xantho hydrophilus* and *Porcellana platycheles* were found under pebbles and small rocks (Vadon 1981; Mateo-Ramírez A., Urra J., Marina P., Rueda J.L., García Raso J.E. unpublished data), and *Processa robusta* and *A. hyndmanni* were found inhabiting soft bottoms, preferentially detritic bottoms for *A. hyndmanni* (García Muñoz *et al.* 2008). The presence of juveniles of *A. hyndmanni* in spring in both *P. oceanica* and *Cymodocea nodosa* meadows (Mateo-Ramírez and García Raso 2012) may indicate that this species uses the seagrass meadows as nursery areas. This connectivity between surrounding habitats, with high levels of movement of species, has been reported in *P. oceanica* meadows throughout the Mediterranean Sea (García Raso 1990a; Scipione *et al.* 1996; Borg and Schembri 2000), in other seagrasses such as *Cymodocea nodosa* (García Raso *et al.* 2006; Mateo-Ramíez and García Raso 2012; Daoulatli *et al.* 2014) and in other faunistic groups with lower mobility than decapods such as mollusks (Urra *et al.* 2013). The ability to inhabit different habitats and the R-reproductive strategies of certain species, such as Alpheus dentipes, *P. hirtellus*, *C. timidus* and *P. longimana* (with long reproductive periods, from January–February to October–November), allow them to display a high colonization capacity, with the presence of juveniles throughout the year and one or two annual recruitment peaks (García Raso and Fernández Muñoz 1987; García Raso 1988, 1990a; López de la Rosa and García Raso 1992; Manjón-Cabeza and García Raso 1994; Belci 2013). These peaks can be delayed or advanced temporally and can show different intensities at different sites or depths in response to environmental changes induced by local factors (e.g. temperature, food availability), entailing changes in the size of the species' populations or decapod assemblages (e.g. *C. timidus*) (Gambi *et al.* 1992; Borg and Schembri 2000). Besides, the high dispersal capacity of many decapod species (adults and larvae; Grantham *et al.* 2003), the local currents and tide influence in the study area, close to the Atlantic Ocean, could intensify the incorporation and/or recruitment of species from adjacent habitats occurring at different areas and depths (Belci 2013).

Temporal dynamics of decapod assemblages and relationships with the environmental variables and seagrass parameters

The studied decapod assemblages showed a significant temporal trend mainly related to the recruitment events of the dominant species, as reflected by the low number of correlations between the ecological indexes and the seagrass parameters. Most of the species occurring in these seagrass beds are sciaphilic ones and therefore not strictly dependent upon the seagrass seasonal cycles associated with the leaf stratum. These species usually search for shelter in sciaphilous micro-habitats, such as seagrass rhizomes and calcareous concretions, especially for juveniles. This could be the reason why the dominant species clustered near the origin in the CCA ordination analysis. Nevertheless, other species such as *Cestopagurus timidus* and *Processa* spp. are more linked to the foliar stratum (Borg and Schembri 2000; Belci 2013; Daoulatli *et al.* 2014), as they usually feed on epiphytes and prey that occur on the seagrass leaves. The relationships with seagrass (leaves) can be indirect, and changes in meadow parameters may act as drivers for recruitment (sometimes with monthly delays, Daoulatli *et al.* 2014). *Cestopagurus timidus* can play a key role in the assemblage dynamics and in the food web at the leaf stratum level, as observed by Gambi *et al.* (1992), even more so than *Hyppolite inermis* because of its higher abundance.

The total abundance (N), species richness (S) and diversity index (H‘) reached their maximum values in fall when *Posidonia oceanica* displayed its minimum leaf height (Figs 2C and 3B). Similar seasonal trends have been observed in decapod assemblages inhabiting *P. oceanica* meadows throughout the Mediterranean Sea (García Raso 1990a; Scipione *et al.* 1996; Borg and Schembri 2000), and also in calcareous algae concretions linked to rhizomes of *P. oceanica* (García Raso 1988). These trends are coincident with the recruitment peaks of some of the dominant species, such as *Athanas nitescens* and *Pilumnus hirtellus* in fall (November) and *Pisidia longimana* in summer (July) (Fig. 4B and C), which are in agreement with the observations made by López de la Rosa and García Raso (1992). Moreover, positive correlations were observed between the total abundance and the abundance of juveniles (small sizes; NJ) with the seawater temperature in both PC and CH (Table 5). All this may suggest that the temporal–seasonal trends of the studied decapod assemblages are mainly related to recruitment events of the dominant species and to seawater temperature rather than to seasonal phenological changes of *P. oceanica* meadows.

Influence of the patchy structure of the seagrass meadows on the decapod assemblages

The studied decapod assemblages occur in fragmented *Posidonia oceanica* meadows located close to the westernmost geographic limit for this seagrass and, therefore, display a different configuration than those located at similar depths in the eastern part of the Alboran Sea or in the Mediterranean Sea (Luque and Templado 2004). The structure of seagrass meadows (continuous or fragmented) and the effect of fragmentation on the associated invertebrate communities are controversial themes. The process of habitat fragmentation, in addition to habitat loss, results in three other effects: an increase in the number of patches, a decrease in patch areas and an increase in the isolation of patches (Bell *et al.* 2001; Fahrig 2003). Thus, different combinations of these effects may promote different responses on the fauna associated with seagrass meadows. Healy and Hovel (2004) found that total epifaunal density was significantly lower in patchy beds than in continuous or very patchy beds, whereas species richness was higher in very patchy beds. In *Zostera marina*, Bowden *et al.* (2001) found a positive species-area relationship and Jackson *et al.* (2006) found that total decapod density increased when seagrass patches form part of a landscape. Other studies have indicated that fragmented seagrass meadows support more decapods than continuous meadows or that decapod density is not related to patch area (Eggleston *et al.* 1998; Hovel and Lipcius 2002).

The integration of the PC and CH meadows with other habitats (e.g. patches of *Cymodocea nodosa*, algae bottoms, rocky and sandy bottoms) generates a macrohabitat, which may reduce the habitat loss effect produced by the fragmentation. This configuration promotes the movement of species and individuals between habitats, which generates relatively high values of species richness, diversity and equitability that are comparable to those reported in decapod assemblages inhabiting continuous *P. oceanica* meadows (17–50 spp.; H' = c. 1.2–2.9 bits; J' = *c.* 0.70, García Raso 1990a, 1988; Borg and Schembri 2000; Box Centeno 2008).

Therefore, seagrass fragmentation is probably affecting some species, but it is not necessarily detrimental for the whole associated faunistic assemblage; also, fragmented seagrass patches may still provide important ecosystem functions for a high number of species and therefore should receive the same attention as non-fragmented ones with regard to habitat conservation and protection, as suggested by Borg *et al.* (2010), especially when considering that fragmentation has already been identified as an important external agent of seagrass decline (Gera *et al.* 2013). In any case, the co-existence of two inter-related assemblages (leaves and rhizomes – photophilous and sciaphilic) in *P. oceanica* meadows, and the further development of the rhizomes may minimize the effects of fragmentation when compared with other small seagrasses occurring on soft bottoms (*e.g. Zostera*, *Cymodocea*).

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CAPÍTULO 5

Asociaciones de crustáceos decápodos ligados a fondos someros de macroalgas infralitorales dominadas por *Halopterys scoparia* en el noroeste del mar de Alboran (Mediterráneo occidental)

Este capítulo se basa en/This chapter is based on:

Crustacean decapod assemblages associated with shallow infralittoral photophilous macroalgal beds dominated by *Halopterys scoparia* in northwestern Alboran Sea (Western Mediterranean Sea)

Mateo-Ramírez A., Urra J., Marina P., Rueda J.L., García Raso J.R. In preparation

Abstract

The temporal dynamics of decapods assemblages associated with the algal fronds and the underlying sediment in two different infralittoral photophilous macroalgal beds dominated by *Halopteris scoparia* were studied in the northwestern Alboran Sea, between July 2007 and April 2008. A total of 35 decapods species were found, with *Hippolyte leptocerus*, *Pilumnus hirtellus*, *Athanas nitescens*, *Sirpus zariquieyi, Achaeus gracilis* and *Acanthonyx lunulatus* as the top-dominant species. The sediment stratum displayed higher values of abundance, species richness and Shannon–Wiener diversity than those of algal fronds. Both strata presented a similar trophic structure in relation to the number of species, with scavengers and predators as dominant groups. The majority of the trophic groups presented an equitable distribution (abundance values) during most of the year. A decoupling between decapod assemblages and algal dynamics was found, probably related to: (1) the trophic strategies of the dominant decapod species that feed on resources present in the sediment; (2) the life cycles of species (recruitment events and movement between habitats); (3) the predator pressure; and (4) the structural complexity of the habitat. A conceptual model based on the results obtained is proposing to explain this decoupling. The high predator abundance, the relatively equitable distribution (in reference to abundance values) of most trophic groups along most of the year and the high values of species richness and evenness, show a healthy status of these assemblages.

Keyword: decapods, composition, dynamics, trophic diversity, macroalgae beds, Alboran Sea

Introduction

Most photophilous macroalgae are habitat-forming species that generate complex habitats with different subsystems, providing refuge for animals from physical stress (e.g. desiccation, wave impact) and protection from predators, acting also as nursery habitats similar to seagrasses (Viejo 1999; Antit *et al.* 2013; Urra *et al.* 2013a; Smith *et al.* 2014). These habitats support a wide variety of plant and animal species with crustaceans, molluscs and polychaetes as important taxa within their associated faunistic communities (Fernández *et al.* 1988; Williams and Seed, 1992; Taylor and Cole 1994). These small invertebrates play an important role in the flux of matters, since are intermediate steps of the food web. In fact, epifauna are the major contributors to the flux of material in rocky reef habitat (Taylor, 1998). However, compared to other faunistic groups such as molluscs (Borja 1986a; Fernández *et al.* 1987, 1988; Chemello and Russo 1997; Urra *et al.* 2013b), information on the ecology of decapods associated with macroalgal beds is sparse, as occurs in a highly biodiverse area as the Iberian Peninsula (Viejo 1999; Lopez de la Rosa *et al.* 2002; 2006; Guerra-García *et al.* 2011a).

In southern Spain, the brown alga *Halopterys scoparia* is one of the most abundant and common algae in infralittoral vegetated habitats (Ballesteros and Pinedo 2004). This is an erect, flexible and perennial species with a dense ramification and large number of interstices (Sanchéz-Moyano *et al.* 2000), forming dense and extensive algal stands that can harbor highly biodiverse faunistic communities (López and Gallego, 2006; Urra *et al.*, 2013b). These stands present two well differentiated strata, the algal frond and the underlying sediment. The latter seem to represent an important micro-habitat for some taxa such as molluscs, which can have higher abundances and species richness values in this stratum than in the algal frond (Urra et al. 2013b). Many species use different habitat and/or microhabitat in different times along the year (Fernández et al. 1998; García Raso et al. 2006; Urra et al. 2013b; Mateo-Ramírez and García Raso 2012; Mateo-Ramírez et al. 2015). However, there are several biotic factors such as the algal architecture, algal biomass or the availability of food (e.g.

detritus, epiphytic) that can influence both in the use of microhabitats and in the seasonal changes of the associated invertebrate communities (Edgar 1983a, b; Taylor 1997; Cacabelos et al. 2010; Antit et al. 2013). This type of information is important for understanding the role of different microhabitats, environmental variables and ecological process on the seasonal patterns of assemblages associated with macroalgal beds, and should be considered for adequate conservation and management plans.

Nowadays, European environmental policies such as the Marine Strategy Framework Directive (MSFD, 2008/56/EC) advocated to get a "Good Environmental Status" of marine ecosystems to 2021. The Directive defines Good Environmental Status (GES) as **"**The environmental status of marine waters where these provide ecologically diverse and dynamic oceans and seas which are clean, healthy and productive". In order to help Member States interpret what GES means in practice, the Directive sets out, in Annex I, eleven qualitative descriptors. Two of these descriptors are biodiversity and food webs. In this line, decapod crustaceans are one of the dominant taxa in shallow and deep benthic habitats (Abelló *et al.* 2002; Cartes *et al.* 2002; Coll *et al.* 2010; UNEP-MAP RAC/SPA 2010; Mateo-Ramírez and García Raso 2012; Matero-Ramírez *et al.* 2015), and could contribute to a large extent in these descriptors. Thus, it would be necessary to get a better knowledge on decapods assemblages associated with one of the dominant habitats along European coastal waters such as macroalgal beds, with important implications for the protection of marine resources.

This study is the first attempt to describe the temporal and spatial variability between decapods assemblages inhabiting different strata of photophilous macroalgae in the western Mediterranean. To do this, we have analyzed the composition, structure and trophic strategies of decapod assemblages associated with the algal fronds and the underlying substratum in two different algal stands dominated by *H. scoparia* in the northwestern Alboran Sea. Additionally, we have analyzed which environmental drivers linked with water column (e.g. seawater temperature) and the algae (e.g. biomass) are most related to the temporal dynamics observed for the decapod assemblages

Material and methods

Study area

The study has been carried out within the Special Conservation Area (SCA) "Calahonda" (code ES6170030), designated under the EC Habitats Directive and included in the Natura 2000 Network. It is located close to the Strait of Gibraltar area in southern Spain (western Mediterranean Sea; Fig. 1). The benthic community associated with the photophilous macroalgae was sampled at 2 m depth in two sites: Punta de Calaburras (hereafter P. Calaburras) (36º30'23" N - 04º38'41"W) which is a more exposed site that results in a high occurrence of bottoms with pebbles surrounding hard bottoms; and Calahonda (36º29'21"N - 04º41'55"W), a more sheltered site with large rocks surrounded by soft sediments. This stretch of coastline is characterized by the presence of littoral rocky outcrops, both intertidally and subtidally, representing one of the few natural rocky areas within the Málaga province (southern Spain). Extensive beds of photophilous algae dominated by *H. scoparia* represent the most widespread vegetated habitat in the SCA (Urra *et al.* 2013b). These shallow algal stands are usually intersperse with *Posidonia oceanica* patches, and occasionally with *Cymodocea nodosa*.

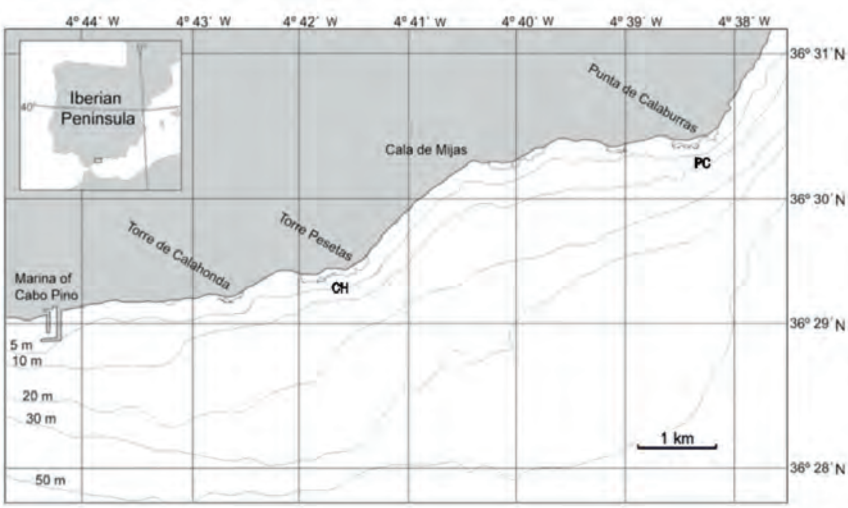

Fig. 1. Study area showing the location of the considered sampling sites in the NW Alboran Sea. PC, Punta Calaburras; CH, Calahonda.

Sample collection and laboratory procedures

Faunistic samples were collected in different times along one year, including July (summer), November 2007 (autumn), January (winter) and April 2008 (spring), with the use of SCUBA. The line intercept method (eight 50 m transects in each site) was used to estimate the algal coverage in the study area. The distinct bionomic strata were sampled separately, first the algal fronds (hereafter 'algae stratum') and then the underlying substratum (hereafter 'sediment stratum'), in each site and season. Algal fronds within a quadrat (0.25 m^2) were collected carefully and enclosed within <0.5 mm mesh bags. Once algae were removed, the sediment below the algae within the same quadrat was collected using an air-lift sampler with a <0.5 mm mesh bag. Suction time was similar (3 minutes) in every sediment sample collected. Five replicate samples were collected per site, stratum and season, resulting in a total of 80 samples. This methodology has previously been used successfully by other authors for collecting samples in similar photophilous algal meadows (Poulicek, 1984; Chemello and Russo, 1997; Bégin *et al.*, 2004), and a similar number of species and individuals were found with this and other sampling techniques (e.g. scraping off individuals from the holdfast (Poulicek, 1984). The air-lift sampling was not used for the fronds in order to avoid collecting individuals from the underlying sediment. In the laboratory, every faunistic sample was sieved over mesh sizes down to 0.5 mm, storing each size fraction in 70% ethanol. Decapods were separated and each species were identified and their individuals counted under a binocular microscope. We distinguished two groups for the dominant species, juveniles-small sizes and adults-large sizes, for which the minimum size of adults was determined from literature (Zariquiey, 1968) and collected data. Wave height (m) information obtained with the High Resolution Limited Area Model and Wave Model numeric models was taken from the Instituto Nacional de Meteorología (Spain) (http:// www.puertos.es).

Water and sediment variables

Water samples for estimating the concentration of chlorophyll *a* (Chl *a*) and seawater temperatures were taken several days before, during and after sampling at each site, in order to study the relation of these variables with the decapods and the algal assemblages. In each sampling event and site, two replicates of 1 litre of seawater were collected at the surface and transported in darkness at low temperature to the laboratory for Chl *a* determination. Water samples were filtered through Whatman GF/C glass filters with a 1.2 µm of pore size. The pigments of the retained cells were then extracted using 100% acetone for 12h in cool and dark conditions. The solution was measured using a spectrophotometer at wavelengths of 630, 647, 664 and 750 nm. The Chl *a* concentrations were obtained using the equation proposed by Jeffrey and Humphrey (1975). The salinity remains almost constant throughout the year due to the low fresh water input in the area, ranging between 36.5 p.s.u. in autumn and 36.8 p.s.u. in spring (Salinity data given in Practical Salinity Scale; GCC, 2014).

Samples of sediment were also taken within the sampled meadows (5 replicates per season and site) in order to estimate the percentage of organic matter (% OM). This percentage was calculated by the weight loss of dry sediment (3 subsamples of 20 gr. per replicate) after ignition at 500ºC for 1h.

Macroalgal characteristics

Macroalgae collected in the samples were also identified and quantified in order to study the structure and composition of the algal assemblage throughout the seasons, as well as their influence on the decapod assemblages. Measurements made on the main collected macroalgal species included: (1) Dry weight (DW), algal weight after drying for 48h at 84ºC and after removal of the epiphytes and animals (Edgar 1983b) (measured in g dw m^{-2}); (2) Volume (V), calculated by the displacement of a known volume of water (Bussell *et al.*, 2007) (measured in cm^3 m^{-2}); (3) Average height of the top-dominant species (*H. scoparia*; HS), length from the holdfast to the distal tip of the plant (measured in cm) of five randomly-selected fronds in each replicate. Finally the sum of the weights and volumes of the different species collected were considered to the total algal dry weight and volume.

Data analysis

Abundance (N) (individuals per sample), Frequency index (%Fi) (percentage of samples in which a particular species is present), Dominance index (%Di) (percentage of individuals of a particular species within the sample) (Glémarec,1964) and the product of Di x Fi/100 (Lopez de la Rosa *et al.* 2002; 2006) were calculated for the species characterization in each time of the year (July, November, January and April), site (P. Calaburras, Calahonda) and stratum (algae stratum and sediment). The characterization of decapods assemblages was done according to several ecological indices, such as the abundance of decapods (N), species richness (S), the Shannon-Wiener diversity index (H´) and the evenness index (J´). These ecological indices were calculated using the software PRIMER 6.0. The trophic groups dominating were analyzed by assigning each decapod species to a trophic category, including deposit feeders (Dep; species that feed on fragmented particulate organic matter from the substratum), filter feeders (Fil.; species that feed on particulate organic matter suspended in the water column), scavengers (Sca; species that feed on dead organic material), grazers (Grz; species that feed on periphyton or other epiphytes) and predators (Pred; species that capture and feed directly on all or part of a living animal species) (Borja *et al.* 2000; Zupo 1993; Grall *et al.* 2006; MarLIN 2006; Zubikarai *et al.* 2014).

Spatial and temporal statistical differences of environmental variables and macroalgal features were tested with a two-factor ANOVA (Analysis of Variance) analysis considering the factors "site" (P. Calaburras *vs.* Calahonda) and "times" (July *vs.* November *vs.* January *vs.* April). Another two-factor ANOVA design with the factors size and times, was used for analysing differences between adults and juveniles abundances in each stratum along the sampling year. Moreover, three-factor ANOVA analyses were carried out for testing statistical differences in values of ecological indices according to site, strata and times. These three analyses were carried out after verifying normality (Kolmogorov-Smirnov) and homogeneity of variances (Levene). Abundance values were transformed in Ln (N). A *post hoc* Tukey test ($P < 0.05$) was used for posteriori multiple comparisons. Kruskal-Wallis and Mann-Whitney analyses were carried out when the homogeneity of variances did not adjust to ANOVA conditions. These statistical procedures were performed using the software SPSS.

Differences in the decapod assemblage were analyzed though a three-way PERmutational MANOVA (PERMANOVA) design with the fixed factors sites, strata and times. Data were square-root transformed prior to analysis to downweight the relevance of the most abundant species and analyses were based on Bray–Curtis similarities (Clarke and Gorley, 2006). The same PERMANOVA design, but based on Euclidian distances, was use to test these differences between trophic groups. The SIMilarity PERcentage (SIMPER) procedure was used to identify those species that contributed to the similarity and dissimilarity between these same groups of samples. ANalysis Of SIMilarity (ANOSIM) was carried out for statistical comparisons of groups of samples (macroalgae species composition) according to factor site. These analyses were executed using the software PRIMER 6.0.

Finally, the relationships between N and ecological indices (S, H') of the whole decapod assemblage (algae + sediment stratum), as well as the abundance of single species, with environmental variables (temperature, Chl *a*, % OM) and algae characteristics (DW, V, HS) were determined by the Pearson correlation. In addition a Canonical Correspondence Analysis was performed to analyze the relationships between environmental variables and the decapods assemblages (taking into account only the top dominant species; Di>2.5%). The statistical significance of the effect of each variable was tested by a Monte Carlo permutation test. Prior to this, the environmental variables were screened and those which presented a correlation of more than 0.9 were not considered further. Environmental data expressed as % were transformed by log (x + 1). These correlations and multivariate analysis were executed using the software SPSS and CANOCO.

Results

Environmental variables

Seawater temperatures were significantly higher in July (maxima, 24.5 °C) and November than in January (minima, 15 °C) and April in both P. Calaburras and Calahonda (two-way ANOVA; factor time: $F = 44.4$, $P < 0.001$; factor site: F

= 1.2, $P > 0.05$). The Chl *a* concentrations displayed significant temporal changes (two-way ANOVA; factor time: $F = 3.3$, $P < 0.05$; factor site: $F = 0.01$, $P > 0.05$), with the highest value recorded in April (11.58 µg l^{-1}) and the lowest in November (5.20 µg l^{-1}), in both cases in Calahonda. Although %OM displayed significant differences between times and sites (two-way ANOVA; factor time: $F = 4.7$, $P < 0.05$; factor site: $F = 36.1$, $P < 0.001$), these values seemed very stable throughout time ranging between 1.11-1.79%, with the maxima in July (3%) at P. Calaburras. Wave height also presented significant differences between sites (Mann-Whitney; U=25, $P < 0.001$) and times (Kruskal-Wallis; $X^2 = 19$, $P < 0.001$ in both sites), with maxima in November at Calahonda (~1 m).

Macroalgal composition and seasonal variability

Macroalgal cover ranged between 74% at P. Calaburras and 61% at Calahonda A total of 13 species were identified, being *Halopteris scoparia* (3868.53 g dw m^{-2}), *Jania rubens* (633.36 g dw m^{-2}) and *Ellisolandia elongata* (183.58 g dw m^{-2}) the three most abundant. Other species were less abundant with values between less than 1 and 90 g dw m^{-2} (e.g. *Cladostephus spongiosus*, *Asparagopsis armata* or *Padina pavonica*).

The structure of the macroalgal assemblages displayed slight, but significant differences between sites ($R_{ANOSIM} = 0.159$; $P < 0.05$). There were certain species that only appeared in P. Calaburras (*Amphiroa rigida*; *P. pavonica*) or in Calahonda (*Dyctiota dycotoma*; *Acrosorium ciliolatum*; *Sphaerococcus coronopifolius*) with values ranging between 1 and 8 g dw m^{-2}. In addition, the dominant species presented some differences in their biomass, for example *H. scoparia* was more abundant in P. Calaburras (2171.95 g dw m^{-2}) than in Calahonda (1696.58 g dw m^{-2}) and *J. rubens* (373.68 g dw m^{-2}; 259.68 g dw m^{-2}) and *E. elongata* (146.89 g m^{-2}; 36.69 g dw m^{-2} respectively) were in Calahonda.

The structure of these assemblages showed significant temporal variations (Table 1). Total macroalgal mean DW and V displayed significant high values in July-April and low values in November-January, but these differences were not significant between sites (Table 1; Fig. 2). Both parameters presented maximum values in April at Calahonda (754.75 ± 87.01 g dw m^{-2} and 2424.80 ± 181.76 cm^3 m^{-2}, respectively; mean ± SE). The dominant species (*H. scoparia*) also presented differences in DW, V and HS between times (Table 1; Fig. 2). Maximum values were observed in P. Calaburras for DW (557.57 ± 44.46 g dw m^{-2}) and in Calahonda for V (1838.4 ± 78.76 cm^3 m^{-2}) and HS (11.42 ± 0.33 cm) during April. The DW and HS showed a significant and high positive correlation with the Chl *a* ($R_{Pearson}$ = 0.50 and $R_{Pearson}$ = 0.83, P < 0.001) while V of

Table 1. Two-way ANOVA analyses for testing differences in the values of algal parameters in relation to sites (Punta Calaburras and Calahonda) and times (July, November, January, April). df, Degree of Free; SS, Squares Sum; MS, Mean Square.

Source of variation	n	df	SS	MS	F	*P*
Macroalgal characteristic						
Biomass	40					
Site		1	1868.962	1868.962	0.057	0.813
Time		3	735,514.02	245,171.34	7.436	**<0.001**
Error		32	1,055,060.56	32,970.64		
Volume	40					
Site		1	34.339.6	37,339.60	0.146	0.705
Time		3	4,615,930.40	1,538,643.50	6.557	**<0.05**
Error		32	7,509,401.60	234,668.80		
Halopterys scoparia						
Biomass	40					
Site		1	14,028.02	14,028.02	1.015	0.321
Time		3	303,168.61	1,001,056.20	7.311	**<0.001**
Error		32	442,292.00	13,821.63		
Volume	40					
Site		1	1768.9	1768.9	0.013	0.909
Time		3	2,098,009.10	699,336.37	5.222	**<0.05**
Error		32	4,285,177.60	133,911.80		
Height	40					
Site		1	0.876	0.876	0.731	0.399
Time		3	15.586	5.195	4.322	**<0.05**
Error		32	38.381	1.199		

H. scoparia displayed the same with %OM ($R_{Pearson} = 0.62$; $P < 0.001$). Some other dominant species such as *J. rubens* and *E. elongata* displayed maximum values in April for DW and V at both sites (Fig. 2). The maximum values were obtained in P. Calaburras with 62.34 ± 29.93 g dw m^{-2} and 104 cm^3 m^{-2} respectively. However, due to large differences between replicates, the temporal variations of DW (Kruskal-Wallis; $X^2 = 10.25$, $P < 0.05$) and V (Kruskal-Wallis; $\chi^2 = 10.86$, $P < 0.05$) were only statistically significant for *J. rubens* at Calahonda. DW and V of *J. rubens* showed a significant positive correlation with Chl *a* ($R_{Pearson} = 0.44$; $R_{Pearson} = 0.47$, $P < 0.05$).

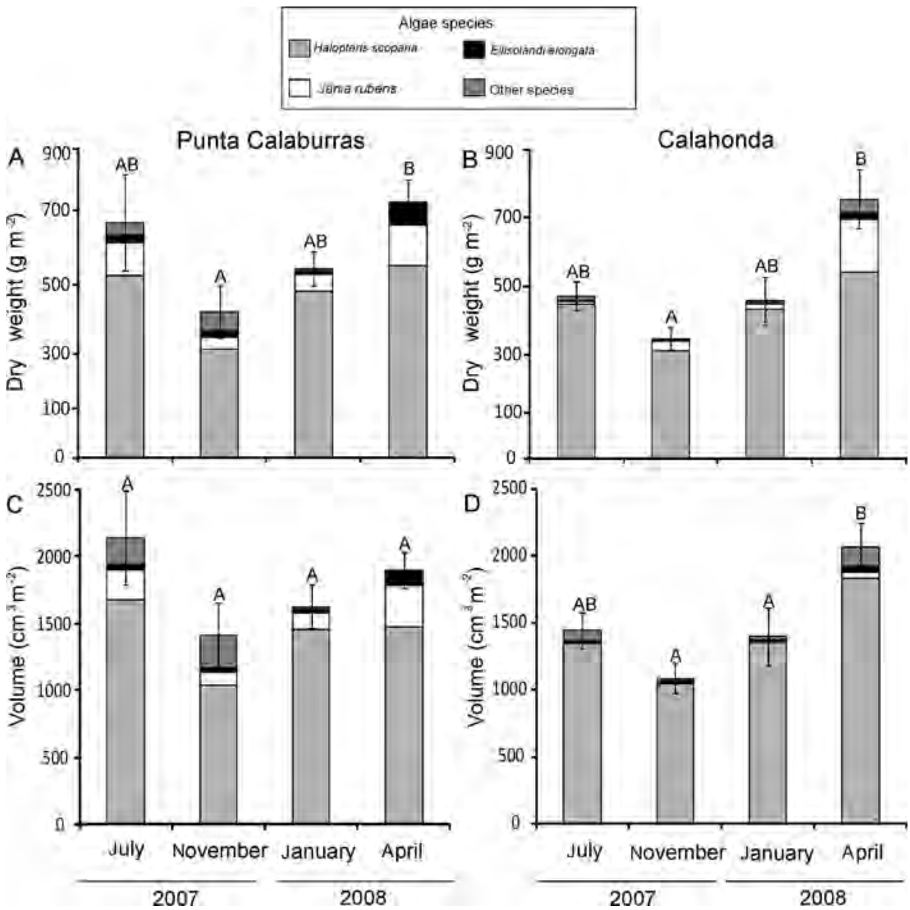

Fig. 2. Seasonal trends of dry weight, (A, B) and volume, (C, D) of dominant species *Halopteris scoparia* (grey bars), *Jania rubens* (empty bars) and *Ellisolandia elongata* (black bars) and less abundant species (dark grey bars) in Punta Calaburras and Calahonda. Mean ± standard error. Letters above error bars display the results of *post hoc* Tukey, different letters indicate significant differences at P<0.05.

Composition, structure and seasonal variability of the decapods assemblages

A total of 35 species were identified from 2654 collected specimens. Hippolitidae and Pilumnidae represented the most abundant families (529 and 479 ind. respectively), and Epialtidae represented the most diverse family (4 species). The top-dominant species were *Hippolyte leptocerus* (481 ind.), *Pilumnus hirtellus*, *Athanas nitescens*, *Sirpus zariquieyi, Achaeus gracilis* and *Acanthonyx lunulatus*. The decapod assemblage showed significant different between sites, strata and times (Table 2, 3, 4). For example, species such as *Pisa carinima*, *Calcinus tubularis*, *Cestopagurus timidus* or *Anapagurus hyndmanni* were more abundant in P. Calaburras, whereas *A. nitescens*, *Philocheras fasciatus* or *Processa robusta* was in Calahonda (Table 2). Regarding to strata; there were species that only were found in one of the strata, e.g. *Pisa nodipes* (Di = 0.14%; Fi = 0.35%) in the algae stratum or *Atelecyclus rotundatus* (0.10%; 0.25%) and *Sicyonia carinata* (0.35%; 0.89%) in the sediment stratum. According to the Di x Fi values, decapods assemblages associated with the algae stratum were dominated by *P. hirtellus* in July, *H. leptocerus* from November to January and *A. lunulatus* in April (Table 4), whereas in the sediment stratum it was dominated by *P. hirtellus* in July and November, *A. gracilis* and *H. leptocerus* in January and *H. leptocerus* in April (Table 4).

The species richness showed significant differences between sites, strata and times (Table 5). The temporal trend observed was similar in both strata, with significant maximum values in November and January, being more acute and with higher values in the sediment stratum (Fig. 3A, B). The highest values were observed in November in the algae stratum (10.20 ± 1.39 species) and in January in the sediment stratum (14.60 ± 1.03 species), in both cases in P Calaburras (Fig. 3A).

The abundance showed significant differences between strata and times, but not between sites (Table 5). The temporal trend was similar to that observed for the species richness, with significant higher values in November in both strata (Fig. 3C, D). The highest abundance values were observed in November in both the algae (50 ± 14.00 ind.) and the sediment stratum (110.80 ± 37.85 ind.) in P. Calaburras. Overall, abundance of adults was higher than that of juveniles in the algae stratum (two-way ANOVA, factor size: $F = 15.580$, $P < 0.001$; factor season:

Table 2. SIMiliraty PERcentage analyses. Species ranked according to their average within-group similarity at sites (Punta de Calaburras and Calahonda) and strata (algae and sediment). Av. Abund, Average abundance; Av. Sim, average similarity; Sim/SD, similarity/ standard deviation; Contrib. %, average contribution to similarity; Cum.%, cumulative percentage of similarity.

Sites					
Punta Calaburras	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
H. leptocerus	2.14	8.25	1.4	21.73	21.73
P. hirtellus	2.09	7.49	1.41	19.73	41.46
S. zariquieyi	1.57	5.64	1.15	14.86	56.32
A. lunulatus	1.07	4.07	0.79	10.72	67.04
P. carinimana	0.97	2.99	0.71	7.88	74.91
A. gracilis	0.9	1.48	0.5	3.89	78.8
C. tubularis	0.66	1.41	0.47	3.71	82.51
P. denticulata	0.62	0.94	0.41	2.46	84.97
C. timidus	0.67	0.88	0.36	2.31	87.28
A. hyndmanni	0.62	0.77	0.26	2.03	89.31
P. longimana	0.51	0.67	0.32	1.76	91.06
Calahonda	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
H. leptocerus	1.92	9.48	1.17	26.77	26.77
P. hirtellus	1.6	5.23	0.8	14.76	41.52
A. lunulatus	1.04	4.7	0.63	13.26	54.78
A. gracilis	1.16	4.12	0.75	11.64	66.42
P. denticulata	0.83	3.25	0.53	9.17	75.59
S. zariquieyi	1.01	2.57	0.59	7.26	82.85
A. nistencens	1.02	1.52	0.45	4.3	87.14
P. longimana	0.62	1.04	0.36	2.93	90.07
Strata					
Alga Stratum	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
A. lunulatus	1.18	8.03	0.88	23.86	23.86
H. leptocerus	1.43	6.83	0.88	20.29	44.15
P. hirtellus	1.35	6.44	0.87	19.12	63.27
S. zariquieyi	0.84	3.41	0.64	10.11	73.38
P. carinimana	0.56	2.05	0.44	6.08	79.46
A. gracilis	0.59	1.82	0.39	5.4	84.86
P. tetraodon	0.3	0.93	0.24	2.77	87.63
C. tubularis	0.34	0.89	0.29	2.65	90.28
Sediment Stratum	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
H. leptocerus	2.62	11.45	2.38	26.18	26.18
P. hirtellus	2.34	6.66	1.31	15.23	41.41
S. zariquieyi	1.73	4.95	1.08	11.32	52.73
P. denticulata	1.19	4.53	0.97	10.36	63.1
A. gracilis	1.48	3.78	0.93	8.64	71.74
A. lunulatus	0.93	2.04	0.67	4.66	76.4
P. fasciatus	0.87	1.95	0.52	4.45	80.86
P. carinimana	0.8	1.46	0.56	3.33	84.18
A. nistencens	1.29	1.3	0.47	2.96	87.14
P. longimana	0.74	1.05	0.39	2.39	89.54
C. tubularis	0.57	0.79	0.39	1.82	91.35

F = 10.646, P< 0.001) and the sediment stratum (two-way ANOVA, factor size: F =8.231, P< 0.01; factor season: F = 10.396, P< 0.001) along the year. However some species presented a higher number of juveniles than adults in all times and in both strata, as in the case of *P. hirtellus* with percentages ranging between 61% in April (sediment stratum) and 93% in November (algae stratum). Other species showed higher number of juveniles in certain times and especially in the sediment stratum such as in the case of *A. gracilis* (59% of juveniles in January), *A. nitescens* and *P. longimana* (94% and 79% in July respectively), *P. carinimana* (87%-62% in November-January) or *A. hyndmanni* (77% in April).

Table 3. PERmutational MANOVA analyses based on Bray-Curtis index for testing differences in the decapod assemblages in relation to sites (Punta Calaburras and Calahonda), strata (algae and sediment) and times (July, November, January, April). df, Degree of Free; SS, Squares Sum; MS, Mean Square.

Source of varation	df	SS	MS	Pseudo-F	P
Sites	1	5956	5956	3.701	**<0.001**
Stratum	1	16256	16256	10.103	**<0.001**
Time	3	24562	8187.3	5.088	**<0.001**
Site * Stratum	1	917.47	917.47	0.570	0.826
Site * Time	3	7726.2	2575.4	1.600	**<0.05**
Stratum * Time	3	10160	3386.5	2.104	<0.01
Site * Stratum * Time	3	5377.3	1792.4	1.114	0.329
Residual	64	102980	1609		
Total	79	173930			

Diversity values of Shannon-Wiener index displayed significant differences between sites, strata and times (Table 4). Values showed a temporal trend with significant seasonal differences in the sediment stratum in P. Calaburras with the maxima in January (2.39 ± 0.18) (Fig. 3E), and in the algae stratum in Calahonda with the maxima in November (1.90 ± 0.08) (Fig. 3F). Finally, evenness only showed significant differences between times (Table 4), and these differences were observed in P. Calaburras in both strata, with the maxima in the algae stratum (0.98 ± 0.01 in July) (Fig. 3G). In Calahonda, evenness values were very similar throughout the year in both strata and ranged between 0.8 and 0.9 (Fig. 3H).

Table 4. Top15 dominant decapod species in each stratum (algae and sediment) and time (July, November, January, April), in function to product of dominance and frequency/100. Di, %dominance; Fi, %frequency; Di*Fi, product of dominance and frequency/100.

	July				November				January				April		
Algal stratum	Di	Fi	Di*Fi		Di	Fi	Di*Fi		Di	Fi	Di*Fi		Di	Fi	Di*Fi
Pilumnus hirtellus(**Pred**)	29.07	70	20.35	*Hippolyte leptocerus*	29.68	100	29.68	*Hippolyte leptocerus*	23.25	90	20.93	*Achantonyx lunulatus*	30.36	90	27.32
Achantonyx lunulatus(**Sca**)	10.47	50	5.23	*Pilumnus hirtellus*	20.05	100	20.05	*Pilumnus hirtellus*	22.48	80	17.98	*Pisa carinimana*	12.5	70	8.75
Athanas nitescens(**Dep**)	10.47	40	4.19	*Sirpus zariquieyi*	9.36	100	9.36	*Achantonyx lunulatus*	12.40	70	8.68	*Hippolyte leptocerus*	10.71	60	6.43
Pirimela denticulata(**Sca**)	11.63	20	2.33	*Athanas nitescens*	10.43	70	7.3	*Achaeus gracilis*	7.75	40	3.1	*Sirpus zariquieyi*	9.82	50	4.91
Sirpus zariquieyi(**Sca**)	5.81	40	2.33	*Achantonyx lunulatus*	6.68	80	5.35	*Pisa carinimana*	5.43	40	2.17	*Calcinus tubularis*	7.14	40	2.86
Pisidia longimana (**Fil**)	4.65	30	1.4	*Achaeus gracilis*	3.74	60	2.25	*Sirpus zariquieyi*	4.65	40	1.86	*Achaeus gracilis*	8.04	30	2.41
Achaeus gracilis(**Sca**)	4.65	30	1.4	*Pisidia longimana*	4.01	50	2.01	*Calcinus tubularis*	3.10	40	1.24	*Pisa tetraodon*	5.36	30	1.61
Hippolyte leptocerus(**Grz**)	4.65	30	1.4	*Alpheus dentipes*	3.21	60	1.93	*Cestopagurus timidus*	3.10	30	0.93	*Pilumnus hirtellus*	4.46	30	1.34
Pisa tetraodon(**Pred**)	3.49	30	1.05	*Pisa carinimana*	2.14	50	1.07	*Pagurus anachoretus*	3.10	30	0.93	*Pagurus anachoretus*	2.68	20	0.54
Anapagurus hyndmanni(**Sca**)	3.49	20	0.7	*Cestopagurus timidus*	2.41	30	0.72	*Pisa tetraodon*	2.32	30	0.7	*Cestopagurus timidus*	1.79	20	0.36
Ebalia edwarsii(**Pred**)	5.81	10	0.58	*Pagurus anachoretus*(**Sca**)	1.07	30	0.32	*Pisidia longimana*	2.32	30	0.7	*Anapagurus hyndmanni*	1.79	10	0.18
Pisa carinimana(**Pred**)	2.33	20	0.47	*Eualus cranchii*	1.07	30	0.32	*Alpheus dentipes*	3.10	20	0.62	*Pirimela denticulata*	1.79	10	0.18
Alpheus dentipes(**Dep**)	1.16	10	0.12	*Calcinus tubularis*	0.8	30	0.24	*Pirimela denticulata*	3.10	20	0.62	*Alpheus dentipes*	0.89	10	0.09
Calcinus tubularis(**Sca**)	1.16	10	0.12	*Achaeus cranchii*	1.07	20	0.21	*Achaeus cranchii*	2.33	10	0.23	*Macropodia czernjawskii* (**Sca**)	0.89	10	0.09
Philocheras fasciatus(**Pred**)	1.16	10	0.12	*Processa robusta*(**Pred**)	1.07	20	0.21	*Athanas nitescens*	0.77	10	0.08	*Pisidia longimana*	0.89	10	0.09
Sediment stratum															
Pilumnus hirtellus	21.07	90	18.97	*Pilumnus hirtellus*	20.34	100	20.34	*Achaeus gracilis*	13.47	100	13.47	*Hippolyte leptocerus*	15.41	100	15.41
Hippolyte leptocerus	17.24	100	17.24	*Athanas nitescens*	21.86	90	19.68	*Hippolyte leptocerus*	13.47	100	13.47	*Pirimela denticulata*	14.66	100	14.66
Sirpus zariquieyi	15.71	70	11	*Hippolyte leptocerus*	18.12	100	18.12	*Pilumnus hirtellus*	15.07	80	12.05	*Anapagurus hyndmanni*	19.92	60	11.95
Pirimela denticulata	9.58	80	7.66	*Sirpus zariquieyi*	5.67	90	5.1	*Sirpus zariquieyi*	12.56	90	11.3	*Sirpus zariquieyi*	10.15	60	6.09
Pisidia longimana	10.73	70	7.51	*Achaeus gracilis*	5.57	70	3.9	*Pisa carinimana*	7.76	80	6.21	*Pilumnus hirtellus*	8.65	70	6.05
Athanas nitescens	6.13	50	3.07	*Achantonyx lunulatus*	3.44	90	3.1	*Achantonyx lunulatus*	3.88	80	3.11	*Achaeus gracilis*	7.14	70	5
Philocheras fasciatus	6.13	50	3.07	*Processa robusta*	2.63	70	1.84	*Processa robusta*	3.88	60	2.33	*Calcinus tubularis*	4.89	60	2.93
Achaeus gracilis	3.07	50	1.53	*Alpheus dentipes*	3.44	50	1.72	*Philocheras fasciatus*	3.65	60	2.19	*Achantonyx lunulatus*	4.51	50	2.26
Anapagurus hyndmanni	4.98	30	1.49	*Cestopagurus timidus*	3.34	50	1.67	*Eualus cranchii*	3.65	60	2.19	*Pisa carinimana*	2.63	50	1.32
Eualus cranchii (**Pred**)	1.92	40	0.77	*Philocheras fasciatus*	2.73	60	1.64	*Pirimela denticulata*	2.74	80	2.19	*Philocheras fasciatus*	2.63	30	0.79
Achantonyx lunulatus	1.15	20	0.23	*Pisidia longimana*	2.33	60	1.4	*Cestopagurus timidus*	3.88	30	1.16	*Alpheus dentipes*	1.5	30	0.45
Achaeus cranchii (**Sca**)	0.38	10	0.04	*Eualus cranchii*	2.13	60	1.28	*Alpheus dentipes*	2.05	50	1.03	*Cestopagurus timidus*	1.13	20	0.23
Atelecyclus rotundatus (**Pred**)	0.38	10	0.04	*Pisa carinimana*	1.62	70	1.13	*Calcinus tubularis*	2.05	50	1.03	*Pagurus anachoretus*	0.75	20	0.15
Cestopagurus timidus (**Sca**)	0.38	10	0.04	*Calcinus tubularis*	1.62	50	0.81	*Athanas nitescens*	2.51	40	1	*Processa robusta*	0.75	20	0.15

Table 5. Three-way ANOVA analyses for testing differences in species richness, abundance, evenness, and diversity index in relation to sites, strata and times. df, Degree of Free; SS, Squares Sum; MS, Mean Square.

Source of variation	n	SS	df	MS	F	*P*
Richness	80					
Site		61.250	1	61.250	9.405	**0.003**
Stratum		352.800	1	352.800	54.173	**<0.001**
Time		370.550	3	123.517	18.966	**<0.001**
Site* Stratum		5.000	1	5.000	0.768	0.384
Site* Time		94.950	3	31.650	4.860	**0.004**
Time * Stratum		37.400	3	12.467	1.914	0.136
Site* Time* Stratum		7.200	3	2.400	0.369	0.776
Error		416.800	64	6.513		
Abundance	80					
Site		0.748	1	0.748	1.825	0.181
Stratum		23.056	1	23.056	56.233	<0.001
Time		24.357	3	8.119	19.802	**<0.001**
Site* Stratum		0.045	1	0.045	0.111	0.740
Site* Time		9.334	3	3.111	7.588	**<0.001**
Time * Stratum		0.635	3	0.212	0.516	0.673
Site* Time* Stratum		0.606	3	00.202	0.493	0.688
Error		26.241	64	0.410		
Shanon-Wiener Diversity	79					
Site		0.844	1	0.844	7.093	**0.010**
Stratum		2.953	1	2.953	24.828	**<0.001**
Time		2.957	3	0.986	8.287	**<0.001**
Site* Stratum		0.016	1	0.016	0.137	0.713
Site* Time		2.096	3	0.699	5.875	**0.001**
Time * Stratum		0.539	3	0.180	1.510	0.221
Site* Time* Stratum		0.035	3	0.012	0.097	0.961
Error		7.493	63	0.119		
Evenness	79					
Site		0.001	1	0.001	0.150	0.700
Stratum		0.022	1	0.022	3.817	0.055
Time		0.099	3	0.033	5.609	**<0.01**
Site* Stratum		0.010	1	0.010	1.723	0.194
Site* Time		0.083	3	0.028	4.696	**<0.01**
Time * Stratum		0.002	3	0.001	0.107	0.956
Site* Time* Stratum		0.023	3	0.008	1.325	0.274
Error		0.370	63	0.006		

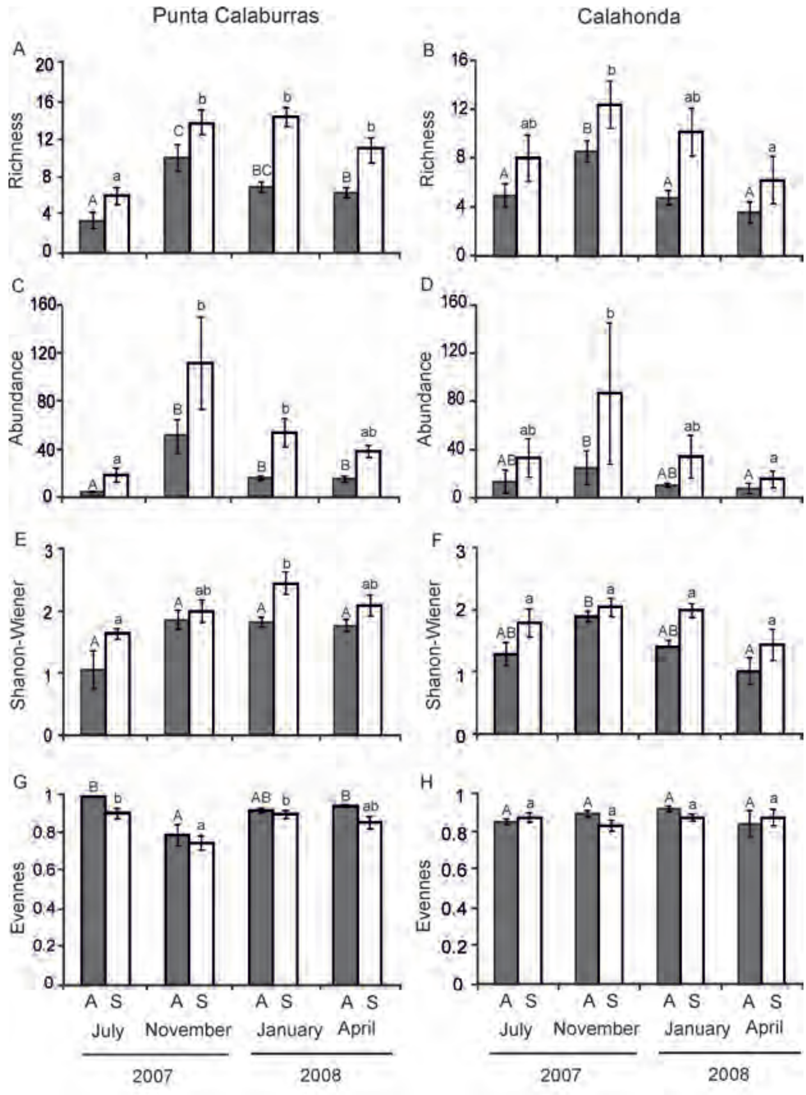

Fig. 3. Seasonal trends of species richness, abundance, Shannon-Wiener diversity and evenness of decapods assemblages inhabiting the A, algae stratum (solid bars) and S, sediment stratum (empty bars) in Punta Calaburras and Calahonda. Mean ± SE. Letters above error bars display the results of *post hoc* analyses, different letters indicate significant differences at P<0.05. Capital letters refers to A comparisons and lower-case to S comparisons.

Trophic structure of decapods assemblages

Regarding trophic groups and species richness, scavengers were the most diverse group throughout the study year in both sites, with 15 species in the sediment stratum and 13 species in the algae stratum. They were followed by predators (14 species in the sediment and 11species in the algae), deposit feeders (3 species in the sediment and 2 species in the algae), grazers (2 species in both strata) and filter feeders (1 species in both strata) (Fig. 4A, C). Regarding abundances, scavengers dominated in the sediment stratum (683 ind.) and in the algae stratum (254 ind.), followed by predators (592 ind. and 200 ind. respectively), grazers (325 ind. and 157 ind. respectively), deposit feeders (293 ind. and 67 ind. respectively) and filter feeders (60 ind. and 23 ind. respectively). All trophic groups displayed significant changes in their abundance values in

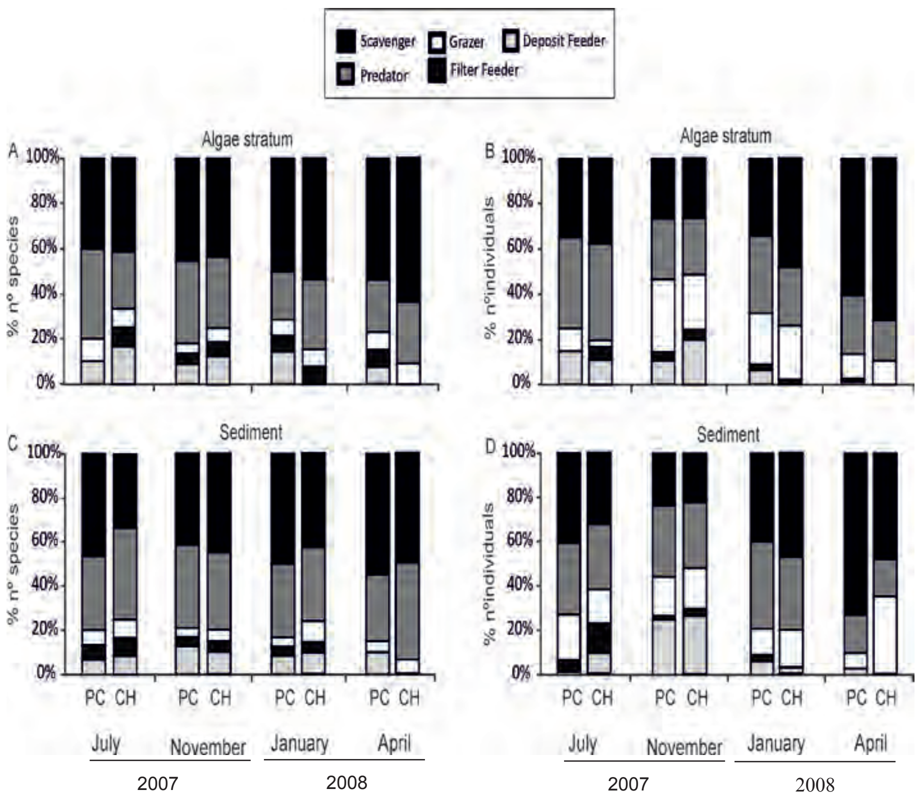

Fig. 4. Seasonal changes on trophic groups of the decapods assemblages inhabiting algae stratum and sediment. PC, Punta Calaburras; CH, Calahonda. A-B, percentage of species number; C-D, percentage of individuals of each trophic groups.

relation to the factor time and stratum (Table 6). The maximum abundances of scavengers were observed in April and were mainly due to the high abundance of juveniles of *P. denticulata* and *A. hyndmanni* as well as of adults of *A. lunulatus* and *S. zariquieyi* in both strata (Fig. 4B, D; Table 2, 4). In the case of deposit feeders, maximum abundances were in November related to the high numbers of *A. nitescens*, especially in the sediment stratum (Fig. 4B, D; Table 2, 4). On the other hand, predators showed the largest differences between strata in November and January, mainly related to the large abundance of *P. hirtellus* in the sediment stratum (Fig. 4B, D; Table 2, 4). Contrary, grazers displayed higher relative percentage in the algae stratum during November and January, in relation to *H. leptocerus* abundances (Fig. 4B, D; Table 4).

Relationships between the assemblage of decapods and environmental-macroalgal variables

Some ecological indices resulted from combining samples from sediment and algae stratum displayed significant correlations with some environmental and macroalgal variables. The abundance showed a negative correlation with DW of *H. scoparia* ($R_{pearson} = -0.352$, $P < 0.05$), whereas diversity displayed a negative correlation with temperature ($R_{pearson} = -0.335$, $P < 0.05$), and evenness showed a negative correlation with wave ($R_{pearson} = -0.363$, $P < 0.05$) and a positive correlation with DW of *H. scoparia* ($R_{pearson} = 0.341$, $P < 0.05$). Juveniles of *A. gracilis* and *P. carinimana* showed a negative correlation with DW of *J. rubens* and temperature respectively, whereas *P. denticulata* showed a positive correlation with DW of *H. scoparia*, *J. rubens* and *E. elongata.*

In the Canonical Correspondence Analysis, the decapod assemblages associated with the sediment stratum were the only one showing significant results in the Monte Carlo test ($P < 0.001$) for all canonical axes. The first two axes accounted for 67.2% of the total variance of species-environment relationships and 26.3% of the species variance. The temperature (-0.630), Chl *a* (0.624), HS (0.572) and DW of *H. scoparia* (0.529) showed the highest correlations with axis I; however, correlations with other axes were less acute. Forward selection indicated temperature ($F = 5.29$, $p < 0.01$) as the variable explaining most of the

Table 6. PERmutational MANOVA analyses based on Euclidian distances for testing differences in abundance of trophic groups of the decapod assemblages in relation to sites (Punta Calaburras and Calahonda), strata (algae and sediment) and times (July, November, January, April). df, Degree of Free; SS, Squares Sum; MS, Mean Square.

	Source	df	SS	MS	Pseudo-F	P
Abundance Deposit Feeders	Site	1	12.8	12.8	0.090	0.782
	Stratum	3	638.45	638.45	44.874	**<0.05**
	Times	1	3037.3	1012.4	7.116	**<0.001**
	Site* Stratum	3	6.05	6.05	0.042	0.855
	Site* Time	1	56.1	18.7	0.131	0.952
	Time * Stratum	3	1395.4	465.15	32.694	**<0.05**
	Site* Time* Stratum	3	24.25	80.833	0.056	0.987
	Residual	64	9105.6	142.28		
	Total	79	14276			
Abundace Filter Feeders	Site	1	28.125	28.125	0.9375	0.344
	Stratum	1	17.112	17.112	57.042	**<0.05**
	Time	3	44.538	14.846	49.486	**<0.01**
	Site* Stratum	1	36.125	36.125	12.042	0.278
	Site* Time	3	24.837	82.792	27.597	0.053
	Time * Stratum	3	16.738	55.792	18.597	0.139
	Site* Time* Stratum	3	11.237	37.458	12.486	0.305
	Residual	64	192	3		
	Total	79	312.89			
Abundance Grazers	Site	1	45	45	13.206	0.284
	Stratum	1	352.8	352.8	10.354	**<0.001**
	Time	3	1966.5	655.48	19.236	**<0.001**
	Site* Stratum	1	48.05	48.05	14.101	0.259
	Site* Time	3	195.9	65.3	19.164	0.108
	Time * Stratum	3	49.5	16.5	0.484	0.744
	Site* Time* Stratum	3	27.45	9.15	0.268	0.902
	Residual	64	2180.8	34.075		
	Total	79	4866			
Abundance Predators	Site	1	238.05	238.05	24.354	0.115
	Stratum	1	1920.8	1920.8	19.651	**<0.001**
	Time	3	3264.9	1088.3	11.134	**<0.001**
	Site* Stratum	1	36.45	36.45	0.373	0.552
	Site* Time	3	445.85	148.62	15.205	0.218
	Time * Stratum	3	1089.3	363.1	37.148	**<0.05**
	Site* Time* Stratum	3	30.25	10.083	0.103	0.961
	Residual	64	6255.6	97.744		
	Total	79	13281			
Abundance Scavengers	Site	1	391.61	391.61	50.842	0.024
	Stratum	1	2300.5	2300.5	29.867	**<0.001**
	Time	3	1047.1	349.05	45.316	**<0.01**
	Site* Stratum	1	148.51	148.51	19.281	0.169
	Site* Time	3	611.54	203.85	26.465	0.052
	Time * Stratum	3	180.44	60.146	0.781	0.519
	Site* Time* Stratum	3	235.04	78.346	10.171	0.401
	Residual	64	4929.6	77.025		
	Total	79	9844.4			

variance in the species data, followed by DW of *J. rubens* ($F = 3.44$, $P < 0.01$), wave height ($F = 2.06$, $P < 0.05$), DW of *H. scoparia* ($F = 2.14$, $P < 0.05$) and DW of *E. elongata* ($F = 2.06$, $P < 0.05$). Samples aggregated in two different groupings: 1) samples from July and November, which were located mainly in the negative part of axis I in correlation with high values of temperature and wave height; and 2) samples from January and April, which were located in the positive part of axis I in correlation with high values of HS and Chl *a* and low temperatures (Fig. 5). The analyses suggests that the seasonality of decapod assemblages associated with the sediment stratum is mainly related to the temperature and algal characteristics

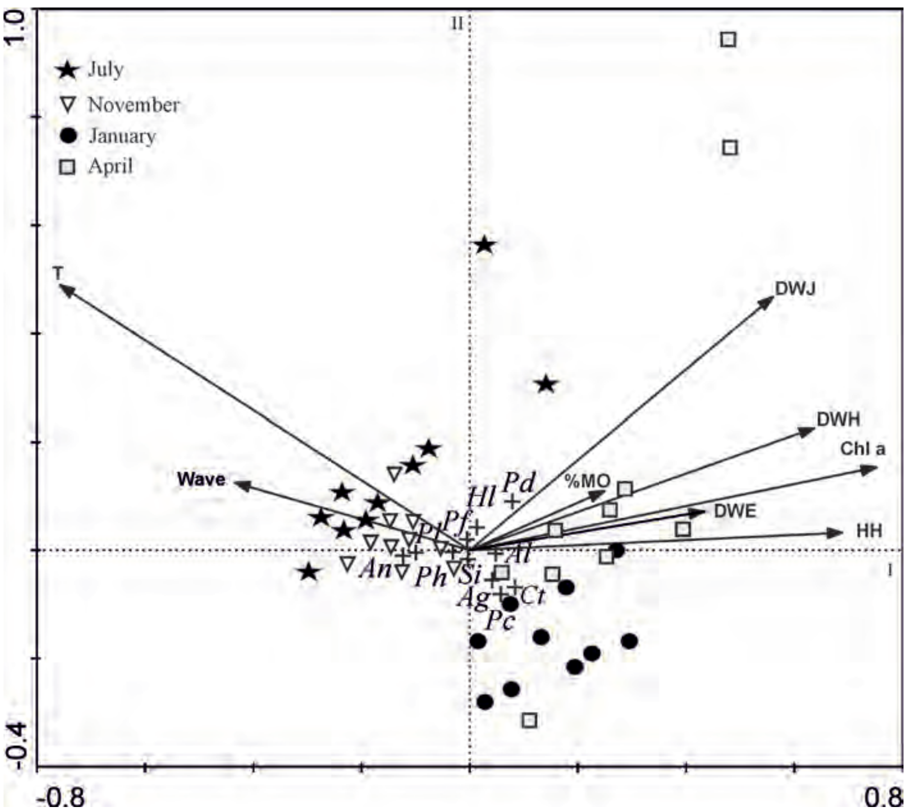

Fig. 5. Canonical correspondence analysis of environmental variables, algae parameters, decapod assemblages and single species associated to sediment stratum in relation to axes I and II (eigenvalues: 0.102 and 0.055 respectively). T, seawater temperature; %OM, percentage of organic matter; Chl *a*, chlorophyll *a* concentration; Wave, wave height; DWH, dry weight of *H. scoparia*; HH, height of *H. scoparia*; DWJ, dry weight of *J. rubens*; DWE and dry weight of *E. elongata*; An, *A. hyndmanni*; Ph, *P. hirtellus*; Pl, *P. longimana*; Pf, *Philocheras fasciatus*; Hl, *H. leptocerus*; Pd, *P. denticulata*; Al, *A. lunulatus*; Ct, *C. timidus*; Pc, *P. carinimana*; Ag, *A. gracilis*; Si, *S. zariquieyi.*

(DW and HS). The majority of the top dominant species are near the origin of the axes, which shows a poorly differentiated profile distribution in relation with the analyses of parameters.

Discussion

Seasonality and composition of the algal community

The macroalgal beds considered for this study seem to correspond to that of Mediterranean sublittoral communities dominated by leafy macroalgae species without the erect stratum of Fucales (Ros *et al.* 1985; Ballesteros 1993). The species composition of macroalgal beds of SCA "Calahonda" are similar to the community from Tossa de Mar (NW Mediterranean Sea), although with some differences such as absence of *Cladophora prolifera* or *Lithophyllum incrustans* and presence of *A. armata* (Ballesteros and Pinedo 2004). The *H. scoparia* beds studied showed a more definite seasonal trend than those reported by Ballesteros (1993) in a NW Mediterranean algal bed which did not present seasonal biomass changes. This seasonal trend was similar to that observed in other Mediterranean and Atlantic beds with maximum development mainly in April (Ballesteros 1984; Borja 1986b). The other two dominant species *J. rubens* and *E. elongata* also presented high development in July, in relation to the high temperature values (Ballesteros 1993) and in April, related to the high concentration of nutrients as observed in the positive correlation between Chl *a* concentration and several algae variables.

Decapod assemblages, temporality and microhabitat use

The decapod assemblages associated with photophilous macroalgal beds of SCA "Calahonda" (northwestern Alboran Sea) showed a high species richness (35 species), and although they were mainly composed by species common in the Mediterranean, some African (*P. carinima*) and Atlantic (*A. hyndmanni*) species were also abundant. The number of species observed here was higher than that found in similar habitats in other Mediterranean areas (25 species) or in the Caribbean Sea (32-27 spp.), and similar to that found in the more complex seascape composed by seagrasses and macroalgae in Florida (38 species) (Gore *et al.* 1981; Castelló *et al.* 1987; Quirós and Campos 2010; Quirós *et al.* 2012). The decapod assemblages in the SCA "Calahonda" were dominated by both species commonly found in macroalgal beds (*P. hirtellus*, *S. zariquieyi*, *A. lunulatus* or *A. gracilis*), and species frequently associated with seagrass meadows (*H. leptocerus* or *A. nitescens*) (Pérès and Picard 1964; Zariquiey 1968; Vadon 1981; Castelló *et al.* 1987; López de la Rosa and García Raso 1992; Ballesteros and Pinedo 2004; Mateo-Ramírez and García Raso 2012; Mateo-Ramírez *et al.* 2015). Furthermore, characteristic species of soft and hard bottoms were also collected in high numbers due to the proximity of these habitats and the movement of species among them (García-Muñoz *et al.* 2008; Mateo-Ramírez and García Raso 2012; Mateo-Ramíre *et al.* 2015). These species were presented in both sampling sites; however *C. tubularis*, *C. timidus*, *P. carinimana* and *A. hyndmanni* were more abundant in P. Calaburras, whereas *P. fasciatus* and *P. robusta* were in Calahonda. These differences were related with the higher quantity of rocks covered by algae and soft bottoms present in P. Calaburras and Calahonda respectively.

Regarding the trophic composition, decapods assemblages associated to macroalgae beds of SCA "Calahonda" were dominated by scavengers and predators. However, most of the trophic groups displayed a certain equitable distribution (in reference to abundance values) during most of the year (November-January) in both strata. An equitable distribution of trophic groups would indicate a healthy ecosystem functioning, which together with a high number of predator species could reflect a higher functional diversity of the entire assemblage (Ngai and Srivastaba 2006; Bremner *et al.* 2006; Zubikarai *et al.* 2014). These data could be used as a reference point for decapods assemblages associated with low impactated habitats such as these macroalgal beds of SCA "Calahonda", when considering the "Good Enviromental Status" (Marine Strategy Framework Directive) of European marine habitats.

Our results indicate a decoupling between the decapod assemblages and the algal characteristics (biomass; volume), with higher values of species richness, abundance and Shannon-Winner diversity during November and January when macroalgal beds showed its lowest development. Macroalgal beds are subjected to seasonal and inter-annual changes in its species composition and coverage (Ballesteros 1993), which can influence the abundance, structure and diversity of invertebrate benthic assemblages (Bustamante *et al.* 2014). Several studies have showed a positive correlation between algal biomass and mollusc and/or crustacean abundance, in relation to the availability of substrate and food (Borja 1986a; López de la Rosa *et al.* 2006; Guerra-García *et al.*, 2011b; Antit *et al.* 2013). Moreover, Urra *et al.* (2013b) observed that the vegetative cycle of algae in the northwestern Alboran Sea played an important role in the abundance of some dominant epifaunal grazers, with high abundance and species richness values coinciding with high biomass of algae. However, other studies have reported similar decoupling than ours (Edgar 1983b, Taylor 1998; Langtry and Jacoby, 2006).

This decoupling could be linked with the feeding strategies of most decapod species inhabiting this habitat (scavengers, *A. lunulatus*, *S. zariquieyi* or *A. gracilis*; predators, *P. hirtellus*, *P. fasciatus* or *P. carinimana*; or deposit feeders, *A. nitescens*) which are not directly dependent to the algal dynamic, since their food resources (MO, detritus, prey) are mainly present in the sediment. Indeed, deposit feeders are the dominant trophic group on the sediment and the basal layer of vegetation in the macroalgae beds of Alboran Sea and Basque Coast (Urra *et al.*2013b; Bustamante *et al.* 2014). In addition, movements of species between surrounding habitats (*P. oceanica*, *C. nodosa*, soft and hard bottoms) as well as vertical movements of certain species between algal fronds and the underlying sediment looking for refuge or food, could be also related to this. This type of movements and use of different microhabitats/strata have been described in others habitats (*C. nodosa* or *P. oceanica* meadows) and species such as the gastropod *Rissoa parva* or the hermit crab *C. timidus*, which make vertical movements between strata looking for food (Fernández *et al.* 1998; Mateo-Ramírez and García Raso 2012; Urra *et al.* 2013b; Mateo-Ramírez *et al.* 2015).

Life cycle of species is another factor that could be related to this decoupling observed between decapods assemblages and algal dynamics. In fact, *A. gracilis*, *P. carinimana*, *P. denticulata* or *P. hirtellus* showed higher abundances in the sediment with maximun values during November or January. These peaks were related to recruitment events, which coincided with the lowest values of algal biomass and temperature (Vadon 1981; López de la Rosa and García Raso 1992). In the case of other species, such as *Hippolyte* spp., abundances usually display a correlation with maximum algal, seagrass or epiphytic development (Mazzella *et al.*, 1989; Lopez de la Rosa *et al.*, 2006). In the SCA "Calahonda", high abundances of *Hippolyte* spp. (mainly juveniles) were observed in July and May in *C. nodosa* meadows (Mateo-Ramírez and García Raso 2012), and in November and January (mainly adults and especially ovigerous females) in macroalgal beds. These data suggest that *Hippolyte* spp. (e.g. *H. leptocerus*) mainly recruit on seagrasses in spring-summer, and then individuals migrate to algal beds for spawning under the protection of algal fronds in autumn-winter.

The low decapods abundance and richness values observed in our study during April and July could be also linked with a high predation pressure from fishes. In this line, several studies have showed that fish assemblage associated with macroalgal beds of European waters present spawning peaks between these months increasing their presence and pressure in these months (Alonso-Fernandez *et al.*, 2011; Raposeiro and Azevedo, 2009). Similar temporal patterns have been observed in seagrass meadows of eastern (Alicante) and southern (Almería) Spain, with a negative relationship between predator and prey abundances (Sánchez-Jerez *et al.*, 1999; García Raso *et al.*, 2006a). Moreover, the larger size of decapods (6-21 mm) in comparison with molluscs (mainly 2-3 mm), amphipods or tanaids (3-5 mm), could force them to look for shelter and protection under the algal cover, as many fishes inhabiting vegetated environments (e.g. *Thalassoma pavo*, *Coris julis*, *Serranus scriba* and *Diplodus annularis*) feed directly on phytal invertebrates and large individuals are more efficiently detected by visual predators (Tortonese, 1975; Mazzoldi and De Girolamo, 1997; Edgar, 1983b).

Finally, the structural complexity of photophilous algal beds is another factor that can influence on the structure of the associated decapods assemblages. We are found a negative correlation between decapods abundance and DW of *H. scoparia*. According to Heck and Orth (1980), an increment of the surface per unit of substrate is related to an increment in epifauna density, but this relationship has a limitation when the vegetative development could prevent the access of new individuals. Probably, the low development (e.g.biomass) of algae in November-January could facilitate the input of species and individuals, increasing the abundance and diversity values. This trend was also found in epifaunal communities associated with *E. elongata* or *Caulerpa prolifera* beds, where the densest faunal populations were found during low or intermediate development stages of the algae (Sánchez-Moyano *et al.* 2001; Kelaher 2003; Guerra-García *et al.* 2011b).

Conclusions

Decapods assemblages inhabiting macroalgal beds dominated by *H. scoparia* in the northwestern Alboran Sea presented a higher number of species than other decapod assemblages inhabiting similar habitats in Mediterranean and Atlantic coastal areas, being composed of species associated with algal beds and others commonly found in surrounding habitats. Furthermore, these assemblages showed a healthy ecosystem functioning with a dominance of scavenger and predator species, as well as a relative equitable distribution of the majority of the trophic groups during most of the year.

They displayed higher individual abundances and species number when algal assemblages showed lower biomass, which indicate that decapods assemblages displayed a temporal pattern not necessarily linked with algae dynamics. Important aspects to be considered behind these observations include different feeding and reproductive strategies, movement of species between surrounding habitats and strata as well as punctual predation pressure. Our results could be indicated that the decapod assemblages need not be present a closed relationship with the algal dynamics. A conceptual model is proposed here to explain this (Fig. 6).

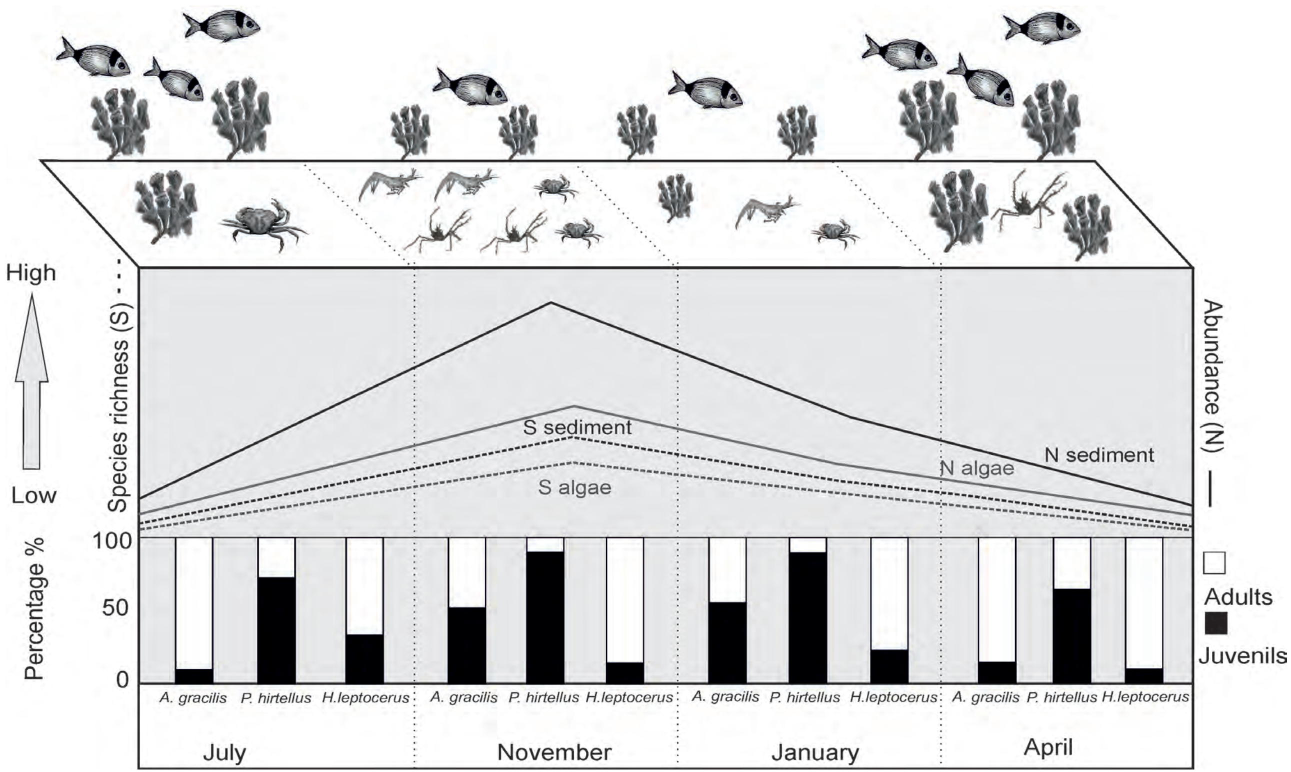

Fig. 6. Conceptual model proposed for explain the decoupling between decapod assemblages and algal dynamic. N sediment, abundances in the sediment; N algae, abundance in the algae stratum; S sediment, species richness in the sediment, S algae, species richness in the algae stratum.

Acknowledgements

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CAPÍTULO 6

Estructura, composición y conectividad de las asociaciones de decápodos ligados a un fondo infralitoral fragmentado

Structure, composition and connectivity of decapod assemblages associated with an infralittoral fragmented seascape

Abstract

The mosaic seascape of the Special Conservation Area (SCA) named "Calahonda", located in the Spanish coasts of the north-western Alboran Sea, were selected to study the structure, composition and connectivity between decapod assemblages associated with *Posidonia oceanica* and *Cymodocea nodosa* patches, and with macroalgal beds. Each habitat was sampled in July 2007 (summer month), November 2007 (fall month), January or February 2008 (winter months) to April or May 2008 (spring months) during daytime by SCUBA divers with the use of an airlift pump and a quadrant of 50 x 50 cm. Environmental and phenological variables such as leaf and frond surface were estimated and compared to temporal changes of the decapod assemblages. A total of 4769 individuals belonging to 48 species and 21 families were captured with the species *Pilumnus hirtellus, Hippolyte leptocerus*, *Athanas nitescens*, *Pisidia longimana* and *Sirpus zariquieyi* being the most abundant (> 50% of the total individuals captured). The surface of shoots and fronds was the variable that explained most of the temporal trend of decapod assemblages associated with this mosaic seascape. All habitats showed high values of evenness and trophic diversity with predators and scavengers opportunistic species being the most important groups. Macrolagal beds presented the lowest values of beta diversity and the lowest percentage of species not represented in the other habitats. Our results suggest that macroalgae beds have an important role during fall and winter months acting like a sink of species. We constated that a complex habitat supports a diverse and resilient decapod assemblages as result of the different uses made of each habitat by the dominant species.

Keywords: decapod, mosaic seascape, conectivity, Alboran sea, resilience

Introduction

Coastal areas worldwide are experiencing loss of seagrass and macroalgae meadows, and although in most cases this loss might due to natural processes (erosion, storms, temporal or climatic change), usually it has been linked to anthropogenic activities such as anchoring, illegal trawling, coastal restructuring (harbours, breakwaters,…), input of organic matter or introduction of invasive species (Short and Wyllie-Echeverria 1996; Walker and Kendrick 1998; Duarte 2002; Ruiz and Romero 2003; Gonzalez-Correa *et al.* 2005; Björk *et al.* 2008; Rueda *et al.* 2008a; Boudouresque *et al.* 2012; Jordà *et al.* 2012). These impacts have a major effect over species with a slow grow rate such as *Posidonia oceanica* (Luque and Templado 2004). This species provides numerous ecological benefits such as the protection of beaches against erosion, diminution of hydrodynamism, stabilization of the sediment which improves the water clarity. It acts as net carbon sink and in addition supports a highly diverse community (Boudouresque and Meinesz 1982; Luque and Templado 2004; Larkum *et al.* 2006; Urra *et al.* 2013a; Mateo-Ramírez *et al.* 2015).

Others seagrass species such as *Cymodocea nodosa* and macroalgae beds offer many of the ecological benefits before cited. Nevertheless, several photophilous macroalgae species are also habitat-forming species. For example, those belonging to genus *Cystoseira*, forming extensive meadows on wave exposed sites, provide habitat and shelter to epiphytes, invertebrates and fish, increasing biodiversity (Smith *et al.* 2014). In the the Special Conservation Area (SCA) named "Calahonda" (ES6170030), located in the NW Alboran Sea, *Cystoseira spp.* are not abundant and they are replaced by *Halopteris scoparia* meadows which represent the most abundant habitat (Urra *et al.* 2013b). The SCA "Calahonda" supports a high faunistic and vegetal marine diversity, being in fact is one of the richest areas of Europe (García Raso *et al.* 2010). The biogeographic location where converge the Lusitanian and Mediterranean provinces (Spalding *et al.* 2007), the high biological productivity of their waters (Rodríguez 1995) and its heterogeneous habitat composed by a mosaic of hard bottoms covered mainly by macroalgae beds, interspersed with *P. oceanica* and *C. nodosa* patches as well as by soft bottoms, promotes this high biodiversity (García Raso *et al.* 2010).

Taking into account that bottoms with seagrasess or macroalgae beds are more diverse than soft bottoms (Edgar *et al.* 1984; Jackson *et al.* 2002; Reed and Hovel 2006; Cowles *et al.* 2009), a loss of meadows should result in a diversity loss (Boström *et al.* 2006). However fragmentation, understood as diminution of proximity and connectivity, could have different effects over the community associated, since different combinations of the number and patch sizes, distances as well as the nature of the matrix present between those, determine the effects of the habitat fragmentation over the associated community (Fahrig 2003). Several studies showed that small patches can support abundant and diverse assemblages (Eggleston *et al.* 1998, 1999; Hirst and Attrill 2008; Mateo-Ramírez and García Raso 2012; Urra *et al.* 2013a; Mateo-Ramírez *et al.* 2015). The mosaic seascape of SCA "Calahonda" offers an exceptional model to study the effects of the fragmentation on the invertebrate community. In addition, decapods are highly appropriate for the study of connectivity between habitats since they are animals with a high capacity for mobility and which can make use of different habitats, sometimes separated by tens of kilometers (Gillianders *et al.* 2003).

In this work we study the decapod assemblages associated with seagrasses (*P. oceanica* and *C. nodosa*) and macroalgae patches, analyzing the structure and composition of each assemblage, connectivity between habitats and the importance of each habitat for the set of decapods associated with this mosaic seascape.

Material and methods

Study area

The study area was located in the Special Conservation Area (SCA) named "Calahonda", included in the EU Natura 2000 network (Decreto 369/2015, BOJA 153 de 07/08/2015), on the Spanish coasts of the north-western

Alboran Sea (Fig. 1). Two sampled sites separated by 7 Km were selected, Punta Calaburras (36º30'23" N - 04º38'41"W) (hereafter P. Calaburras) and Calahonda (36º29'21"N - 04º41'55"W). Both sites present a mosaic seascape where infralittoral rocks covered by photophilous macroalgae and dominated by *H. scoparia*, are the most abundant habitat (cover range between 62%-74%), followed by fragmented meadows of *P. oceanica* (~14%) and *C. nodosa* (< 5%). However, P. Calaburras is located in a more exposed zone results in a higher presence of pebbles (13%) and in a lower occurrence of soft bottoms (7%) than in Calahonda, where represent 17.5%. All coverage values were obtained by the line intercept method, used eight 50 m transects in each site with a depth range between 1-6m.

Water and sediment variables

Water samples for estimating the concentration of chlorophyll *a* and seawater temperatures were taken several days before, during and after sampling at each site. In each sampling event and site, two replicates of 1 litre of sea water were collected at the surface and transported in darkness at low temperature to the laboratory for chlorophyll *a* determination. Water samples were filtered through

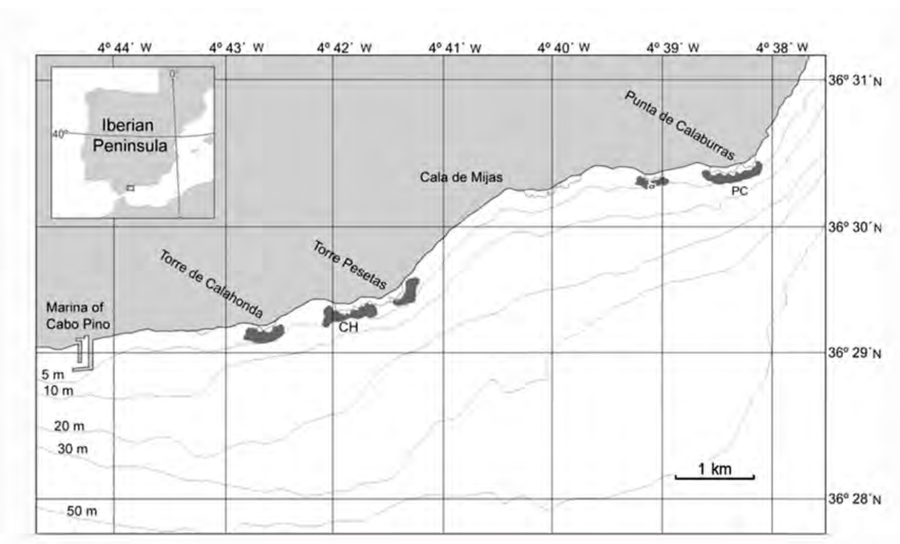

Figure 1. Study area showing the location of the sampled sites. The area in black indicates the location of the mosaic seascape. PC, Punta Calaburras and CH, Calahonda.

Whatman GF/C glass filters. The pigments of the retained cells were then extracted using 100% acetone for 12h in cool and dark conditions. The solution was measured using a spectrophotometer at wavelengths of 630, 647, 664 and 750 nm. The chlorophyll *a* concentrations were obtained using the equation proposed by Jeffrey and Humphrey (1975). The salinity remains almost constant throughout the year due to the low fresh water input in the area, ranging between 36.5 p.s.u. in autumn and 36.8 p.s.u. in spring (Salinity data given in Practical Salinity Scale; GCC, 2014).

Samples of sediment were also taken within the sampled seagrass meadows or macroalgal beds (5 replicates per site, season and habitat) in order to estimate the percentage of organic matter (% OM). This percentage was calculated by the weight loss of dry sediment (3 subsamples of 20gr. per replicate) after ignition at 500ºC for 1h.

Fauna sampling collection and laboratory procedures

In order to analyze the connectivity between the decapod assemblages associated to the vegetated habitats presents in the SCA "Calahonda", we sampled its three main habitats (patch meadows of *P. oceanica* and *C. nodosa* and macroalgae beds) in different dates from July 2007 (summer month), November 2007 (fall month), January or February 2008 (winter months) to April or May 2008 (spring months). The samples were taken during daytime by SCUBA divers with the use of an airlift pump and a quadrant of 50 x 50 cm. The suction time was 3 minutes. Five replicates in each site, habitat, and sampling date were collected, resulting in a total of 120 samples. In algae samples, two distinct strata were sampled separately, algal fronds and the underlying substratum (Urra *et al.* 2013b; chapter 5), but in this study we analyzed together both strata, in order to be able to compare with the seagrass samples, in which these two strata were sampled together. In the laboratory, every faunistic sample was sieved over mesh sizes down to 0.5 mm, storing each size fraction in 70% ethanol. With the use of a binocular microscope decapods were separated and identified down to species level and their individuals were counted. The evolution of the sizes of the dominant species was analysed to distinguish two groups: juveniles-small sizes / adults-large sizes, for which the minimum size of adults was determined from literature (Zariquiey, 1968; Manjón-Cabeza and García Raso 1994) and our personal data (collected samples).

Seagrass and macroalgae characterization

In order to estimate the leaf phenological variables within of each quadrant used to take the fauna samples, ten shoots of *P. oceanica* and of *C. nodosa* were randomly selected. In each of them, the number of leaves per shoot was counted, and the shoot height (from the basal part of the sheath to the blade tip) and leaf width (at the mid-point between the sheath and the blade tip) of the highest leaf were measured *in situ* to the nearest mm (n = 50 shoots per site, month and seagrass species).

For macroalgae, in every quadrant where the fauna sample was taken, average height (length from the holdfast to the distal tip) and width (length between more distal tips) of five randomly selected fronds of *H. scoparia* (top-dominant specie) were measured.

With these data, relative available surface in each habitat was estimated. For seagrasses, the surface was calculated multiplying leaf area per number of leaves, so we obtained the mean area per shoot. For algae, we multiplied the average height and width per frond.

Data analysis

The decapod assemblages were characterized according to abundance (N), species richness (S), Shannon-Wiener diversity index (H') and evenness index (J´). These ecological indices were calculated using the software PRIMER v6. The trophic groups dominating in each habitat were analyzed by assigning a trophic category for each decapod species. These categories included: deposit feeder (Dep; species that feeds on fragmented particulate organic matter from the substratum), filter feeder (Fil.; species that feeds on particulate organic matter, suspended in the water column), scavenger (Sca; species that actively feeds on dead organic material), grazer (Grz; species that feeds periphyton or other epiphytes) and predator (Pred; species that feeds by preying on other organisms, killing them for food). (Zupo and Fressi 1985; Chesa *et al.* 1989; Zupo 1993; Borja *et al.* 2000; Grall *et al.* 2006; MarLIN 2006; Zubikarai *et al.* 2014). The index of trophic diversity was calculated as ITD =(g_1^2 + g_2^2+g_3^2…+g_n^2) where g is the relative contribution of the number of individuals of each trophic group to the total number of individuals, and n is the number of trophic groups (Gambi *et al.* 2003). As the highest trophic diversity scores the lowest values, we used here a modified version of this index as 1-ITD to better visualize the changes in trophic diversity (Danovaro *et al.* 2004).

To test potential significant differences in the decapod species composition between sites, habitat and sampling dates, a three way multivariable PERmutational Multivariate ANalyses of Variance (PERMANOVAs) based on Bray–Curtis index were performed. In this design: sites (P. Calaburras and Calahonda), habitats (Algae, *P. oceanica*, *C. nodosa*) and sampling dates (summer, fall , winter, spring months) were treated as fixed factors. The data were square root transformed prior to analysis. In addition, the data grouped by habitat and site were subject to Principal Coordinates Analysis (PCO) in order to visually assess variations in the species composition. Finally a SIMilarity PERcentanges analysis (SIMPER) was applied to detect which species were responsible of these differences. The differences among ecological indexes, abundance as well as for the abundances of the main species were analyzed with a three-way PERMANOVA based on Euclidean distances (Anderson, 2001) and following the abovementioned design. In addition a *post-hoc* PAR-WISE test was used to check differences between sites, habitats and sample dates. The significance of P values was determined through 9999 permutations of residuals under a reduced model or of raw data (when test was running with only one factor) (Anderson *et al.* 2008). Multivariate multiple regression analyses (DISTLM) tested the significance of these contributions by fitting a linear model based on Bray Curtis dissimilarities using 999 permutations and the R2 and step-wise criteria. Software used PRIMER v6.

On the other hand, magnitude in the changes of the species composition in each habitat was calculated through the use of beta-diversity values. Beta-diversity was calculated according to Whittaker (1960), useing the formula $\beta W = (\gamma/\alpha)-1$, where ($\alpha$; Alfa diversity) is diversity within each habitat and was calculated like species richness per sample (*RSs*) (Gray 2000) and (γ; gamma diversity) is the total species number per habitat. However Whittaker's measurement only provides a single value per habitat so can not be used to test differences among groups in beta diversity. For this, PERMutational analysis of multivariate DISpersion (PERMDISP) analysis based on Jaccard similarities were used (Anderson *et al.* 2008). Software used PRIMER v6.

Finally, differences between sites, habitats and dates (fixed factors) in temperatures values, chlorophyll *a* concentrations, % OM and the area of each habitat were analyzed with two or three way ANOVA or PERMANOVA based on Euclidean distances test. Software used SPSS 18 and PRIMER v6.

Results

Water and sediment variables

Seawater temperatures did not show differences between sites. High values were obtained in the summer months (maxima, 24.5 ^{o}C) and fall months, and lows in the winter (minima, 15 ^{o}C) and spring months in both P. Calaburras and Calahonda (two-way ANOVA; factor site: F =1.2, P > 0.05; factor date: F= 44.4, P < 0.001).

The chlorophyll *a* concentrations displayed temporal variations (two-way ANOVA; factor site: F= 0.01, P > 0.05; factor date: F= 3.3, P < 0.05) with the highest values recorded in the spring months (11.58 µg l^{-1}) and the minimum in the fall months (5.20 µg l^{-1}) both in Calahonda.

The general values of organic matter concentration showed differences between sites, habitats and dates. The highest values were obtained in Calahonda (2.12±0.07%; PERMANOVA, factor site, P-F=21.12; P < 0.001), in *C. nodosa* (2.40±0.09%; follow by *P. oceanica* 1.99±0.07% and algae 1.63±0.06%; PERMANOVA, factor habitat, P-F=65.423; P < 0.001), and in the summer month (3.03±0.41% in *C. nodosa*, 2.16±0.12 % in *P. oceanica* and 1.96±0.28 % in algae; PERMANOVA, factor date, P-F=11.849; P < 0.001).

Seagrass and macroalgae characterization

Seagrasses and macroalgae showed a similar temporal trend, with a higher development in the summer and spring months (Mateo Ramírez and García Raso 2012; Mateo Ramírez *et al.* 2015; chapter 5), whereas the leaf number and leaf width in *P. oceanica* were higher in the winter months (Mateo Ramírez *et al.* 2015).

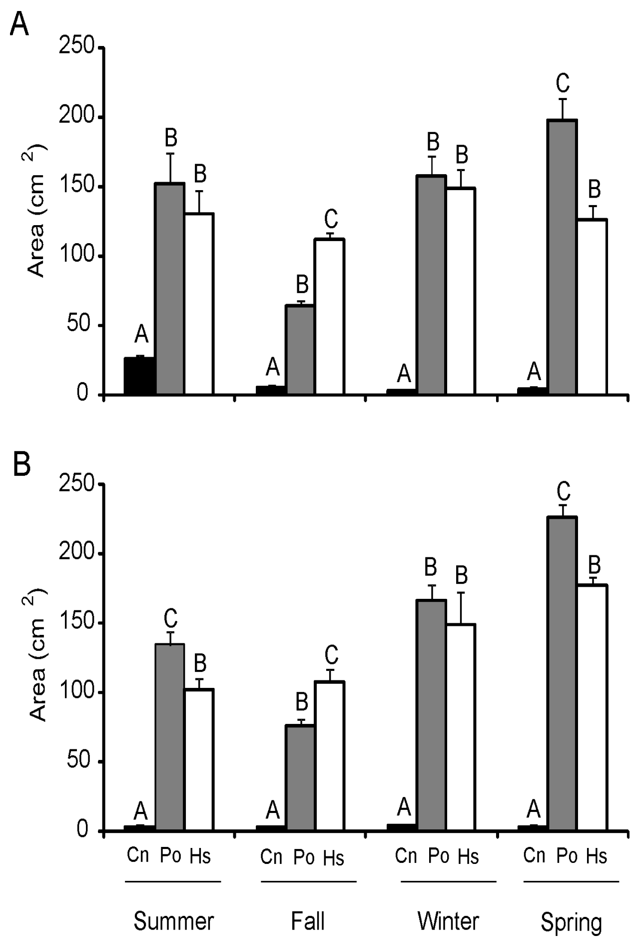

Figure 2. Temporal trends of the available surface of shoots and fronds in P. Calaburras (A) and Calahonda (B). Cn, *Cymodocea nodosa* (black bars); Po, *Posidonia oceanica* (grey bars) and Hs, *Halopteris scoparia* (empty bars). Mean + SE. Letters above error bars display the results of PAR-WISE tests; different letters indicate significantly different means inside each date at P < 0.05.

Regarding surface of shoots or fronds, the highest values for seagrass species were registered in the summer month for *C. nodosa* (26.59±1.64 cm^2 in P. Calaburras) and in the spring months for *P. oceanica* (226.53±9.67 cm^2 in Calahonda) (Fig. 2). Conversely, during the fall and winter months, values for *H. scoparia* were higher than, or similar to values for *P. oceanica* in both sites respectively (PERMANOVA; factor habitat*date: P-F=18.044; $P < 0.001$) (Fig. 2).

Composition, structure and seasonality of the decapod assemblages associated with the vegetated bottoms

A total of 4769 individuals belonging to 48 species and 21 families were captured. The families Hippolytidae and Inachidae with 5 species, followed by the family Epialtidae with 4 spp were the most diverse. In relation to abundance, the families Hippolytidae, Pilumnidae, Alpheidae and Paguridae were the most important, with an accumulated percentage of 54.5%. The species *Pilumnus hirtellus* (699 ind.), *Hippolyte leptocerus* (651 ind.), *Athanas nitescens* (510 ind.), *Pisidia longimana* (313 ind.) and *Sirpus zariquieyi* (274 ind.) were the most abundant (> 50% of the total individuals captured).

The decapod assemblages associated with the three vegetated bottoms studied presented differences between sites, habitats and months (PERMANOVA; factor sites*habitats*date: Pseudo-F =1.804; $P < 0.05$; Table 1). These differences correspond to changes in species composition and their relative contributions. Therefore, the decapod assemblage associated with *C. nodosa* presented two clearly different assemblages, related to the different substrates found in each site (Mateo Ramírez and Garcia Raso 2012) (Fig. 3). In Calahonda, the substrate is composed by fine sand and therefore features species associated with this type of substrate such as *Pirimela denticulata*, *Processa edulis edulis* or *Syciona carinata* (Table 2). However in P. Calaburras where *C. nodosa* grows over a mixed substrate of pebbles and mud, appear species such as *Calcinus tubularis*, *Clibanarius erythropus* or *Xantho poressa*.

Table 1. PERmutational MANOVA analyses based on Bray-Curtis index for testing differences in the decapod assemblages in relation to sites (Punta Calaburras and Calahonda), habitats (Macroalgae, *P oceanica*, *C. nodosa*) and sampling dates (summer, fall, winter, spring months). df, Degree of Free; SS, Squares Sum; MS, Mean Square.

Source	df	SS	MS	Pseudo-F	P
Sites	1	14230	14230	9.43	**< 0.001**
Habitats	2	69709	34854	23.09	**< 0.001**
Date	3	27466	9155.4	6.07	**< 0.001**
SixHa	2	8856.8	4428.4	2.93	**< 0.001**
SixDa	3	9622.7	3207.6	2.12	**< 0.001**
HaxDa	6	30002	5000.4	3.31	**< 0.001**
SixHaxDa	6	16336	2722.7	1.80	**< 0.001**
Res	94	141860	1509.2		
Total	117	317070			

This decapod assemblage showed similarities, in relation to species composition, with the macroalgae and *P. oceanica* assemblages as can be seen on the PCO plot (Fig 3; Table 2). Nonetheless, both meadows share species such as *Philocheras fasciatus*, *H. leptocerus*, *Liocarcinus navigator* or *Anapagurus hyndmanni*, although with different percentages of contribution, for example the former had the highest percentage of contribution in Calahonda (Table 2).

The decapod assemblages associated with *P. oceanica,* showed a mix assemblage with species usually found in *P. oceanica* such as *Pisidia longimana*, *Cestopagurus timidus* or *C. tubularis* and to algae bottoms such as *P. hirtellus*, *Achaeus gracilis* or *A. nitescens* (Table 2). However species like *Processa robusta* in Calahonda or *Ebalia edwardsii* in P. Calaburras, marked the differences between sites (Table 2).

Finally macroalgae beds presented a decapod assemblage principally formed by species which are common in this habitat, such as *P. hirtellus*, *S. zariquieyi*, *A. gracilis* or *Pisa carinimana* (Table 2). Notwithstanding, some species associated with other habitats such as *H. leptocerus* were also present. *Calcinus tubularis*, *A. hyndmanni* or *Alpheus dentipes* only had an important contribution in P. Calaburras (Table 2).

Regarding structure, N and the ecological indexes (S, H') showed significant differences between sites, habitats and dates (Table 3; 4). The highest values of N, S and H' were found in P. Calaburras (Fig. 4; Table 3). The decapod assemblages associated with macroalgae beds showed the highest values of N, S and H', whereas those associated with *P. oceanica* and *C. nodosa* presented intermediate and low values respectively (Fig. 4; Table 3). Finally, J' always displayed values above 0.8 in all habitats (Table 3; 4). On the other hand, the values of beta diversity (ßw; Jaccard) as well as the percentage of species present only in one habitat, showed a contrary trend. Therefore, decapod assemblages associated with *C. nodosa* and *P. oceanica* showed higher numbers of unique species than macroalgae bottoms, which presented the lowest values of beta-diversity (Table 3).

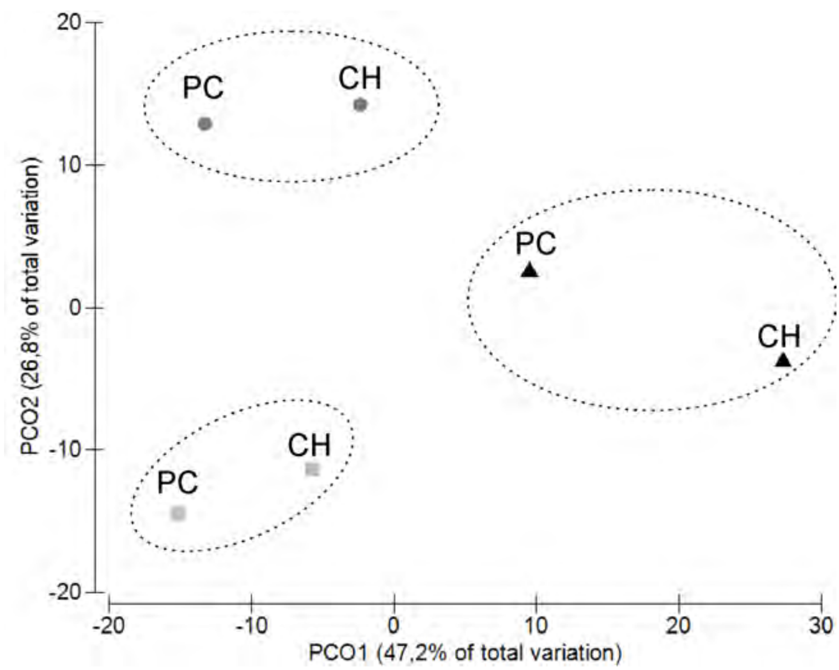

Figure 3. Principal Coordinates Analysis (PCO) based on Bray-Curtis index in order to visualize the similarity between decapod assemblages associated with *Cymodocea nodosa* (black triangles), *Posidonia oceanica* (grey circles) and macroalgae beds (grey quadrant). PC, Punta Calaburras and CH, Calahonda.

Table 2. SIMiliraty PERcentage analyses. Species ranked according to their average within-group similarity at habitats (Macroalgae, *Posidonia oceanica*, *Cymodocea nodosa*) in both sites (Punta de Calaburras and Calahonda). Av. Abund., Average abundance; Av. Sim. average similarity; Sim / SD, similarity/ standard deviation; Contrib. %, average contribution to similarity; Cum. %, cumulative percentage of similarity.

	PUNTA CALABURRAS						CALAHONDA				
Cymodocea nodosa	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	*Cymodocea nodosa*	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Calcinus tubularis	1.79	8.65	1.43	24.13	24.13	*Philocheras fasciatus*	1.29	6.3	0.8	22.44	22.44
Hippolyte leptocerus	1.68	6.13	1.15	17.11	41.24	*Anapagurus hyndmanni*	0.89	6.01	0.74	21.4	43.84
Clibanarius erythropus	1.24	3.99	0.61	11.14	52.38	*Hippolyte leptocerus*	1.34	5.88	0.83	20.93	64.76
Cestopagurus timidus	0.97	3.22	0.77	8.99	61.36	*Pirimela denticulata*	0.78	2.62	0.55	9.33	74.1
Anapagurus hyndmanni	1.3	3.22	0.65	8.97	70.33	*Achaeus gracilis*	0.45	1.14	0.35	4.06	78.16
Hippolyte inermis	1.08	1.91	0.51	5.33	75.67	*Liocarcinus navigator*	0.37	1.14	0.32	4.06	82.21
Liocarcinus navigator	0.63	1.49	0.53	4.15	79.82	*Processa edulis edulis*	0.63	0.94	0.35	3.35	85.57
Athanas nitescens	0.9	1.44	0.46	4.02	83.84	*Sirpus zariquieyi*	0.47	0.86	0.29	3.07	88.64
Philocheras fasciatus	0.56	1.37	0.42	3.82	87.66	*Sicyonia carinata*	0.28	0.71	0.18	2.54	91.18
Xantho poressa	0.63	0.89	0.33	2.48	90.14						
Posidonia oceanica	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	*Posidonia oceanica*	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Pisidia longimana	2.1	7.89	1.08	20.28	20.28	*Pisidia longimana*	1.8	7.74	1.08	23.3	23.3
Pilumnus hirtellus	1.9	5.95	1.08	15.3	35.58	*Pilumnus hirtellus*	1.45	6.01	0.96	18.11	41.4
Athanas nitescens	1.93	4.63	0.99	11.92	47.49	*Achaeus gracilis*	0.98	3.62	0.74	10.89	52.3
Cestopagurus timidus	1.25	3.52	0.87	9.05	56.55	*Processa robusta*	0.88	3.17	0.54	9.54	61.84
Calcinus tubularis	1.34	3.14	0.68	8.08	64.63	*Cestopagurus timidus*	0.92	2.9	0.63	8.75	70.58
Anapagurus hyndmanni	1.12	3.07	0.62	7.9	72.53	*Calcinus tubularis*	0.65	2.17	0.46	6.53	77.11
Xanho hydrophilus	0.91	2.47	0.75	6.35	78.88	*Eualus cranchii*	0.52	1.37	0.41	4.13	81.23
Achaeus gracilis	0.87	1.82	0.5	4.67	83.55	*Xanho hydrophilus*	0.52	1.22	0.36	3.67	84.9
Ebalia edwardsii	0.67	1.71	0.52	4.41	87.95	*Athanas nitescens*	0.62	1.13	0.36	3.41	88.31
Sirpus zariquieyi	0.59	1.4	0.49	3.61	91.56	*Hippolyte leptocerus*	0.41	0.86	0.37	2.59	90.90
Macroalgae	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	Macroalgae	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Hippolyte leptocerus	3.2	8.65	3	17.83	17.83	*Hippolyte leptocerus*	3	11.43	2.95	23.33	23.33
Pilumnus hirtellus	3.13	7.55	2.11	15.56	33.38	*Pirimela denticulata*	1.45	5.72	1.36	11.67	35
Sirpus zariquieyi	2.4	6.31	1.7	13.01	46.39	*Achaeus gracilis*	1.91	5.7	1.4	11.65	46.65
Achantonyx lunulatus	1.67	4.08	1.41	8.42	54.81	*Achantonyx lunulatus*	1.69	5.56	1.16	11.35	58
Pisa carinimana	1.62	3.95	1.66	8.15	62.96	*Pilumnus hirtellus*	2.39	5.07	0.95	10.36	68.36
Pirimela denticulata	1.22	2.79	1.05	5.74	68.7	*Sirpus zariquieyi*	1.75	4.49	1.13	9.17	77.53
Achaeus gracilis	1.52	2.41	0.8	4.96	73.66	*Athanas nitescens*	1.62	1.85	0.56	3.77	81.31
Calcinus tubularis	1.12	2.02	0.84	4.17	77.83	*Philocheras fasciatus*	1.02	1.85	0.62	3.77	85.08
Anapagurus hyndmanni	1.19	2	0.5	4.11	81.94	*Pisa carinimana*	0.72	1.56	0.6	3.18	88.26
Philocheras fasciatus	0.76	1.13	0.43	2.32	84.27	*Pisidia longimana*	1.01	1.37	0.51	2.79	91.05
Pisidia longimana	0.84	1.08	0.46	2.22	86.49						
Alpheus dentipes	0.96	1.05	0.53	2.17	88.65						
Athanas nitescens	1.33	1.02	0.49	2.11	90.76						

Table 3. Diversity indexes of the habitats studied in Punta Calaburras and Calahonda. Mean ± SE. H', Shannon-Wiener diversity index; J' evenness index; Range, number of species range; St, total species richness (gamma diversity); βW Whittaker's beta diversity. The proportion of species that are unique (species restricted to single site or habitat) is also included. Jaccard's index (another beta diversity measure); ITD, index of trophic diversity per sites and habitat. Cymo, *Cymodocea* nodosa; Posi, *Posidonia oceanica*; Algae, macroalgae; CH, Calahonda and PC, Punta Calaburras.

Habitat	Number of replicates	H'	J'	Range	St	ßw	Uniques (%)	Unique*Habitat (%)	Jackard (%)	ITD	ITD Habitat
Cymodocea nodosa Calahonda	19	1.57±0.11	0.9±0.01	1-12	26	3.08	6.25	14.58	53.965	0.65	0.68
Cymodocea nodosa P.Calaburras	20	1.74±0.12	0.82±0.04	3-17	29	2.25	6.25		49.151	0.64	
Posidonia oceanica Calahonda	19	1.68±0.09	0.86±0.02	3-16	29	2.87	2.08	12.5	51.13	0.72	0.74
Posidonia oceanica P. Calaburras	20	1.85±0.08	0.87±002	4-16	28	2.04	6.25		45.788	0.73	
Macroalgae Calahonda	20	1.96±0.07	0.84±0.010	5-19	30	1.764	0	10.47	39.824	0.75	0.72
Macroalgae P. Calaburras	20	2.10±0.07	0.84±0.02	4-17	31	1.366	6.25		38.924	0.72	
Total		1.70±0.50	0.87±0.09		48	4.87				0.74	

≠ Post-hoc differences (PAIRwise) of H' at P<0.05

CymoCH≠PosiPC;AlgaePC;AlgaeCH/CymoPC≠AlgaePC/PosiCH≠AlgaeCH / PosiPC≠AlgaePC

≠ Post-hoc differences (PAIRwise) of Jackard% at P<0.05

CymoCH≠AlgaeCH;PosiPC;AlgaePC / PosiCH≠AlgaeCH;AlgaePC / AlgaeCH≠CymoPC / CymoPC≠AlgaePC / PosiPC≠AlagePC

R_`jc 2, PERMutational ANOVA analyses based on Euclidean distances for testing differences in the S, species richness; N, abundance; J', evenness and H', Shannon-Wiener index between sites (Punta Calaburras and Calahonda), habitat (Macroalgae, *P oceanica*, *C. nodosa*) and sampling dates (summer, fall, winter, spring months). Df, Degree of Free; SS, Squares Sum; MS, Mean Square.

Species richness (S)	df	SS	MS	Pseudo-F	P
Sites	1	140.99	140.99	19.158	**< 0.001**
Date	3	279.41	93.138	12.656	**< 0.001**
Habitat	2	433.51	216.75	29.452	**< 0.001**
SixDa	3	90.075	30.025	40.798	**< 0.01**
SixHa	2	39.625	19.813	0.269	0.768
DaxHa	6	355.01	59.169	8.04	**< 0.001**
SixDaxHa	6	72.843	12.141	1.65	0.146
Residual	95	699.15	7.359		
Total	118	2078.9			
Abundance (N)	df	SS	MS	Pseudo-F	P
Sites	1	9279.9	9279.9	89.291	**< 0.01**
Date	3	37631	12544	12.069	**< 0.001**
Habitat	2	42695	21347	20.54	**< 0.001**
SixDa	3	7034.9	2345	22.563	0.083
SixHa	2	135.12	67.562	0.065	0.939
DaxHa	6	43756	7292.7	7.017	< 0.001
SixDaxHa	6	6740	1123.3	10.809	0.382
Residual	95	98733	1039.3		
Total	118	248450			
Evennes index (J')	df	SS	MS	Pseudo-F	P
Sites	1	0.017	0.017	2.101	0.145
Date	3	0.043	0.014	1.760	0.156
Habitat	2	0.011	0.005	0.666	0.522
SixDa	3	0.020	0.007	0.827	0.486
SixHa	2	0.055	0.028	3.352	**< 0.05**
DaxHa	6	0.133	0.022	2.693	**< 0.05**
SixDaxHa	6	0.063	0.010	1.265	0.274
Residual	93	0.766	0.008		
Total	116	1.104			
Shannon-Wiener index (H')	df	SS	MS	Pseudo-F	P
Sites	1	0.901	0.901	6.608	**< 0.05**
Date	3	1.528	0.509	3.736	**< 0.05**
Habitat	2	3.101	1.551	11.378	**< 0.001**
SixDa	3	0.713	0.238	1.743	0.165
SixHa	2	0.013	0.006	0.046	0.957
DaxHa	6	2.862	0.477	3.500	**<0.01**
SixDaxHa	6	1.040	0.173	1.272	0.275
Residual	93	12.674	0.136		
Total	116	22.435			

	Cymodocea nodosa	Posidonia oceanica	Halopteris scoparia
S	CH 6.37 ± 0.75	7.50 ± 0.81	10.85 ± 0.74
	PC 8.90 ± 0.85	9.20 ± 0.82	13.10 ± 0.92
	CH: Cymo≠Posi;Cymo=Algae; Posi=Algae	PC: Cymo=Posi;Cymo≠Algae; Posi≠Algae	
N	CH 16.53 ± 3.57	20.25 ± 3.11	56.55 ± 10.81
	PC 30.80 ± 5.84	39 ± 8.42	76.15 ± 16.57
	CH: Cymo=Posi;Cymo≠Algae; Posi≠Algae	PC: Cymo=Posi;Cymo≠Algae; Posi≠Algae	

Figure 4. Diagram of the structural design of each vegetal species studied. Values of S, species richness and N, abundance of the three habitats studied in PC, Punta Calaburras and CH, Calahonda. Cymo, *Cymodocea* nodosa; Posi, *Posidonia oceanica*; Algae; macroalgae. (≠) significant differences at P < 0.05 (PAIR-WISE test).

In relation to temporal trends, the highest values of N and S were found in *P oceanica* and macroalgae beds during the fall and winter months (Fig. 5). The results of multivariate multiple regression analyses show that the available surface of the habitats is the main variable that explains the temporal trend of the total decapod assemblages, explaining up to 15 % of the total variation. The combination of variables which is most strongly correlated to faunal assemblages is organic matter and habitat surface, which explain up to 23 % of the temporal variability (Table 5).

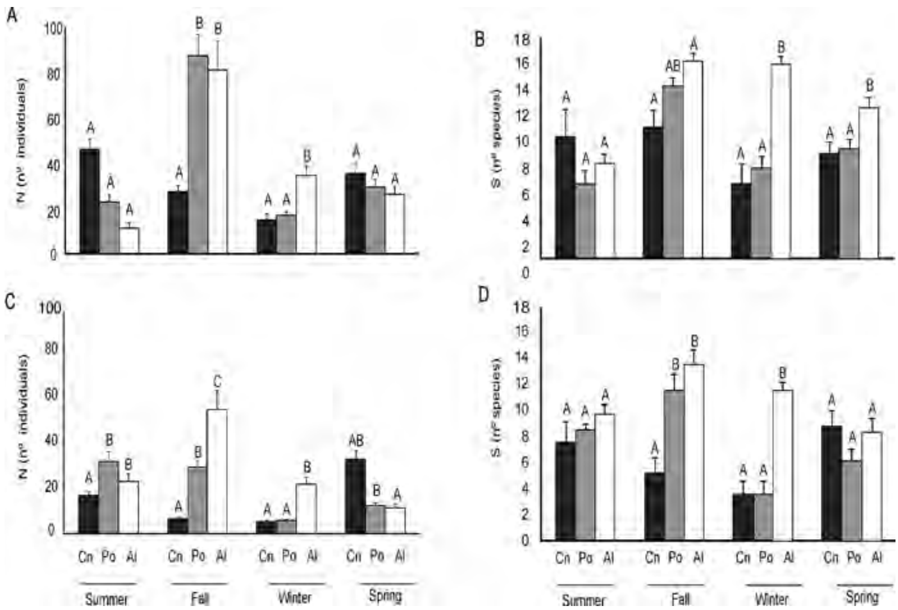

Figure 5. Temporal trends of the N, abundances and S, species richness of each habitat in P. Calaburras (A, B) and Calahonda (C ,D). Cn, *Cymodocea nodosa* (black bars); Po, *Posidonia oceanica* (grey bars) and Al, macroalgae (empty bars). Mean + SE. Letters above error bars display the results of PAR-WISE tests; different letters indicate significantly different means inside each date at P < 0.05.

Table 5. Results of multivariate multiple regression analyses (DISTLM) of environmental variables and surface of shoots and fronds (habitat area) with taxonomic composition of the total decapod assemblages associated with the three habitats studied.

Variable	Pseudo-F	P	Prop
1 Temperature	1.246	0.254	0.054
2 Chlorophyll *a*	0.706	0.702	0.031
3 Organic Matter	2.507	**< 0.01**	0.102
4 Habitat Area	4.413	**< 0.01**	0.153
R2 *best solution*		3&4	0.234
		All	0.339

Prop: proportion of variation explained by each variable.

These temporal differences were marked by changes both in species composition and in abundance of the dominant species in all three habitats analyzed (Table 6; Fig. 6). For example, *H. leptocerus* presented high abundances in macroalgae beds during the fall months (Table 6; Fig. 6A, B). These abundances correspond principally to adults, since juveniles are the dominant fraction in *P. oceanica* and *C. nodosa* during the summer and spring months (Fig. 6A, B). In the summer month *P. longimana* presented also recruitment events, principally in *P. oceanica* (Fig.6C, D). *Pilumnus hirtellus* always presented higher proportion of juveniles than adults along the year in all habitats. However, recruitment peaks were recorded during the fall month in *P. oceanica* and macoalgae beds (Fig. 6E, F). Likewise, *A. gracilis* showed high abundances in *P. oceanica* and macroalgae beds, mainly in the fall and winter months related to recruitment peaks. On the other hand, *A. nitescens* displayed maxima abundances in the fall month for macroalgae beds and *P. oceanica* in relation with an input of juveniles (Fig. 6G, H).Adults of *C. timidus* showed an inverse trend between seagrasses and macroalgae beds, displaying higher abundances in *P. oceanica* and *C. nodosa* during the summer and spring months and low between fall and winter months. During these last seasons the highest abundances of *C. timidus* were found in the macroalgae beds. *Anapagurus hyndmanni* presented their highest abundances during the spring months in the three habitats in relation with recruitment events (Fig. 6I, J).

Trophic analyses

Regarding trophic groups, decapod assemblages associated with the three vegetated habitats studied, were dominated by predators (20 species) such as *P. hirtellus*, *P. fasciatus*, *P. robusta* or *P. carinimana*, followed by scavengers (14 species) with species such as *S. zariquieyi*, *A. gracilis*, *C. tubularis* or *Achantonyx lunulatus* (Fig. 7). However some differences were detected, for example grazer species such as *Hippolyte spp* (4spp) were more important in *C. nodosa* of P. Calaburras, and deposit species such as *A. hyndmanni*, *C. timidus*, were more important in *C. nodosa* of Calahonda (Fig. 7A).

The relative abundance of the trophic groups was different between habitats and sites (Fig. 7B). In the *C. nodosa* meadows of Calahonda, predators were the

Table 6. PERMutational ANOVA analyses based on Euclidean distances for testing differences in species abundance between sites (Punta Calaburras and Calahonda), habitat (Macroalgae, *P oceanica*, *C. nodosa*) and sampling dates (summer, fall, winter, spring months). P-F, Pseudo-F; Df, Degree of Free; SS, Squares Sum; MS, Mean Square.

Source of variation		*Hippolyte leptocerus*				*Pisidia longimana*				*Athanas nistencens*				*Anapagurus hyndmanni*			
	df	SS	MS	P-F	P	SS	MS	P-F	P	SS	MS	P-F	P	SS	MS	P-F	P
Sites	1	0.437	0.437	0.480	0.496	0.361	0.361	0.409	0.522	15.973	15.973	9.650	**< 0.01**	18.753	18.753	30.377	**< 0.001**
Date	2	156.160	78.081	85.695	**< 0.001**	65.042	32.521	36.833	**< 0.001**	22.757	11.379	6.874	**< 0.01**	4.370	2.185	3.540	**< 0.01**
Habitat	3	23.766	7.922	8.695	< 0.001	21.989	7.330	8.302	**< 0.001**	101.770	33.924	20.495	**< 0.001**	24.591	8.197	13.278	**< 0.001**
SixDa	2	1.968	0.984	1.080	0.347	0.711	0.356	0.403	0.673	9.542	4.771	2.883	0.056	2.457	1.229	1.990	0.141
SixHa	3	1.564	0.521	0.572	0.635	4.284	1.428	1.617	0.196	3.803	1.268	0.766	0.525	17.979	5.993	9.708	**< 0.001**
DaxHa	6	49.940	8.323	9.135	**< 0.001**	10.150	1.692	1.916	0.085	44.034	7.339	4.434	**< 0.01**	5.973	0.995	1.613	0.147
SixDaxHa	6	3.661	0.610	0.670	0.676	8.760	1.460	1.654	0.135	14.002	2.334	1.410	0.217	2.931	0.488	0.791	0.592
Residual	94	85.648	0.911			82.995	0.883			155.590	1.655			58.029	0.617		
Total	117	328.370				194.210				372.670				136.860			
Source of variation		*Achaeus gracilis*				*Pilumnus hirtellus*				*Cestopagurus timidus*				*Achantonyx lunulatus*			
	df	SS	MS	P-F	P	SS	MS	P-F	P	SS	MS	P-F	P	SS	MS	P-F	P
Sites	1	0.809	0.809	1.131	0.293	7.615	7.615	5.424	**< 0.05**	11.735	11.735	21.351	**< 0.001**	0.372	0.372	1.010	0.318
Date	2	37.401	18.701	26.127	**< 0.001**	100.780	50.390	35.893	**< 0.001**	6.477	3.238	5.892	**< 0.01**	56.523	28.262	76.740	**< 0.001**
Habitat	3	14.047	4.682	6.542	< 0.01	50.383	16.794	11.963	**< 0.001**	9.627	3.209	5.839	**< 0.01**	8.881	2.960	8.038	**< 0.001**
SixDa	2	0.223	0.112	0.156	0.858	6.434	3.217	2.292	0.106	1.446	0.723	1.316	0.274	0.104	0.052	0.142	0.871
SixHa	3	1.121	0.374	0.522	0.668	7.287	2.429	1.730	0.170	11.580	3.860	7.023	**< 0.001**	0.526	0.175	0.476	0.692
DaxHa	6	16.228	2.705	3.779	**< 0.01**	53.209	8.868	6.317	**< 0.001**	17.758	2.960	5.385	**< 0.001**	8.301	1.384	3.757	**< 0.01**
SixDaxHa	6	5.695	0.949	1.326	0.254	16.891	2.815	2.005	0.074	11.560	1.927	3.505	**< 0.01**	3.131	0.522	1.417	0.214
Residual	94	67.281	0.716			131.970	1.404			51.663	0.550			34.618	0.368		
Total	117	144.420				378.720				122.280				111.720			

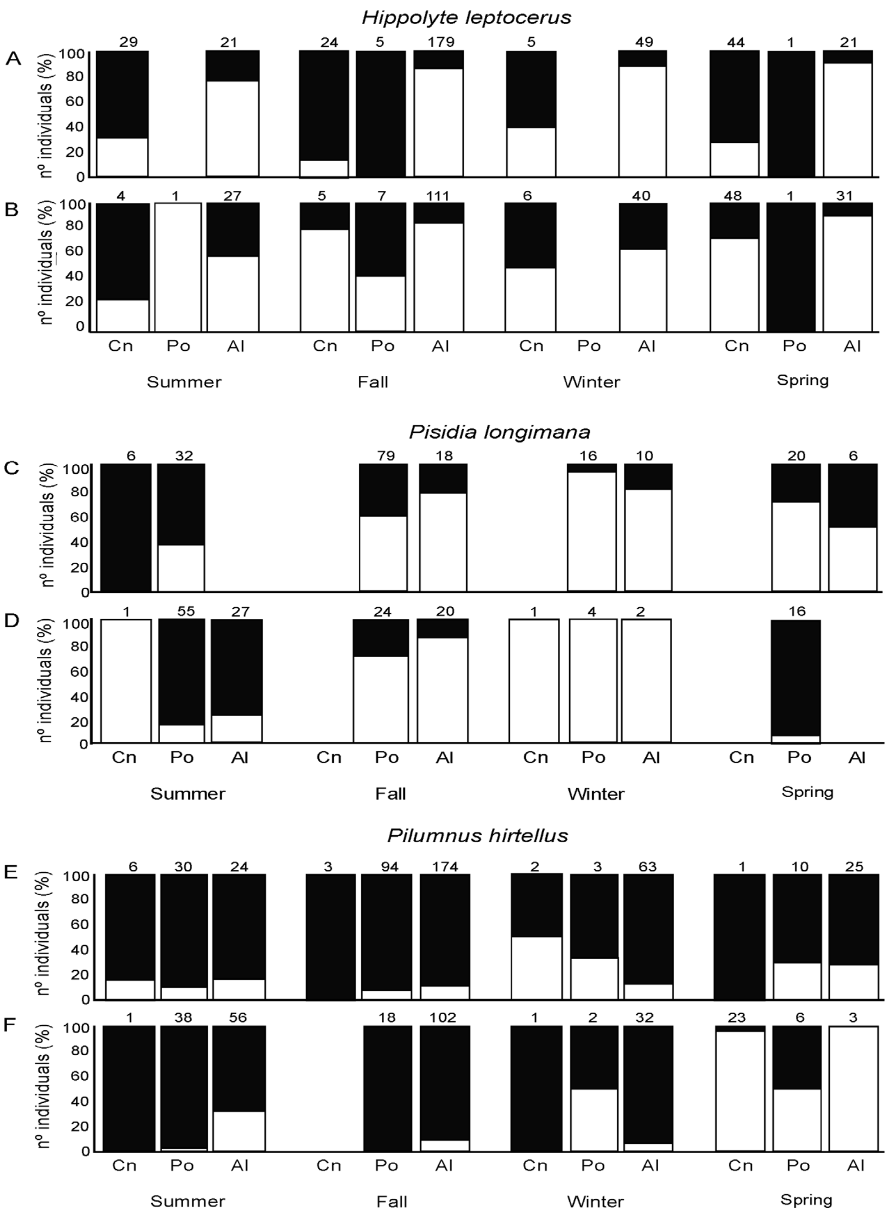

Figure 6. Percentage of adults (empty bars) and juveniles (black bars) along the sampling dates. Cn, *Cymodocea nodosa*; Po, *Posidonia oceanica* and Al, macroalgae. Numbers on bars indicates a total of individuals.

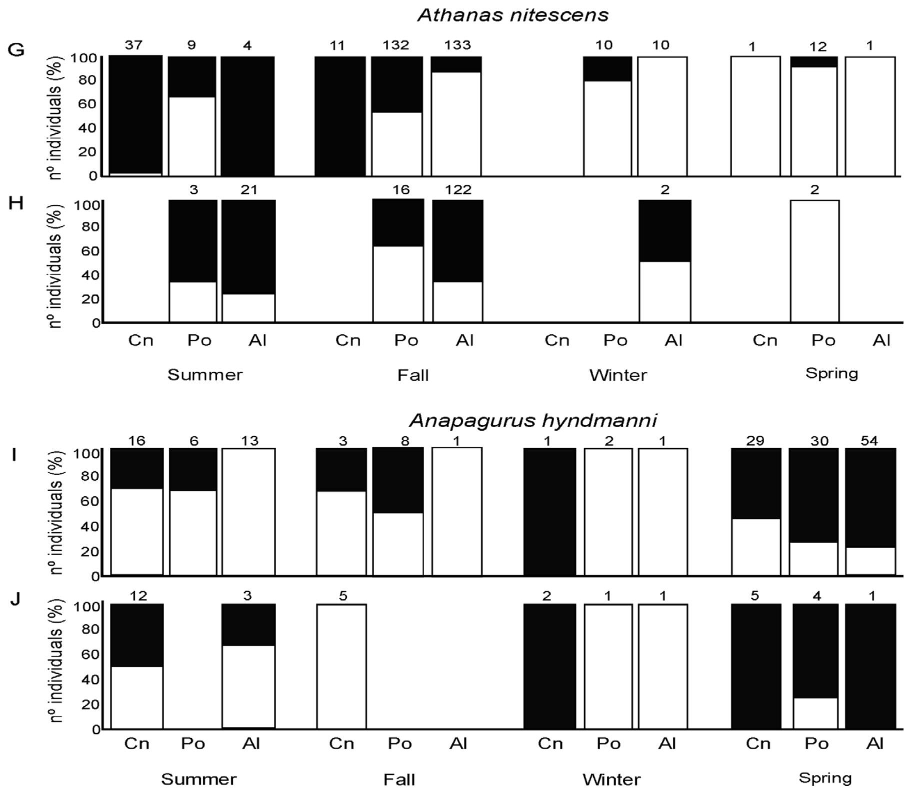

Figure 6, continuation. Percentage of adults (empty bars) and juveniles (black bars) along the sampling dates. Cn, *Cymodocea nodosa*; Po, *Posidonia oceanica* and Al, macroalgae. Numbers on bars indicates a total of individuals.

most important group, principally in relation to the abundances of *P. fasciatus* (55 ind.) and *P. edulis edulis* (28 ind.) (Fig. 7B). In the P. Calaburras meadows, scavenger species such as *C. tubularis*, *Clibanarius erythropus* or *A. hyndmanni* were the most abundant. Grazer species had higher percentages of individuals in *C. nodosa* than in macroalgae and *P. oceanica* meadows, principally due to *H. inermis* and *H. lepotocerus* which were always more abundant in P. Calaburras (66 and 92 ind. respectively) (Fig. 7B). Predators and scavengers were also the dominant groups in *P. oceanica* meadows of P. Calaburras and Calahonda respectively. However, filter feeders presented a higher percentage of individuals in *P. oceanica* than in the other two habitats, mainly due to the abundance of *P.*

longimana (99 ind. in Calahonda and 128 ind. in P. Calaburras). In addition, deposit feeders were more abundant in the meadows of P. Calaburras due to the high abundance of *A. nitescens* in this site. (Fig. 7B). The trophic guilds of the macroalgae beds were the most constant between sites. Predators, dominated by *P. hirtellus* (193 ind. and 286 ind. for Calahonda and P. Calaburras) and by *S. zariquieyi* (94 ind. and 142 ind. respectively) and scavengers with species such as *A. gracilis* (98 and 80 ind.), or *A. lunulatus* (75 ind. in both sites) were the most abundant groups in this habitat (Fig. 7B).

All decapod assemblages showed high values of trophic diversity, being *P. oceanica* and macroalgae beds the most diverse (Table 3).

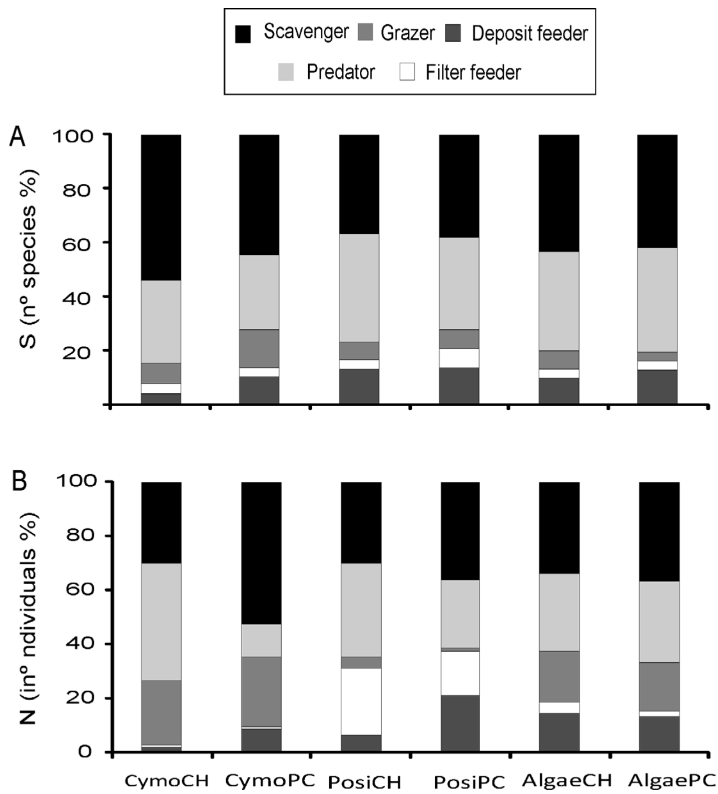

Figure 7. A, Species richness and B, abundances of decapods according to different trophic groups. Cymo, *Cymodocea* nodosa; Posi, *Posidonia oceanica*; Algae; macroalgae; CH, Calahonda and PC, Punta Calaburras.

Discussion

Habitat complexity, composition and connectivity between vegetative habitats

The seascape of the SCA "Calahonda", although is composed by fragmented seagrass meadows and macroalgal beds, present high values of species diversity and trophic diversity. It is known that an increasing of habitat complexity produces an increase of biodiversity (Kovalenko *et al.* 2012). At the patch scale, habitat complexity can increase species richness more effectively than the effects of patch sizes (Taniguchi *et al.* 2003; Matias *et al.* 2010). However, recent studies performed in this SCA, showed highly diverse assemblages of mollusc and decapods associated with small and medium sized patches of *P. oceanica* and *C. nodosa* (Mateo-Ramírez and García Raso 2012; Urra *et al.* 2013a; Mateo-Ramírez *et al.* 2015). The complex seascape of the SCA "Calahonda" generates numerous micro-habitats which can be used by many species. Each of the habitats studied have two well differentiated strata, for example, *C. nodosa* has the leaves and the sediment on which the meadow grows. The nature of the sediment has an influence on the species composition and trophic groups of the decapod assemblages that inhabit it (Mateo-Ramírez and García Raso 2012; present study). In the same way, *P. oceanica* has a leaf stratum and a rhizome stratum which support photophilous and sciaphilic assemblages respectively (Luque and Templado 2004; García Raso *et al.* 2006; Mateo-Ramírez *et al.* 2015). Finally, the macroalgal beds dominated by *H. scoparia* are differentiated between the algal frond with narrow interstitial space, and the underlying sediment stratum (chapter 5). This compartmentalization allows coexistence of organisms with a wider range of body sizes, increasing the number of pathways for resource utilization, e.g. larger, omnivorous predators can no longer access all habitat patches, thus giving competitive advantage to smaller intermediate predators, increasing community persistence and ecosystem stability (Kovalenko *et al.* 2012). The elevated dominance of predator species could be indicating also a high complexity of this seascape, since similar studies found a positive relationship between the number of predator species and habitat complexity (Burlakova *et al.* 2012; Kovalenko *et al.* 2012).

Each habitat studied presented a characteristic decapod assemblage. In good agreement with the findings of others authors in Mediterranean and Atlantic seagrass and macoalgal beds, species such as *S. zariquieyi*, *A. gracilis*, *P. carinimana* or *A. lunulatus* were found associated with algal bottoms, *P. fasciatus*, *H. leptocerus*, *H. inermis, P. edulis edulis* and *L. navigator* with *C. nodosa* and *P. longimana*, *A. nitescens* and *E. cranchii* with *P. oceanica* (Pérès and Picard 1964; Vadon 1981; Castelló *et al.* 1987; López de la Rosa and García Raso 1992; López de la Rosa *et al.* 2002; 2006; García Raso 1990a,b; Ballesteros and Pinedo 2004; García Raso *et al.* 2006; Mateo Ramírez and García Raso 2012; Daoulatli *et al.* 2013; Mateo Ramírez *et al.* 2015; chapter 5). On the other hand, other species shows a preference for a particular kind of substrate, which explains the differences between the two *C. nodosa* meadows studied. For example, *P. denticulata* prefers soft bottoms (Zariquiey 1968), therefore it is an important species in the *C. nodosa* meadows of Calahonda, and in macroalgal beds, associated to the sediment present under the algal cover. Conversely, species like *C. tubularis* are associated with hard substrates: this specie presented an elevated contribution in the *C. nodosa* meadows and algal bottoms of P. Calaburras as well as in *P. oceanica* meadows (García Raso 1990a). In the first case this is due to the more rocky bottoms present in P. Calaburras and in the second with the nature of *P. oceanica* rhizomes; which function as a hard substrate (rock) with a lot of cavities where the species can find refuge.

However these habitats shared a lot of species. For many species, and especially for decapods, their habitat is the sum of different partial habitats, each of them used for different functions such as reproduction, nursery, shelter or feeding (Amanieu *et al.*. 1981; García Raso 1990; García Raso *et al.* 2006; García Muñoz *et al.* 2008; Mateo Ramírez and García Raso 2012; Mateo Ramírez *et al.* 2015). The high values of evenness, low numbers of unique species, moderate values of beta diversity, and homogeneous values of trophic diversity presented in the decapod assemblages associated with the vegetated bottoms of the SCA"Calahonda" indicate that there is high connectivity between them.

The multivariable analysis suggested that the relative surface of the shoots and algal fronds which conform the mosaic seascape of the SCA"Calahonda" was the variable which explains most of the temporal trend of the decapod assemblages. Macroalgal beds seem to have an important role in the general context of the three habitats studied, principally during the fall and winter months when the habitat displayed the highest available surface. Many species such as *P. hirtellus*, *A. nitescens* or *A. gracilis* which recorded recruitment peaks during these seasons (Mateo-Ramírez and García Raso 2012; Mateo-Ramírez *et al.* 2015) seem to find shelter under the algal cover. Other species such as *H. leptocerus* or *C. timidus* that presented high abundance of adults, many of them ovigerous female, may be using macroalgal beds as spawning habitat during these months. On the other hand, during the summer and spring months, seagrasses, principally *P. oceanica*, played an important function. Species such as *H. leptocerus*, *A. hyndmanni* and *C. timidus* recorded highest abundances during these months when the seagrasses also displayed the highest development. However, the correlation between *H. inermis* and *H. leptocerus* with the phenology of *P. oceanica* and *C. nodosa* was previously reported by Zupo (1994) and Mateo Ramírez and García Raso (2012), respectively. The case of *A. hyndmanni* is remarkable because it is an abundant species in deeper detritic bottoms of the study area (García Munoz *et al.* 2008) and only presented high abundances in the shallow bottoms studied during spring, principally in P. Calaburras, which may indicate that this species uses shallow rocky bottoms covered by seagrasses and macroalgae as a nursery habitat. Probably the higher density of these species during summer and spring months, apart from recruitment events, could be related with the higher availability of food resources such as epiphytes or diatoms which have a higher leaf area to grow on (Zupo 1994; Mateo Ramírez and García Raso 2012).

Does fragmented habitats enhance capacity to resist impacts?

Ecosystem resilience reflects the ability of a system to undergo changes and yet retain the same controls on function and structure (Holling *et al.* 1995). It includes the degree to which the system is capable of reorganizing and building its capacity to adapt to changes (Gunderson 2000). The *P. oceanica* meadows of the SCA"Calahonda" have demonstrated a high resilience. Although the presence of dead rhizome indicates that, in past, it occupied a larger and more continuous area; nowadays these meadows present a good conservation status with high shoot densities and flowering events. (chapter 2; appendix 1). This persistence could be related to *Ecological memory* which refers to the composition and distribution of organisms and their interactions in space and time and includes the life-history experience with environmental fluctuations. Ecological memory is a part of spatial resilience and a critical component in the reorganization of ecosystems (Nyström and Folke 2001). According to Schaefer (2009) mature landscapes that are a mosaic of patches with a variety of successional stages has more ecological memory and in consequence a higher spatial resilience. This could apply also to a seascape such as the mosaic habitat of SCA "Calahonda" which resilience also allows a resilience of the associated communities. In this way, the matrix of habitat that forms this seascape plays an important role. Our results indicate that the macroalgae beds are very important for the decapod assemblages associated with seagrasses, because they provide shelter to a high number of individuals and species, principally during the fall months when *H. scoparia* was the habitat with a higher available surface of fronds. The lowest values of unique species and beta diversity reaffirm the sink function of macroalgae beds.

According to Nyström and Folke (2001), ecological memory consists in three basic and interacting parts. 1) biological and structural legacies that is, species, and patterns of persisting dead structures such as rhizomes of *P. oceanica*; 2) the mobile link (species that migrate passively or actively) and 3) support area for mobile link, in our case other patches of *P. oceanica* and *C. nodosa* and macroalgae beds. Each of these components consists of several functional groups interacting and a higher redundancy of species within each group relates with a higher resilience of the ecosystem (Nyström and Folke 2001). Our results indicate that the decapod assemblages associated with the three vegetative habitats studied displayed an elevated redundancy in their trophic groups, especially in scavenger and predator species. The latter are mainly important because predator species influence the structural and functional diversity of the rest of the assemblages, e.g. preying selectively on the organisms, especially the less mobile ones (Giere 1993; Danovaro *et al.* 1995, 2008).

Thus, the mosaic seascape of SCA "Calahonda" formed by *P. oceanica* and *C. nodosa* patches and macroalgae beds as well as their decapod assemblages associated seem to have a high resilience which is related with the resilience of this seascape and connectivity between habitats.

Conclusion

The seascape of the SCA "Calahonda" presents a high structural complexity and high diversity of decapods. Although each of the three habitats (*P. oceanica*, *C. nodosa* and macroalgal beds) studied presented a characteristic decapod assemblage, the high values of evenness and the redundancy in the trophic groups, principally predators and scavengers, shows a high connectivity between them. The species seem to make a different use of each habitat along the time studied, e.g. used seagrass patches like nursery or feeding habitat during the spring and summer months. On the other hand, macroalgal beds have an important role during the fall and winter moths when they provide shelter to a high number of individuals and species. Finally this mosaic seascape and its associated decapod assemblages seem to have a high resilience which could be related with its structural complexity, ecological memory and connectivity between habitats.

CAPÍTULO 7

Discusión General

Discusión general

En el mar de Alborán se pueden diferenciar tres subregiones (occidental, central y oriental), en función de las características oceanográficas y las especies que en ellas habitan y dominan. Así el sector oriental, se caracteriza por sus condiciones más oligotróficas, las cuales favorecen el desarrollo de extensas asociaciones de macrófitos de crecimiento lento como la fanerógama *Posidonia oceanica* y de macrolagas pertenecientes al grupo de *Cystoseira ericaefolia* (Pinedo *et al.* 2007; Bermejo *et al.* 2015). Por el contrario en el sector occidental, dentro del cual se encuentra la zona de estudio (Zona Especial de Conservación de Calahonda; ES6170030), es una zona mucho más productiva como consecuencia de los constantes afloramientos que se producen en ella, lo que favorece la dominancia de especies filtradoras como *Mytilus* spp. frente a los macrófitos antes citados (Rodríguez 1995; Bermejo *et al.* 2015). Estas características oceanográficas parece ser las responsables de la estructura fragmentada que presentan tanto las praderas de *Posidonia oceanica* como de *Cymodocea nodosa* dentro del ZEC "Calahonda". La turbidez de las aguas, como consecuencia de la alta productividad de esta zona, hace que el límite inferior de estas praderas sea muy somero (~ 5m), quedando más expuestas a la influencia del oleaje (capítulo 2; Fonseca *et al.* 1983; Turk and Vukovic 1998; Reyes *et al.* 1995; Ballesta *et al.* 2000). Probablemente, las hojas cortas, la alta densidad de haces, así como el hecho de que *P. oceanica* solo se encuentra sobre rocas, sean adaptaciones de estas especies para soportar el estrés hidrodinámico (capítulo 2; Marbá *et al.* 1996; de lo Santos *et al.* 2013). La dinámica temporal de ambas especies se corresponde con la de otras praderas mediterráneas y atlánticas. No obstante, ciertos parámetros fenológicos presentaron una variabilidad anual menor e intermedia para *P. oceanica* y *C. nodosa*, con respecto a otras praderas mediterráneas y atlánticas respectivamente; probablemente como consecuencia de los constantes afloramientos, los cuales generan unas condiciones ambientales más estables (capítulo 2: Bermejo *et al.* 2015).

Tanto las características oceanográficas del ZEC "Calahonda" como la estructura en parches de sus praderas y su situación biogeográfica, que incluye la ecorregión del mar de Alborán, la plataforma Atlántica Europea del sur y los Afloramientos saharauis (Spalding *et al.* 2007), tienen una influencia sobre las asociaciones de decápodos que las habitan.

En relación a las asociaciones de decápodos ligadas a las praderas de *C. nodosa*, encontramos como especie dominante a *Hippolyte leptocerus*, que es una especie típicamente asociadas a esta fanerógama (Ledoyer 1968, 1984; Scipione *et al.* 1996; Reed & Manning 2000; García Raso *et al.* 2006). No obstante la diferente naturaleza del sustrato sobre el que crecen las praderas en Punta Calaburras y Calahonda tiene un importante peso en la composición específica y en la estructura de cada una de las asociaciones. Así en el primer caso, donde la pradera está más expuesta al oleaje, el sustrato está formado por una gran cantidad de guijarros, apareciendo especies asociadas a fondos duros como *Clibanarius erythropus* o *Calcinus tubularis* (Gherardi 1990; García Raso 1990). Sin embargo en Calahonda, donde los parches están protegidos por grandes rocas, dominan las arenas finas bien calibradas, con especies como *Philocheras fasciatus* o *Sycciona carinata* contribuyendo de forma significativa en la caracterización de estas asociaciones (Pérès y Picard 1964; García Raso *et al.* 2006; López de la Rosa *et al.* 2006).

Estas asociaciones presentaron una correlación positiva con la fenología de la planta, mostrando un alto número de individuos y especies durante el periodo de máximo desarrollo de la planta (mayo-julio). No obstante otros factores externos como la temperatura o picos de reclutamiento de ciertas especies también tuvieron un peso importante en los altos valores de abundancia y riqueza específica (capítulo 3). Contratiamente, no se encontró ninguna relación entre el tamaño de parche y estos dos índices, lo que corrobora lo mencionado por otros autores: pequeños fragmentos de una pradera pueden seguir manteniendo unas asociaciones de decápodos bien estructuradas y diversas (capítulo 3; Bell *et al.* 2001; Hirst y Attrill 2008). Posiblemente esto sea consecuencia de un aumento del "efecto borde", pues al disminuir el tamaño de del parche, la zona de transición entre la fanerógama y los hábitats circundantes es mayor, lo que favorece el flujo de especies (Tanner *et al.* 2005).

En el caso de las praderas de *P. oceanica*, las asociaciones de decápodos estuvieron dominadas por especies principalmente ligadas al rizoma de esta fanerógama, como: *Pisidia longimana*, *Pilumnus hirtellus*, *Athanas nitescens*, *C. tubularis* y *Cestopagurus timidus*. Este estrato presenta una gran cantidad de recovecos los cuales crean un ambiente esciáfilo, donde adultos y juveniles de diferentes especies pueden encontrar refugio en él (capítulo 4). La última especie aunque habita en el rizoma de *P. oceanica*, también tiene un peso importante en el estrato de las hojas, a las cuales parece ser que se desplaza para alimentarse (capítulo 4; Borg y Schembri 2000; Belci 2013; Daoulatli *et al.* 2014). Aunque la composición faunística es similar a la de otras praderas del Mediterráneo hay algunas singularidades, como por ejemplo la presencia de especies atlánticas, como *Anapagurus hyndmanni*, o la ausencia de especies mediterráneas, como *Pagurus chevreuxi* que si están presentes en praderas del Mediterráneo Central y Occidental (Templado 1984; García Raso 1990a; Borg y Schembri 2000; García Muñoz *et al.* 2008).

Contrariamente a lo que sucede en las praderas de *C. nodosa*, los índices ecológicos presentaron un bajo número de correlaciones con la fenología de *P. oceanica*. Esto puede deberse a que la mayoría de las especies no están estrictamente relacionadas con el ciclo estacional de las hojas (capítulo 4). Muchas de ellas presentaron picos de reclutamiento durante el otoño, coincidiendo con los máximos valores de abundancia, riqueza específica y diversidad de Shannon-Wiener, así como con valores mínimos en la longitud de las hojas. Dinámicas similares se han encontrado en otras asociaciones de decápodos ligadas a otras praderas a lo largo del Mediterráneo (capítulo 4; García Raso 1990a; Scipione *et al.* 1996; Borg y Schembri 2000). Por lo tanto, parece ser que la dinámica temporal de las asociaciones de decápodos ligadas a las praderas de *P. oceanica* del ZEC “Calahonda”, están principalmente relacionados con los eventos de reclutamiento de las especies dominantes así como con la temperatura del agua, ya que se encontró una correlación entre la abundancia de juveniles y esta.

Los fondos de macroalgas fotófilas, dominadas por *Halopteris scoparia*, son los realmente dominantes en la zona de estudio, presentando un porcentaje de cobertura de entre el 62-74% (capítulo 5). Las asociaciones de decápodos que habitan estos fondos están compuestas principalmente por especies comunes en hábitats fotófilos poco profundos, como: *H. leptocerus*, *P. hirtellus*, *A. nitescens*, *Sirpus zariquieyi*, *Achaeus gracilis* y *Acanthonyx lunulatus* (Pérès y Picard 1964; Vadon 1981; Castelló *et al.* 1987; López de la Rosa y García Raso, 1992).

Desde un punto de vista trófico la mayoría de las especies analizadas fueron carroñeras o predadoras. No obstante, los grupos tróficos presentaron una relativa distribución homogénea, en referencia a los valores de abundancia, durante gran parte del año de estudio (capitulo 5). Esto, junto con los altos valores de equirrepartición y de riqueza específica (35 especies) parecen estar indicando que las asociaciones estudiadas presentan un buen estado de salud (Bremner *et al.* 2006; Ngai y Srivastaba 2006; capítulo 5), y que por lo tanto podrían ser tomadas como referencia a la hora de establecer el "Buen Estado Ambiental" de las aguas costeras de Europa, como establece la Directiva de la Estrategia Marina (MSFD, 2008/56/EC).

La comunidad de macroalgas presentó una estacionalidad bien definida, con un desarrollo máximo (biomasa y volumen) en julio y abril. Sin embargo, las asociaciones de decápodos mostraron un desacoplamiento con la dinámica del alga, ya que fueron más diversas y abundantes durante los meses que esta tuvo un menor desarrollo (noviembre y enero). Otros autores obtuvieron resultados similares tanto para decápodos como para el resto de la fauna fital (capítulo 5; Edgar 1983b, Taylor 1998; Langtry y Jacoby 2006). Esto parece indicar que las asociaciones de decápodos que habitan los fondos de macroalgas, incluida la del ZEC "Calahonda", no tienen porque estar directamente relacionadas con la dinámica de la comunidad de macroalgas. Probablemente el ciclo de vida de las especies (eventos de reclutamiento), el equilibrio ente la complejidad del hábitat, la disponibilidad de espacio y/o de alimento (Orth 1992; Edgar y Robertson 1992), así como la presencia de depredadores pueden estar detrás de este desacoplamiento (capitulo 5).

Aunque cada una de las asociaciones de decápodos presentó una composición de especies característica, es cierto que comparten un gran número de especies (capítulo 6). La estructura en mosaico de los fondos del ZEC ”Calahonda” permite un flujo de especies entre los diferentes hábitats, generando unas asociaciones de decápodos ricas y bien estructuradas (Mateo-Ramírez y García Raso 2012; Mateo Ramírez *et al.* 2015, capítulo 6). Además la presencia de diferentes estratos o microhábitat (hojas-frondes y rizomas-sedimento), genera una compartimentalización que permite la coexistencia de organismos con diferentes rangos de tamaños y edades, incrementando el número de vías para la utilización de los recursos, lo que incrementa la persistencia de la comunidad y la estabilidad del ecosistema (Kovalenko *et al.* 2012).

Los altos valores de equirrepartición, los bajos o medios valores de especies únicas y de beta-diversidad, en comparación con otros grupos como los moluscos (Urra 2012b), así como la similitud en cuanto a diversidad trófica encontrada en los hábitas vegetales presentes en el ZEC “Calahonda”, muestran una homogeneidad en cuanto a la composición y estructura de las asociaciones, fruto de la conectividad existente entre todos ellos (capítulo 6). Esta conectividad está relacionada con el diferente uso que hacen las especies de cada uno de los hábitas a lo largo del año. Así, por ejemplo *H. leptocerus* o *C. timidus*, que son especies principalmente ligadas a fanerógamas (Zupo 1994; García Raso 1990a; Belci *et al.* 2012; Mateo-Ramírez y García Raso 2012), presentan altas abundancias en ellas durante los meses de primavera y verano, cuando estas tienen un mayor desarrollo. Mientras que en los meses de otoño e invierno, es en los fondos de macroalgas donde se encuentran la mayores abundancias. En el primer caso están relacionadas con picos de reclutamiento y con la mayor disponibilidad de alimento (perifiton y epífitos) presente sobre las hojas. Mientras que en el segundo caso, podrían estar relacionadas con la protección que les ofrece las macroalgas durante esos meses, cuando las fanerógamas presentan una superficie menor (capítulos 5, 6). Por lo tanto los fondos de macroalgas juegan un papel importante para la estabilidad de las asociaciones de decápodos, actuando como sumidero de especies e individuos durante los meses del año que ofrecen una cobertura mayor que la del resto de macrófitos.

La complejidad estructural de los fondos del ZEC ”Calahonda”, formado por diferentes parches de fanerógamas (*P. oceanica*; *C. nodosa*) y macroalgas, así como los diferentes estratos o microhábitats que presentan y la conectividad entre ellos, permite la existencia de unas asociaciones de decápodos diversas, bien estructuradas y con una alta resiliencia.

CAPÍTULO 8

Conclusiones/Conclusions

Conclusiones

Las conclusiones que se han extraído en esta Tesis Doctoral son:

1 Las praderas de *Posidonia oceanica* y *Cymodocea nodosa* del ZEC ”Calahonda” presentaron dinámicas estacionales específicas para cada especie. Estas dinámicas fueron similares a las de otras praderas del área Atlánto-Mediterránea.

2 La baja transparencia de las aguas del ZEC “Calahonda”, unido a su alta productividad, hace que las praderas de *P. oceanica* y *C. nodosa* presenten una localización más somera, lo que las expone a un oleaje casi continuo. Esto junto con la presencia de aguas frías atlánticas y de afloramientos casi constantes, tienen una influencia tanto sobre los parámetros fenológicos (altas densidades de haces, hojas cortas y una baja variabilidad anual de ciertos parámetros) como en la configuración fragmentada de estas praderas. Aún así, mantiene un buen estado de salud, con episodios de floración.

3 Las asociaciones de decápodos ligadas a los rodales de *C. nodosa* presentaron una estructura similar tanto en Punta Calaburras como en Calahonda. No obstante, los diferentes sustratos sobre los que crecen cada una de las praderas, así como los hábitats colindantes, tuvieron una importante influencia sobre la composición faunística de cada asociación. No se encontró relación alguna entre la abundancia y la riqueza de especies con el tamaño del parche. Por otro lado, la dinámica estacional de estas asociaciones estuvo relacionada con la dinámica de la planta y con los reclutamientos de las especies dominantes.

4 Las especies dominantes de decápodos asociadas a las praderas fragmentadas de *P. oceanica*, fueron especies ligadas principalmente al rizoma, el cual es frecuentemente utilizado como zona de cría - guardería. Estas asociaciones presentaron una dinámica estacional relacionada principalmente con la temperatura del agua y con eventos de reclutamiento de las especies dominantes. Aunque estas praderas presentan una estructura fragmentada, la presencia de un rizoma bien desarrollado y la integración de estos parches dentro de un fondo mixto, minimizan el efecto de la fragmentación sobre las

asociaciones de decápodos ligadas a estas praderas, manteniendo altos valores de diversidad y equirrepartición.

5 Las asociaciones de decápodos ligadas a los fondos de macroalgas estuvieron compuestas por especies principalmente asociadas a ambientes fotófilos superficiales. Cada uno de los estratos (alga y sedimento) presentaron diferencias en cuanto a la composición faunística y estructura de sus respectivas asociaciones, encontrándose valores de abundancia y riqueza específica mayores en el sedimento. No obstante, ambas asociaciones fueron similares en relación a los grupos tróficos que las representaban. Estas asociaciones mostraron un desacoplamiento con la dinámica de la comunidad de macroalgas; indicando que los patrones estaciónales de las asociaciones de decápodos no tiene porque estar necesariamente ligados con el de las algas.

6 Los fondos de macroalgas juegan un papel muy importante dentro del mosaico de hábitats que conforman los fondos del ZEC ”Calahonda”, dando cobijo durante los meses de otoño e invierno a un gran número de individuos y especies provenientes de los hábitats colindantes.

7 Aunque cada uno de los hábitats presentan unas asociaciones de decápodos características, estás comparten un gran número de especies, como consecuencia del flujo de especies entre hábitats y el diferente uso (alimentación, guardería, desove, protección) que hacen de cada uno de ellos durante el año.

8 Depredadores y carroñeros fueron los grupos tróficos más importantes. La alta dominancia de los primeros junto con los altos valores de riqueza específica (48 especies) y de equirrepartición, como consecuencia de la conectividad entre hábitats, indican que los fondos del ZEC ”Calahonda” presentan una alta complejidad estructural y un buen estado de salud. Por ello podrían ser utilizados como una zona de referencia del “Buen Estado Ambiental” de las aguas costeras, para la Directiva de la Estrategia Marina europea (MSFD, 2008/56/EC).

Conclusions

The conclusions obtained in this Doctoral thesis are:

1 The *Posidonia oceanica* and *Cymodocea nodosa* meadows of the SAC "Calahonda" showed specific seasonal dynamics for each species. These dynamics were similar to that of others seagrass meadows of the Atlanto-Mediterranean area.

2 The low transparency of the water of SAC "Calahonda", linked to their high productivity, makes that the *P. oceanica* and *C. nodosa* meadows present are shallower than usual, which exposes them to almost continuous wave action. This along with the presence of cold Atlantic waters and quasi-persistent upwellings, has an influence both on phenological parameters (high shoot density, short leaves and low annual variability of certain parameters) and on the fragmented configuration of these meadows. Still, these meadows have a healthy status with flowering episodes.

3 The decapod assemblages associated with *C. nodosa* patches showed a similar structure in both Punta Calaburras and Calahonda. However, the different substrates on which the meadows grow, as well as the neighbouring habitats; had an important influence on the faunistic composition of each assemblage. Abundance and species richness did not show a relation with patch area. On the other hand, the seasonal dynamics of these assemblages were related with the seagrass dynamics and with the recruitment of the dominant species.

4 The dominant decapod species associated with *P. oceanica* meadows were linked to the rhizome stratum, which is often used as nursery. The seasonal dynamics of this assemblage was mainly related to water temperature and recruitment events of the dominant species. Although these meadows are fragmented, the presence of a well developed rhizome and the integration of these patches into a mixed botttoms minimized the impact of the fragmentation on the decapod assemblages, which maintained high values of diversity and evenness.

5 The decapod assemblages associated with macroalgae bottoms were composed by species principally associated with shallow photophilous environments. Each stratum (algae and sediment) showed differences in relation to the faunistic composition and structure of their assemblages, with higher values of abundance and species richness in the sediment. However, both assemblages were similar in terms of trophic groups represented. These assemblages displayed a decoupling with the dynamic of the macroalgal community, which indicates that temporal patterns of decapods assemblages are not necessarily linked with the algal dynamics.

6 The macroalgae beds play an important role inside the mosaic of habitat that form the bottoms of SCA "Calahonda", since they offer shelter to a high number of individuals and species belonging to neighbouring habitat during fall and winter months.

7 Although each of the habitats has a characteristic decapod assemblage, these assemblages share a large number of species, as result of the flow of species between habitats and the different uses (food, nursery, spawning, protection) that species make of each of them along year.

8 Predators and scavengers were the most important trophic groups. The high dominance of the former, as well as the high species richness (48 species) and evenness, due to connectivity between habitats, indicate that the bottoms of SAC "Calahonda" have a high structural complexity and good state of health. Therefore they could be used as a reference area of "Good Environmental Status" of coastal waters, for the Directive of the European Marine Strategy (MSFD, 2008/56 / EC).

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APÉNDICES

Artículos publicados relacionados con la presente memoria de tesis doctoral

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Short communication

First records of *Posidonia oceanica* flowering at its westernmost distributional limit (Málaga, Alboran Sea)

Javier Urra, Ángel Mateo, Pablo Marina, José L. Rueda* and J. Enrique García Raso

Departamento de Biología Animal, Universidad de Málaga, Campus de Teatinos s/n, 29071 Málaga, Spain, e-mail: biologiamarina@uma.es

* Corresponding author

Abstract

Flowering events of *Posidonia oceanica* (over two consecutive years) are reported for the first time in meadows located close to its westernmost distribution limit (Málaga, southern Spain). Shoots with inflorescences were found in fragmented meadows (patches between 1–130 m^2) at a mean depth of 2.5 m. In March 2009, flowering was only observed in Calaburras (0–28 inflorescences m^{-2}) and not in Calahonda. In November 2009, massive flowering events were observed in both Calaburras (4–144 inflorescences m^{-2}) and Calahonda (8–184 inflorescences m^{-2}). On this occasion, developing fruits were also observed. From 2003 to 2009, mean annual water temperatures increased in this area, with maximum values in late summer and autumn of 2007 and 2008, and these warm waters may have induced the massive flowering events. Flowering in these *P. oceanica* meadows located close to the Atlantic Ocean may imply favourable environmental conditions and a good health status, which should be considered in improving conservational strategies for these meadows.

Keywords: Alboran; flowering; Mediterranean; *Posidonia oceanica*.