Changes in seagrass polychaete assemblages after invasion by *Caulerpa racemosa* var. *cylindracea* (Chlorophyta: Caulerpales): community structure, trophic guilds and taxonomic distinctness

ANTONIO BOX [1], DANIEL MARTIN [2] and SALUD DEUDERO [1]

[1] Laboratorio de Biología Marina, Universidad de las Islas Baleares (UIB), Ctra Valldemossa Km 7.5, 07122 Mallorca, Islas Baleares. Spain. E-mail: toni.box@uib.es
[2] Centre d'Estudis Avançats de Blanes (CEAB), Consejo Superior de Investigaciones Científicas (CSIC), Carrer d'accés a la cala Sant Francesc 14, 17300 Blanes, Girona, Catalunya, Spain.

SUMMARY: A two-year study focusing on the associated polychaete assemblages revealed that the degradation of the *Posidonia oceanica* seagrass meadows, together with the colonisation of rhizomes by invasive *Caulerpa racemosa* in the Balearic Islands, have produced important changes in the ecosystem functioning, and have therefore affected the benthic faunal communities. The highest abundance and number of species occurred in *C. racemosa* from August to December. The species composition of the polychaete assemblage in *C. racemosa* is similar to that of *P. oceanica* but abundances of shared species differ between *Caulerpa* and *Posidonia*. Abundance, number of species and diversity were positively correlated with *C. racemosa* biomass. The spatial complexity provided by the network of *C. racemosa* fronds and stolons seemed to combine with that of the remaining seagrass mat to support a well developed polychaete assemblage. Although invaded meadows harboured significantly modified polychaete assemblages when compared with living *P. oceanica* meadows, the main impacts seem to be non-harmful (i.e. increased abundance and number of species) and mainly affect their seasonal patterns, which is a direct consequence of the corresponding biomass seasonality of *C. racemosa*.

Keywords: *Posidonia oceanica, Caulerpa racemosa,* Polychaeta, species diversity, trophic guilds, taxonomic distinctness, introduced species, Mediterranean.

RESUMEN: CAMBIOS EN LA COMUNIDAD DE POLIQUETOS ASOCIADOS A LA INVASIÓN DE *CAULERPA RACEMOSA* VAR. *CYLINDRACEA* (CHLOROPHYTA: CAULERPALES): ESTRUCTURA DE COMUNIDAD, ESTRATEGIAS TRÓFICAS Y DISTINCIÓN TAXONÓMICA. – En las Islas Baleares, la degradación de las praderas de *Posidonia oceanica* junto con la colonización de los restos de rizoma por *Caulerpa racemosa* conllevan importantes cambios en el funcionamiento del ecosistema, los cuales afectan especialmente a las comunidades de invertebrados. El presente estudio muestra que, a lo largo de dos años, las mayores abundancias y diversidades de poliquetos en rizomas invadidos por *C. racemosa* se han encontrado en agosto y septiembre. La composición específica en dichos rizomas invadidos es muy similar a la propia de las praderas de *P. oceanica*, si bien algunas de especies coincidentes difieren claramente en abundancia. La biomasa de *C. racemosa* muestra una correlación positiva con la abundancia, número de especies y diversidad de poliquetos. La complejidad espacial asociada a los frondes y estolones de *C. racemosa* se combinan con los restos de rizoma, generando un hábitat capaz de mantener una comunidad de poliquetos bien estructurada. Sin embargo, a pesar de las diferencias encontradas entre las respectivas comunidades de poliquetos, el impacto de la invasión parece no ser negativo (e.g. aumentan la abundancia de algunas especies y la diversidad específica) y afecta principalmente a su pauta estacional, siendo consecuencia directa de la estacionalidad del ciclo vegetativo de *C. racemosa*.

Palabras clave: *Posidonia oceanica, Caulerpa racemosa,* poliquetos, diversidad de especies, estrategias tróficas, distinción taxonómica, especies introducidas, Mediterráneo.

INTRODUCTION

The presence of alien species in the Mediterranean, currently about 662 (Gollasch, 2006), is an increasing problem that still needs to be studied to clarify its consequences. Invasive species are considered a serious threat to natural ecosystems (Mack *et al.*, 2000), as well as one of the major drivers of biodiversity loss (Sakai *et al.*, 2001). Invaders could be highly competitive and their interaction with native species may cause a global decrease in biodiversity (Bax *et al.*, 2003). Negative effects of invasive species on the local biota have been recently reported, especially for macroalgal communities (Piazzi and Cinelli, 2000; Meinesz *et al.*, 2001; Balata *et al.*, 2004; Meinesz, 2004). In the Mediterranean Sea, 84 introduced macrophytes have been reported to date (Boudouresque and Verlaque, 2002), and two of them belong to the green algae genus *Caulerpa*: *C. taxifolia* and *C. racemosa* (Ceccherelli and Sechi, 2002). Their presence induces drastic changes in faunistic composition and abundance of the affected systems, and thus they have become a serious problem in the western Mediterranean (Pandolfo and Chemello, 1995; Bellan-Santini *et al.*, 1996; Argyrou *et al.*, 1999; Buia *et al.*, 2001). *Caulerpa* species produce anti-herbivorous secondary metabolites (Amade and Lemee, 1998; Jung *et al.*, 2002), the main one being caulerpenyne, which negatively affect grazing organisms (Boudouresque *et al.*, 1996; Parent-Massin *et al.*, 1996; Amade and Lemee, 1998; Pesando *et al.*, 1998; Sureda *et al.*, 2006; Sureda *et al.*, 2008) and chemically change the environmental conditions of the habitat (Amade and Lemee, 1998; Sureda *et al.*, 2006).

Posidonia oceanica (L.) Delile meadows are among the most important Mediterranean ecosystems, with an estimated extension of between 2.5 and 5.5 million hectares (Buia *et al.*, 2001). *Posidonia* beds are characterised by having a foliar canopy and a root-rhizome layer, and this structure strongly influences the associated fauna. Even dead (i.e. after losing the foliar structures) *Posidonia* beds still support a rich macrofauna in terms of the number of species and diversity (Borg *et al.*, 2006). However, the particular characteristics of *P. oceanica* meadows make them highly sensitive to competitors, such as the invasive species of the genus *Caulerpa* (Ceccherelli *et al.*, 2002), which leads to a large decrease in shoot density (Molenaar *et al.*, 2009).

Local species being replaced by invaders is nowadays a worldwide phenomenon (Montefalcone *et al.*, 2007), and the Mediterranean *Posidonia* meadows are no exception. Our study focuses particularly on the invading *Caulerpa racemosa*, which has already been reported in 12 Mediterranean countries: Italy, Greece, Albania, Cyprus, France, Turkey, Malta, Spain, Tunisia, Croatia, Algeria and Libya (Klein and Verlaque, 2008). *Caulerpa racemosa* spreads in sheltered and exposed areas, colonising all kinds of substrates from 0 to 70 m depth (Argyrou *et al.*, 1999; Piazzi and Cinelli, 1999; Zuljevic *et al.*, 2003). Introduced species often become more invasive in impacted ecosystems. For instance, the brown alga *Sargassum muticum* substitutes *Zostera marina* in damaged beds of the French Atlantic coast (Givernaud *et al.*, 1991), and the green alga *Enteromorpha radiata*, which spreads in deteriorated mixed beds of *Zostera noltii* and *Z. marina* on the coasts of Great Britain (Der Hartog, 1994). In particular, regressive *Posidonia oceanica* meadows are more prone to being invaded by *C. racemosa* var. *cylindracea* than healthy ones (Ceccherelli *et al.*, 2000).

The invertebrate assemblages, including those associated with seagrass beds, may also be affected by the presence of invasive species, which may either enhance (Argyrou *et al.*, 1999; Antoniadou and Chintiroglou, 2007) or decrease (Galil and Zenetos, 2002; Zenetos *et al.*, 2003; Streftaris and Zenetos, 2006) diversity. Among benthic invertebrates, the polychaetes are considered to be excellent descriptors of the structure of faunal assemblages, including those in association with seagrasses (Gambi *et al.*, 1998; Brito *et al.*, 2005). Although *Posidonia oceanica* beds lack exclusive polychaete species, the structure of their assemblages is very characteristic and tends to differ among the leaf stratum and the rhizomes and "matte". Polychaete abundance and diversity tend to be lower in the leaf stratum whilst, in general, there are no dominant species in the matte, where there is a higher richness of relatively less abundant species (Gambi *et al.*, 1995).

In turn, diversity and abundance of soft-bottom polychaetes have been reported to increase in the presence of *Caulerpa racemosa* (Argyrou *et al.*, 1999). Therefore, our study aimed to describe the structure (both in terms of species and trophic diversity) and seasonal patterns of the polychaete assemblages associated with dead *Posidonia* meadows invaded by *C. racemosa*, and to compare them with those associated with living *Posidonia* meadows.

MATERIALS AND METHODS

Study area

The study was carried out at Mallorca Island (Balearic Islands, Western Mediterranean), where *Caulerpa racemosa* var. *cylindracea* has overgrown dead *Posidonia* meadows forming patches surrounded by bare sand and living seagrass meadows. Samples of *C. racemosa* var. *cylindracea* (hereafter called *Caulerpa* mats) were collected in the proximities of Portals Vells, southwest Mallorca (N39°28.321'/E2°31.320', 5 to 8 m deep). For the comparisons, samples of living *Posidonia oceanica* (hereafter called *Posidonia* meadows) were collected in the proximities of Cala D'Or, southeast Mallorca (N39°22.164'/E3°13.887' and N39°22.028', 5 to 8 m deep), which was not invaded by *Caulerpa*.

Sampling

From February 2004 to February 2005, *Caulerpa* mats and *Posidonia* meadows were sampled bimonthly in three sampling areas per meadow (each separated by 100 m). According to Sanchez-Moyano *et al.* (2001), we used a 20 x 20 cm frame inserted 5 cm into the sediment to collect samples, which were then placed in a plastic mesh bag (0.5 mm pore size), fixed in a 4% formaldehyde-seawater solution and preserved in 70% ethanol prior to being sorted in the laboratory. *Caulerpa racemosa* was sorted and dry-weighted (24 h at 60°C), as well as the rhizomes, roots and sheaths of the dead *Posidonia* mat. For the living *Posidonia* meadows, leaves were also sorted and dry-weighted (24 h at 60°C). All biomasses were expressed as percentages.

The polychaete specimens were sorted under a stereomicroscope, identified at the lowest possible taxonomic level, and grouped into trophic guilds: carnivorous, herbivorous, omnivorous, deposit feeders and filter feeders (according to Fauchald and Jumars, 1979; Gambi *et al.*, 1995; Martin *et al.*, 2000; Antoniadou and Chintiroglou, 2006).

In parallel, three additional corers per meadow and sampling date (inserted 5 cm into the sediment) were collected to analyse the granulometry of the surrounding sediments. The sediment was dried for 24 h (after being treated with H_2O_2 for 24 h) and the grain size fractions were estimated following the scale established by Wentworth (1972).

Data analysis

Five different categories of substrata were considered for analysing the polychaete assemblages associated with *Caulerpa* mats: *Caulerpa* networks and *Posidonia* rhizomes, sheaths, dead leaves and roots. Living leaves were also included in the case of *Posidonia* meadows. The observed differences in the polychaete assemblages were tested by two-way analysis of variance (two-way ANOVA) including meadow type and time as factors. Principal component analysis (PCA) was used to analyse the influence of the structural parameters (i.e. *Posidonia* fractions and *Caulerpa* network biomasses, grain size fractions) on sample seasonal trends.

For statistical purposes (except for TAXDTEST, PRIMER 6.0), the species of Paraonidae, Capitellidae, Sabellidae and Maldanidae were pooled at family level due to the misidentification of several individuals. A species was considered as dominant when its abundance was more that 1% of the total.

The structure of the polychaete assemblages was analysed using PRIMER 6.0 software. A cluster analysis was performed on a resemblance matrix (Bray-Curtis index) based on a fourth-root transformed abundance per sample matrix (replicate samples pooled by meadow and sampling date). No reduction in species was applied. The multidimensional scaling (MDS) routine was used for a two-dimensional representation. The differences between cluster groups were assessed by the ANOSIM routine. The species responsible for the observed differences were identified by means of the SIMPER routine. The DIVERSE routine was used to calculate the density, number of species per sample, diversity and evenness for the obtained cluster groups.

The relationships between *C. racemosa* biomass, polychaete assemblage descriptors and trophic groups were assessed by pairwise Pearson correlations. Changes in trophic guilds were tested by one-way ANOVA (meadow as factor). The seasonal trends of the assemblages were analysed by two-way ANOVA (meadow and time as factors) based on the polychaete species with higher resemblance contributions (SIMPER routine).

In order to compare the species composition and seasonality of the polychaete assemblages inhabiting *Posidonia* meadows and *Caulerpa* mats, we used the taxonomic distinctness (AvTD, Δ^+) and its variation (VarTD Δ^+) obtained with the TAXDTEST routine of the PRIMER 6.0 software (Clarke and Warwick,

2001). This allowed us to calculate the average taxo-nomic relatedness for samples or treatments, as well as compare this to the range of values calculated by repeatedly taking random samples of the same size (as number of species) from an appropriate master list (Clarke and Warwick, 2001; Warwick and Light, 2002; Smith, 2008). In our case, this list was based on the exhaustive inventory of *Posidonia* invertebrates from the Balearic Islands (18 stations, 0 to 35 m deep) made by Ballesteros *et al.* (1987), complemented with the species from Cala d'Or meadows to avoid species omissions (Smith, 2008). The master list finally included 140 polychaete spe-cies. TAXDTEST was also applied to data pooled as *Posidonia* meadow, and low- and high- *Caulerpa* biomass periods (samples with low/null (less than 5 g/m² DW) or high biomass respectively).

RESULTS

Sample characterisation

Sheaths were the dominant fraction both in *Caul-erpa* mats and *Posidonia* meadows, followed by roots and living leaves respectively (Fig. 1a).

Fine sand was the dominant grain size both in *Caulerpa* mats and *Posidonia* meadows, but in *Caul-erpa* mats there was a higher contribution of large grain size fractions (Fig. 1b). The maximum algal biomasses in *Caulerpa* mats occurred from August to December, and were highly influenced by the warm conditions in the last months of 2004 (Fig. 2).

In the PCA (Fig. 3), the first axis (eigenvalue 10.4, 74.1% of the explained variance) was most-ly related to *Caulerpa* (eigenvector 0.607) and biomasses of living Posidonia leaves (eigenvector -0.602). The second axis (eigenvalue 1.94, 13.8% of the explained variance) was mostly related to the living *Posidonia* leaf (eigenvector 0.683) and sheath (eigenvector -0.584) biomasses. *Caulerpa* mats and *Posidonia* meadows are clearly sepa-rated along the first axis (positive and negative sectors respectively), and there is a distinction be-tween little and highly invaded sampling periods (the later with more positive eigenvalues). In turn, the second axis distinguishes the *Posidonia* mead-ows with low leaf biomass in autumn and winter (positive eigenvalues) from those with high leaf biomass in spring and summer (negative eigenval-ues) (Fig. 3).
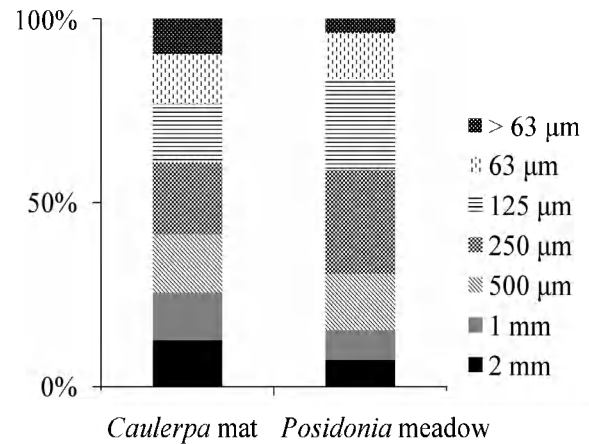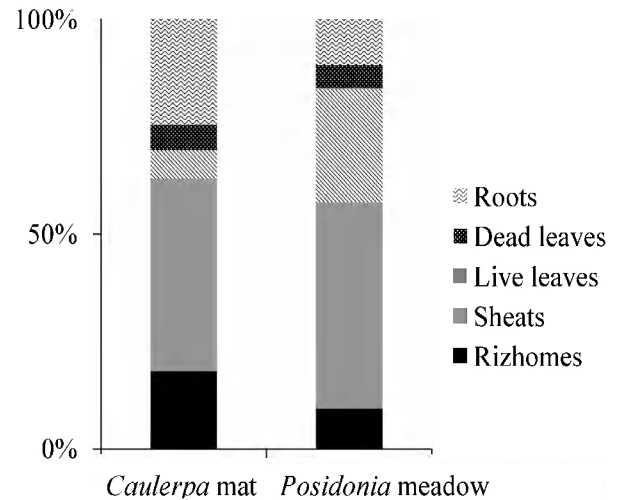

FIG. 1. – *Caulerpa* mat and *Posidonia* meadow annual means of: A, Biomass of the Posidonia fractions (percentage in weight); B, granulometry (Wentworth scale).
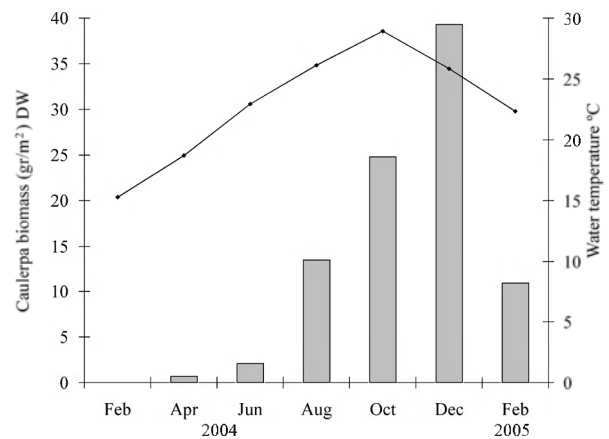

FIG. 2. – Seasonal patterns in *Caulerpa racemosa* biomass and water temperature.
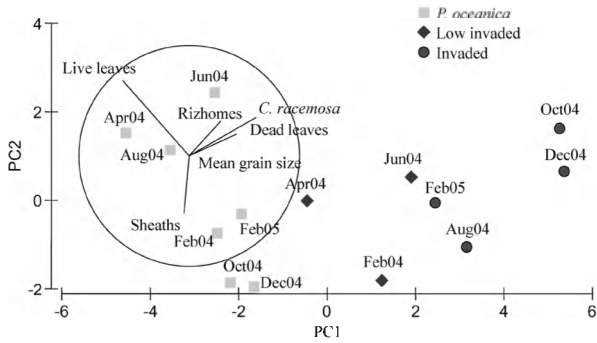
FIG. 3. – Principal component analysis of the seasonal *Posidonia* meadows and *Caulerpa* mats related to the measured structural parameters. Low *Caulerpa* biomass samples are those with biomasses lower than 5 g/m² DW. Variable vector is in the circle on the left of the plot.

Faunistic composition

1863 polychaetes from 43 taxa were identified in *Caulerpa* mats, with Nereididae and Sigalionidae being the most abundant throughout the year. The species richness was high and 25 species were dominant through the year. *Neanthes agulhana, Pelogenia arenosa, Polyophthalmus pictus* and *Lumbrineris latreilli* were the most abundant (Table 1). *Neanthes agulhana* was present in all sampled periods, while *P. arenosa, P. pictus, Arabella iricolor* and *Sthenelais boa* showed frequencies over 70% (Table 1). The internal similarity of the assemblages from *Caulerpa* mats was 32.57% and *N. agulhana, P. arenosa, P. pictus*, Capitellidae, *A. iricolor, L. latreilli, S. boa, Harmothoe spinifera, Pholoe inornata, Pontogenia chrysocoma* and *Syllis garciai* accounted for more than 80%.

1475 polychaetes from 44 taxa were identified in *Posidonia* meadows, with Eunicidae and Nereididae being the most abundant throughout the year. The species richness was high, with 29 dominant species. *Nematonereis hebes, Aponuphis bilineata* and *Neanthes agulhana* were the most abundant (Table 2). *Lumbrineris gracilis, A. bilineata* and *N. agulhana* showed frequencies over 70% (Table 2). The internal similarity of the assemblages from *Posidonia* meadows was 25.01%, and Capitellidae, *A. bilineata, L. gracilis, N. agulhana, N. hebes*, Maldanidae, *Polyophthalmus pictus, Eunice vittata, Lumbrineris latreilli* and Terebellidae were the taxa that made the highest contributions (≥ 80%) and accounted for more than 80%.

The structure of the polychaete assemblages showed seasonal differences (Fig. 4). At 60% similarity, Group 1 includes all *Caulerpa* mats

with higher algal biomass (i.e. August, October and December). Then, at 40% similarity, all remaining *Caulerpa* mats (except February 2005) joined Group 1 successively, while the February 2005 mat was clustered with the October 2004 *Posidonia* meadow (Group 2). Group 3 included late winter, spring and early summer *Posidonia* meadows from 2004, while both the 2004 and 2005 winter *Posidonia* meadows formed Group 4. Finally, the single summer *Posidonia* meadow remained isolated in Group 5.

There were significant differences among all cluster groups (ANOSIM, global $R = 0.769$, number of used permutations = 20000, significance level = 0.1%) (Table 3). The dissimilarity between Group 1 and all other groups were mainly caused by *Polyophthalmus pictus, Neanthes agulhana, Lumbrineris latreilli* and Capitellidae (Table 3).

In *Caulerpa* mats, the maximum densities and highest number of species occurred in October, while the maximum diversities and evenness corresponded to August/December and August respectively. Ac-
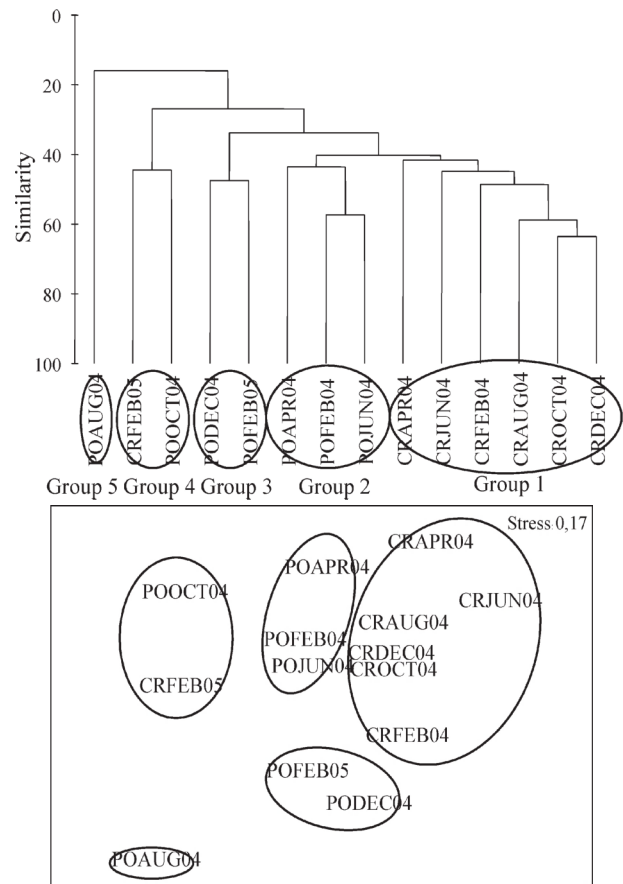

FIG. 4. – Cluster and MDS representation of polychaete assemblages from *Caulerpa* mats and *Posidonia* meadows.

TABLE 1. – Seasonal changes in the *Caulerpa racemosa* polychaete abundances expressed as individuals/m² ±standard error sampled in Cala d'Or. Frequency = n° samples with presence/total n° seasonal samples. Dominance = total number of individuals of any given species/total polychaete abundance (expressed as a percentage).

Species	CRFEB04	CRAPR04	CRJUN04	CRAUG04	CROCT04	CRDEC04	CRFEB05	Mean	Frequency	Dominance
Neanthes agulhana (Day, 1963)	17±8.33	25±14.44	25±2401	8±8.33	58±8.33	25±14.44	8±8.33	167	100.00	8.94
Pelogenia arenosa (Delle Chiaje, 1830)	17±8.33	8±8.33	8±8.33	17±8.33	8±8.33	42±41.01	42±30.04	133	85.71	7.16
Polyophthalmus pictus (Dujardin, 1839)	25±14.44	33±8.33	42±22.05	17±8.33	8±8.33	8±8.33		133	85.71	7.16
Capitellidae Grube, 1862		17±16.33		25±16.66	8±8.33	58±22	17±16.67	125	71.43	6.71
Lumbrineris latreilli Audouin & Milne Edwards, 1834	42±41.67		17±25.00	8±8.33	33±16.67	33±8.33	8±8.33	117	57.14	6.26
Harmothoe spinifera (Ehlers, 1864)				25±25	42±22.05	25±25.00		92	57.14	4.92
Arabella iricolor (Montagu, 1804)	8±8.33	17±16.67	8±8.33	8±8.33	8±8.33	17±8.33		83	85.71	4.45
Sthenelais boa (Johnston, 1833)	17±8.33		8±8.33	8±8.33	25±14.43	17±16.67		75	71.43	4.45
Syllis garciai (Campoy, 1982)	8±8.33	42±41.66		17±16.67		8±8.33		75	57.14	4.03
Pontogenia chrysocoma (Baird, 1865)		25±25.00		17±16.67	17±8.33			75	57.14	4.03
Pherusa eruca (Claparède, 1869)		17±8.33		33				67	42.86	3.58
Pholoe inornata Johnston, 1839		17±16.67						58	57.14	3.13
Platynereis dumerilii (Audouin & Milne Edwards, 1833)	8±8.33		17±16.67	17±8.33	25±14.44	17±16.67		58	57.14	3.13
Lumbrineris gracilis Ehlers, 1868					42±30.05		8±8.33	50	42.86	2.68
Maldanidae Malmgren, 1867					17±16.67			50	28.57	2.68
Lagis koreni Malmgren, 1866	17±16.67		17±8.33		8±8.33	17±16.67		50	42.86	2.68
Aponuphis bilineata (Baird, 1870)	8±8.33	8±8.33		8±8.33		8±8.33		42	57.14	2.24
Neanthes caudata (Delle Chiaje, 1827)		17±16.67			17±16.67	17±16.67		42	57.14	2.24
Sphaerosyllis pirifera Claparède, 1868		25±14.44	25±25.00			8±8.33		42	42.86	2.24
Spirobranchus polytrema (Philippi, 1844)			17±16.67			17±8.33		42	42.86	2.24
Haplosyllis spongicola (Grube, 1855)					8±8.33			25	14.29	1.34
Malmgreniella lunulata (Delle Chiaje, 1830)	8±8.33			8±8.33		17±8.33		25	28.57	1.34
Amphictene auricoma (O.F. Müller, 1776)					17±16.67	8±8.33		25	28.57	1.34
Paraonidae Cerruti, 1909	8±8.33	8±8.33			8±8.33	8±8.33		25	28.57	1.34
Eunice vittata (Delle Chiaje, 1828)					8±8.33	8±8.33		24	42.86	1.31
Syllis variegata Grube, 1860	17±16.67		17±16.67					17	42.86	0.89
Vermiliopsis striaticeps (Grube, 1862)			17±16.67					17	14.29	0.89
Harmothoe sp. Kinberg, 1856		8±8.33	8±8.33					17	14.29	0.89
Glycera sp. Savigny, 1818				8±8.33	8±8.33		8±8.33	17	28.57	0.89
Parapionosyllis brevicirra Day, 1954						17±16.67		17	28.57	0.89
Fimbriosthenelais minor (Pruvot & Racovitza, 1895)						8±8.33		17	14.29	0.89
Chrysopetalum debile (Grube, 1855)	8±8.33	8±8.33				8±8.33		16	28.57	0.86
Terebellidae Malmgren, 1865				8±8.33				16	28.57	0.86
Syllis gerlachi (Hartmann-Schröder, 1960)		8±8.33						8	14.29	0.45
Syllis westheidei San Martín, 1984		8±8.33						8	14.29	0.45
Schistomeringos rudolphii (delle Chiaje, 1828)		8±8.33						8	14.29	0.45
Sabellidae Fauchald, 1977							8±8.33	8	14.29	0.45
Lumbrineriopsis paradoxa (Saint-Joseph, 1888)							8±8.33	8	14.29	0.45
Sphaerosyllis austriaca Banse, 1959							8±8.33	8	14.29	0.45
Lysidice ninetta Audouin & Milne-Edwards, 1833				8±8.33				8	14.29	0.45
Nematonereis hebes Verrill, 1900	8±8.33							8	14.29	0.45
Exogone dispar (Webster, 1879)	8±8.33							8	14.29	0.45
Exogone rostrata Naville, 1933		8±8.33						8	14.29	0.43
Cirratulidae Ryckholt, 1851						8±8.33		8	14.29	0.43

TABLE 2. – Seasonal changes in the *Posidonia oceanica* polychaete abundances expressed as individuals/m^2 ±standard error sampled in Cala d'Or. Frequency = n° samples with presence/total n° seasonal samples. Dominance = total number of individuals of any given species/total polychaete abundance (expressed as a percentage).

	POFEB04	POAPR04	POJUN04	POAUG04	POOCT04	PODEC04	POFEB05	Total number	Frequency	Dominance
Capitellidae Grube, 1862	50±14.44	33±22.05	33±22.05		17±16.67			141	71.43	9.68
Nematonereis hebes Verrill, 1900	33±22.05		33±8.33			42±8.33	8±8.33	116	57.14	7.96
Aponuphis bilineata (Baird, 1870)	17±8.33	8±8.33			33±8.33	17±8.33	25±14.45	100	71.43	6.86
Maldanidae Malmgren, 1867	17±8.33	42±30.04				8±8.33	25±8.33	92	57.14	6.31
Neanthes agulhana (Day, 1963)	25±14.43	25±14.43	25±14.43	8±8.33	8±8.33			91	71.43	6.25
Lysidice ninetta Audouin & Milne-Edwards, 1833	58±30.05		8±8.33		17±8.33			83	42.86	5.70
Paraonidae Cerruti, 1909	8±8.33					50±50	25±14.43	83	57.14	5.70
Eunice vittata (Delle Chiaje, 1828)	42±8.33	8±8.33	17±8.33			8±8.33		75	42.86	5.15
Terebellidae Malmgren, 1865	33±22.05		17±16.67					67	57.14	4.60
Lumbrineris gracilis Ehlers, 1868	17±16.67	17±8.33	8±8.33		17±16.67	8±8.33	8±8.33	66	85.71	4.53
Polyophthalmus pictus (Dujardin, 1839)	17±8.33	8±8.33	8±8.33				25±14.44	58	57.14	3.98
Lumbrineris latreilli Audouin & Milne Edwards, 1834	25±14.44				17±8.33	17±16.67		42	42.86	2.88
Platynereis dumerilii (Audouin & Milne Edwards, 1833)						8±8.33		41	42.86	2.81
Hydroides niger Zibrowius, 1971			17±16.67			17±16.67		34	28.57	2.33
Sabellidae Fauchald, 1977	8±8.33						25±14.44	33	28.57	2.26
Pterocirrus macroceros (Grube, 1860)				25±14.44				25	14.29	1.72
Syllis variegata Grube, 1860	17±8.33		8±8.33					25	28.57	1.72
Arabella iricolor (Montagu, 1804)	8±8.33	17±8.33						25	28.57	1.72
Cirratulidae Ryckholt, 1851	8±8.33		8±8.33		8±8.33			24	42.86	1.65
Chrysopetalum debile (Grube, 1855)			8±8.33	8±8.33			8±8.33	24	42.86	1.65
Spirobranchus polytrema (Philippi, 1844)			17±16.67					17	14.29	1.17
Phyllodoce mucosa Oersted, 1843		17±16.67						17	14.29	1.17
Pelogenia arenosa (Delle Chiaje, 1830)						17±16.67		17	14.29	1.17
Neanthes caudata (Delle Chiaje, 1827)			17±16.67					17	14.29	1.17
Syllis gerlachi (Hartmann-Schröder, 1960)			8±8.33					17	14.29	1.17
Sthenelais boa (Johnston, 1833)			8±8.33			8±8.33		16	28.57	1.10
Pherusa eruca (Claparède, 1869)	8±8.33	8±8.33						16	28.57	1.10
Glycera sp. Savigny, 1818		8±8.33			8±8.33			16	28.57	1.10
Haplosyllis spongicola (Grube, 1855)		8±8.33						16	28.57	1.10
Sphaerosyllis pirifera Claparède, 1868							8±8.33	16	28.57	1.10
Lagis koreni Malmgren, 1866	8±8.33							8	14.29	0.55
Syllis garciai (Campoy, 1982)							8±8.33	8	14.29	0.55
Schistomeringos rudolphii (delle Chiaje, 1828)						8±8.33		8	14.29	0.55
Poniogenia chrysocoma (Baird, 1865)			8±8.33					8	14.29	0.55
Lumbrineriopsis paradoxa (Saint-Joseph, 1888)			8±8.33					8	14.29	0.55
Lumbrineris impatiens Claparède, 1868	8±8.33							8	14.29	0.55
Harmothoe sp. Kinberg, 1856		8±8.33						8	14.29	0.55
Eunice harassii Audouin & Milne Edwards, 1834	8±8.33							8	14.29	0.00

TABLE 3. – ANOSIM and SIMPER analysis between groups established after Cluster analysis.

| GROUPS	ANOSIM R statistic	Sig level%	SIMPER Average Dissimilarity	Species most contributing to dissimilarity (up to 60%)
Group 1-2	0.432	1.2	67.81	Capitellidae, *N. hebes*, Maldanidae, *L. ninetta, L. latreilli, E. vittata, L. gracilis, P. arenosa,* Terebellidae, *P. pictus, H. spinifera, S. garciai. P. dumerilii, S. boa, P. eruca*
Group 1-3	0.646	3.6	76.35	Paraonidae, *N. agulhana, N. hebes, L. latreilli, P. pictus,* Capitellidae, *A. bilineata,H. spinifera, A. iricolor,* Maldanidae, Sabellidae, *P. arenosa, L. gracilis, S. garciai.*
Group 1-4	1	3.6	81.21	*P. pictus, P. arenosa, L. latreilli, A. bilineata, N. agulhana,* Capitellidae, *A. iricolor, H. spinifera, S. garciai, S. boa, P. chrysocoma, P. eruca, P. inornata, L. gracilis.*
Group 1-5	1	14.3	92.50	*P. macroceros, P. pictus, L. latreilli, N. agulhana,* Capitellidae, *P. arenosa, A. iricolor, H. spinifera, S. garciai, S. boa, L. gracilis, P. chrysocoma.*
Group 2-3	0.667	10	73.74	Paraonidae, Capitellidae, *N. agulhana, N. hebes, L. ninetta,* Maldanidae, *E. vittata,* Terebellidae, *A. bilineata,* Sabellidae, *P. pictus.*
Group 2-4	0.917	10	75.54	Maldanidae, *P. arenosa,* Capitellidae, *N. hebes, E. vittata, L. ninetta, N. agulhana, A. bilineata,* Terebellidae, *L. latreilli, P. pictus.*
Group 2-5	1	25	88.23	Capitellidae, *P. macroceros,* Maldanidae, *N. hebes E. vittata, N. agulhana, L. ninetta,* Terebellidae, *P. pictus*
Group 3-4	1	33.3	77.56	Paraonidae, *N. hebes, P. arenosa,* Maldanidae, *A. bilineata, P. pictus,* Sabellidae, Capitellidae.
Group 3-5	1	33.3	89.63	Paraonidae, *P. macroceros, N. hebes, A. bilineata,* Maldanidae, *P. pictus.*
Group 4-5	1	33.3	85.24	*P. macroceros, P. arenosa,* Capitellidae, *A. bilineata, L. latreilli*
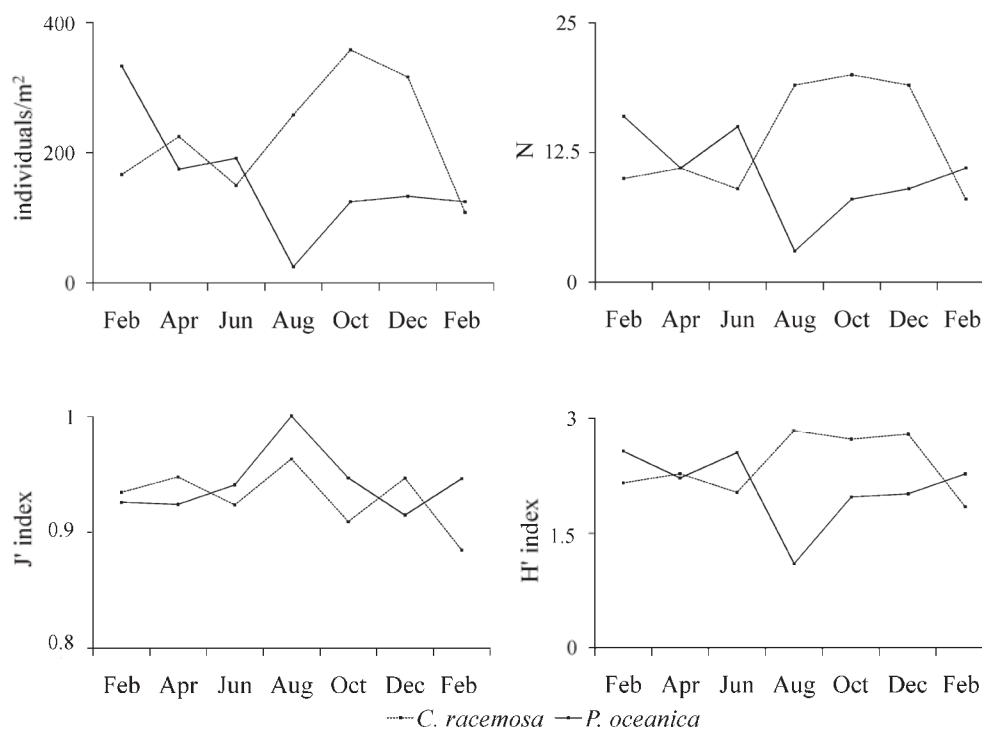
FIG. 5. – Total Polychaeta abundances per square meter and number of species (N), Jaccard index (J) and Shannon-Wiener index (H') in *Posidonia* meadows and *Caulerpa* mats with seasonal changes (February 04 to February 05).

TABLE 4. – Significance of the differences in abundance between habitats (*Caulerpa* mats and *Posidonia* meadows) and sampling dates tested by two-way ANOVA. Species selected according to the SIMPER percentages of similarity. ***: $p<0.001$,**: $p<0.01$; *: $p<0.05$.

Source of variation	Df	Arabella iricolor MS	Paraonidae MS	Capitellidae MS	Cirratulidae MS	Chrysopetalum debile MS	Eunice vittata MS
Habitat	1	2,526	0.256	0.436	2.411*	0.023	0.471
Date	9	0.895	0.774	0.995	0.441	0.222	1.208
Habitat*Date	9	0.589	0.723	4.776***	0.677	0.556	1.838
Residual	40	0.846	0.640	1.081	0.553	0.500	0.806

		Harmothoe spinifera	Aponuphis bilineata	Lumbrineris gracilis	Lumbrineris latreilli	Lysidice ninetta	Maldanidae
Habitat	1	2.824*	0.688	0.433	7.428**	3.775*	2.113
Date	9	0.566	1.507	0.792	2.653**	0.725	1.068
Habitat*Date	9	0.875	2.036	2.772**	1.231	1.012	1.882*
Residual	40	0.678	1.128	0.854	1.547	0.573	0.822

		Neanthes agulhana	Nematonereis hebes	Lagis koreni	Pelogenia arenosa	Pholoe inornata	Platynereis dumerilii
Habitat	1	7.546*	5.179**	2.083*	12.198**	6.117**	0.055
Date	9	1.973	1.729**	0.380	0.767	0.361	0.926
Habitat*Date	9	1.566	2.198***	0.601	0.694	0.361	1.348
Residual	40	1.232	0.457	0.500	0.990	0.687	0.739

		Polyophthalmus pictus	Pontogenia chrysocoma	Sthenelais boa	Syllis garciai	Terebellidae	
Habitat	1	6.300*	0.333	3.390	5.851***	4.169*	
Date	9	1.738	1.496*	0.816*	2.375**	1.394	
Habitat*Date	9	1.419	1.892*	0.626	1.183**	0.742	
Residual	40	1.006	0.652	0.720	0.649	0.990	

cordingly, *Caulerpa* biomass was positively correlated with density, number of species and diversity ($r = 0.839$, $r = 0.907$ and $r = 0.868$; $p = 0.05$). Conversely, in *Posidonia* meadows, maximum densities, number of species and diversity occurred in February 2004, while maximum evenness was observed in August (Fig. 5). No significant correlations were found between any polychaete descriptors and the biomass of the different *Posidonia* fractions in *Caulerpa* mats and *Posidonia* meadows.

The analysis of the main species in *Caulerpa* mats and *Posidonia* meadows shows that there were significant differences in the abundances of several polychaete species, such as *Harmothoe spinifera, Lumbrineris latreilli, Lysidice ninetta, Neanthes agulhana, Pelogenia arenosa*, among others (Table 4)

Trophic guilds

No significant seasonal differences for the different trophic guilds were found either in *Caulerpa* mats or *Posidonia* meadows, the main guilds being (according to their abundance) deposit feeders, carnivores and omnivores. In both types of samples, herbivores and filter feeders were the least abundant guilds.
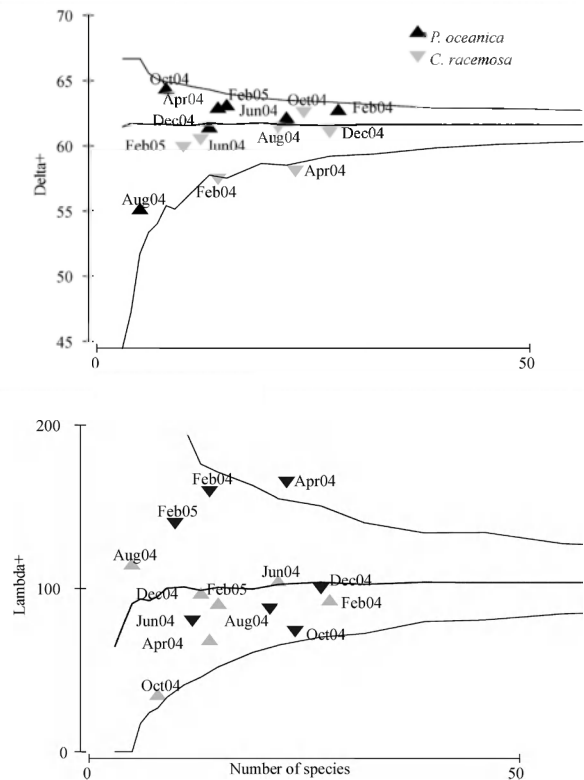

FIG. 6. – Confidence funnels (mean and 95% probability intervals) of the average taxonomic distinctness (Δ^+) and its variation (Λ^+) generated from the master list showing the range of values displayed by the seasonal *Caulerpa* mats and *Posidonia* meadows
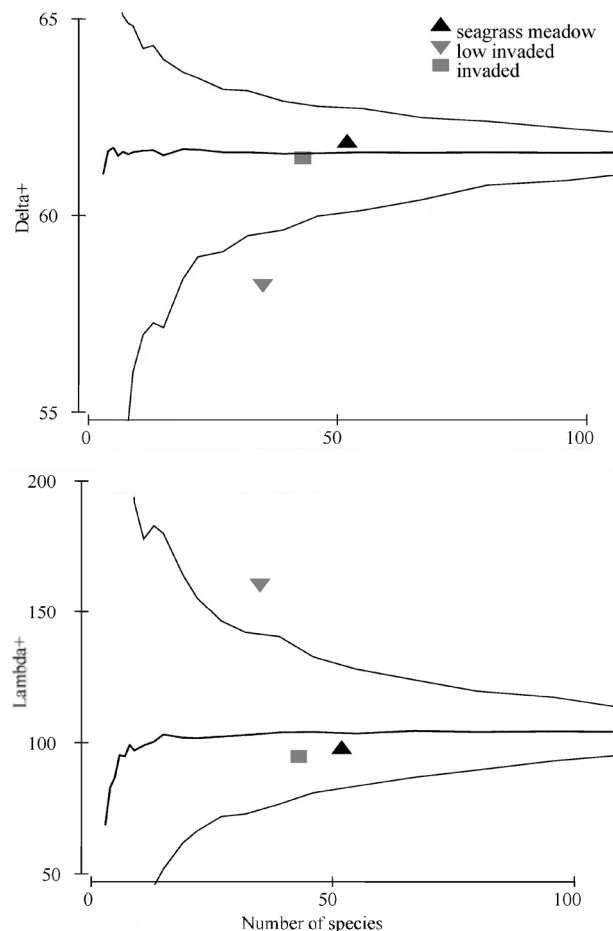
Fig. 7. – Confidence funnels (mean and 95% probability intervals) of the average taxonomic distinctness (Δ^+) and its variation (Λ^+) generated from the master list showing the relative position of the *Posidonia meadows*, high *Caulerpa* biomass and low *Caulerpa* biomass.

Taxonomic distinctness

Polychaete species composition in both *Caulerpa* mats and *Posidonia* meadows was similar, and thus when their seasonal variability was compared with the Balearic Islands master list, both the average taxonomic distinctness and its variation were also similar, except for the April *Caulerpa* mats (average taxonomic distinctness $P=0.003$ and variation in taxonomic distinctness $P=0.022$) (Fig. 6). In turn, both the average taxonomic distinctness and its variation fell inside the 95% probability funnel for both the *Posidonia* meadows and the *Caulerpa* mats during the periods with the highest *Caulerpa* biomass (Δ^+ $P=0.83$ Λ^+ $P=0.66$ and Δ^+ $P=0.64$ Λ^+ $P=0.59$, respectively), while the indices for the *Caulerpa* mats during the periods with low *Caulerpa* biomass periods fell outside the 95% confidence interval ($P=0.008$ and $P=0.006$ respectively) (Fig. 7).

DISCUSSION

Polychaete assemblages associated with the invasive *Caulerpa racemosa* spreading along the western Mediterranean appear to have characteristic patterns of abundance, diversity and seasonal dynamics. The most influencing factors are the loss of *Posidonia oceanica* aboveground structures (leaves and vertical sheaths) in mats invaded by *C. racemosa*, which changes the habitat structure (with the short fronds and complex stolon network of the algae), and the marked seasonal dynamics of the algal biomass. When compared to living *P. oceanica* meadows, the effects of the invasion were shown to be non-negative. In fact, the abundance and number of species of the polychaete assemblages tended to increase, as previously reported for soft-bottoms colonised by *C. racemosa* (Argyrou *et al.*, 1999).

The species composition of the polychaete assemblages associated with *Caulerpa* mats did not show a clear differentiation between samples. In other words, the assemblages were very uniform, most of them also included common soft bottom species, as reported for living *Posidonia* meadows (Gambi *et al.*, 1995; Gambi *et al.*, 1998; Brito *et al.*, 2005). In the study area, several of the most abundant species in *Caulerpa* mats also occurred in *Posidonia* meadows and *viceversa* (i.e. *Pelogenia arenosa, Polyophthalmus pictus, Lumbrineris latreilli* and *Arabella iricolor*, on one side, and *Nematonereis hebes, Aponuphis bilineata, Lysidice ninetta* and *Eunice vittata* on the other). In fact, the increase or decrease in abundances of coincident polychaete species seems to be a characteristic trend when living *P. oceanica* and dead mats invaded by *C. racemosa* are compared. However, only *Neanthes agulhana* was dominant in both habitats, although it was significantly more abundant in *Caulerpa* mats.

The most abundant family in *Caulerpa* mats (and the second most abundant in *Posidonia* meadows) was the Nereididae, as previously reported for seagrass systems (Gambi *et al.*, 1998). In addition to *Neanthes agulhana*, nereidids were represented by the omnivorous species *Neanthes caudata* and *Platynereis dumerilii*. The second most abundant family in *Caulerpa* mats was the carnivorous Sigalionidae (also relatively less abundant in *Posidonia* mats). As a general trend, carnivorous species tended to increase their abundance in *Caulerpa* mats. We postulated that a major availability of preys in *Caulerpa* mats, i.e. other polychaetes (this paper) and molluscs

(Box, 2008), could be responsible for this increased presence of carnivores, both polychaetes (this paper) and crustaceans (Box, 2008).

In turn, a characteristic trend of the polychaete assemblages harboured by *Caulerpa* mats was the particular seasonal dynamics, which showed the highest density, species richness and diversity during summer and autumn. This pattern clearly differs from that of the assemblages associated with *Posidonia* meadows, which were most dense and diverse in winter (Gambi *et al.*, 1995). Our results demonstrate that these seasonal peaks were linked to maximums of *Caulerpa* biomass. Thus, we postulated that the increasing spatial complexity provided by a high biomass of their stolons and fronds (Longepierre *et al.*, 2005) growing over the dead seagrass mat layer, increased the complexity of the habitat and enhanced the structuring of the polychaete assemblage. During summer and autumn, the invasive algae grew quickly and formed extensive mats of stolons, which trapped sediments to the extreme that the lower vegetation layers may be affected (Balata *et al.*, 2004). The stolon/frond network was less complex in winter and spring and, correspondingly, low polychaete densities and diversities were found. The co-generic invasive *Caulerpa taxifolia* also develops a network of stolons on the substratum surface and has a rhizoid system that allows it to colonise virtually all substrates (Levi and Francour, 2004). As a result, specialised species such as the fish *Mullus surmuletus* underwent strong decreases in densities in the presence of *C. taxifolia* (Longepierre *et al.*, 2005). *Caulerpa racemosa* also developed a similar complex network, and thus has similar effects on *M. surmuletus* and other benthic-feeder fish such as *Spondyliosoma cantharus* (Box personal observations). However, the sharp decrease in its biomass during winter may reduce the overall impact on the invaded communities.

The presence of *Caulerpa racemosa* seemed to cause a significant reduction in the density of several polychaetes that are characteristic of *Posidonia* meadows, such as the eunicids *Nematonereis hebes* and *Lysidice ninetta*, which were also among the major contributors to the dissimilarity among *Caulerpa* mats and *Posidonia* meadows in the SIMPER analysis. However, the reasons for this negative effect are not clear, as it is not possible to assess whether it has a trophic basis, these species feed at *P. oceanica* scales according to Gambi *et al.* (2003, 2005), or a chemical basis linked to the secondary metabolites produced by the algae that may either affect grazing directly or indirectly through inhibiting growth or death of *P. oceanica* (Raniello *et al.*, 2007).

Moreover, the marked changes in the associated polychaete assemblages induced by the increasing *Caulerpa racemosa* biomass tended to be stable through time, as revealed by the high similarity of the samples collected in August, October and December (which strongly influence the observed seasonal patterns). In addition, minimum *C. racemosa* biomasses were observed during the coldest months (i.e. February 2004 and April 2005), in parallel with a reduction in the polychaete abundance and diversity in the *Caulerpa* mats. *Posidonia* meadows did not show a seasonal pattern, and the assemblage descriptors were more homogeneous and stable through the year and relatively higher in winter. Compared with a bare sandy bottom, the presence of meadows increases the amount of fine particles and organic matter (Brito *et al.*, 2005), but this is also true when compared to the winter, less dense, *Caulerpa* mats in the study area. The polychaete assemblages in living *Posidonia* meadows were less abundant and less rich than those in the dead mats in summer (Borg *et al.*, 2006). However, this seems more likely to be related to the dynamics of the dead mat assemblages, as their lowest annual diversity also occurs in summer (Gambi *et al.*, 1995). Non-invaded dead mats were absent from the studied area, so that it has not been possible to isolate this particular effect in our analyses.

The taxonomic distinctness analysis showed that the species composition of the polychaete assemblages from *Caulerpa* mats was always very similar to that of *Posidonia oceanica* assemblages, with the only exception being those associated with samples with low or null *C. racemosa* biomass, which had a lower number of species, and thus fell outside the confidence intervals of the analyses. Altogether, this suggests that the coverage of dead seagrass meadows by the invasive *C. racemosa* provides a suitable habitat for *P. oceanica* polychaete assemblages.

The introduction of exotic species, together with habitat degradation, fragmentation and overexploitation (among other processes), may cause a reduction in species richness at large spatial scales (Rosenzweig, 2001), in association with a local modification of the overall biodiversity of each recipient benthic community. However, the effects may either be negative (Galil and Zenetos, 2002; Zenetos *et al.*, 2003; Streftaris and Zenetos, 2006) or positive (Viejo, 1999; Crooks, 2002; Buschbaum *et al.*, 2006), with the enhanced diversity of the invaded communities being mainly due to the

increased habitat complexity. In fact, recent colonisations by exotic plants, animals and microbes have been reported to increase species richness locally (Rosenzweig, 2001; Sax and Gaines, 2003). Previous studies on rocky bottoms invaded by *C. racemosa* showed that the invasion mainly caused habitat modifications, and this altered the amphipod assemblage (Vazquez-Luis *et al.*, 2008). In the case of the introduction of *Caulerpa racemosa* in the Balearic Islands, the analysis of the polychaete assemblages does not reveal a negative effect, as their overall species composition is coincident with that of the typical *P. oceanica* assemblages, and can be considered as locally positive, taking into account that the invaded mats also have the highest polychaete abundances. Our data supports that the introduction of exotic species may have diverse impacts at both local and temporal scales. Thus, we agree with Buschbaum *et al.* (2006) in that the effects of an invasion cannot be generalised, as each invasive event requires an independent study.

In summary, the invasive colonisation of *Posidonia oceanica* meadows by *Caulerpa racemosa* induces changes in the structure and functioning of the associated polychaete assemblages, both at the spatial and temporal scales. Our results demonstrate that the species composition was similar in living and dead (i.e. invaded) *Posidonia* meadows, with only a few characteristic species being replaced. In turn, the assemblages showed clear seasonal differences in abundance, mainly because the invasive *C. racemosa* generated a complex stolon/frond network which represents a new, suitable habitat for polychaetes. In fact, not only is the microhabitat availability enhanced, but the *Caulerpa* network also constitutes an effective barrier against fish predators (Longepierre *et al.*, 2005). In the Balearic Islands, however, this is only valid for the warm period, when *C. racemosa* has significant biomasses.

In spite of the structural and seasonal changes, our results also show that it is of interest to study and assess functional aspects (e.g. bottom up and cascade effects, trophic web shifts) of the polychaete assemblages affected by the invasion, as well as their relationships with the entire benthic community.

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