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Mobile epifaunal assemblages associated with *Cystoseira* beds: comparison between areas invaded and not invaded by *Lophocladia lallemandii*

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Summary: The study compared the structure of mobile epifaunal assemblages associated with Mediterranean *Cystoseira* beds between areas invaded and not invaded by *Lophocladia lallemandii*. A total of 150 taxa were identified: 42 Polychaeta, 78 Arthropoda, 26 Mollusca and 4 Echinodermata. Epifaunal assemblages differed between areas invaded and not invaded by *Lophocladia lallemandii* when the invasive species reached maximum values of cover and biomass, while differences between conditions were not significant in other periods of the year. The main differences were the greater abundance of amphipods, isopods and polychaetes in invaded areas and the greater abundance of molluscs and decapods in non-invaded areas, while richness and total abundance of organisms were not significantly different between conditions. The effects of *Lophocladia lallemandii* invasion on *Cystoseira*-associated assemblages seem to be limited to the period of vegetative growth of the alga and reversible during the period of its vegetative rest.

Keywords: biological invasions; *Cystoseira crinita*; *Lophocladia lallemandii*; Mediterranean Sea; mobile epifauna.

Comunidad de epifauna móvil asociada a las bosques de *Cystoseira*: comparación entre áreas invadidas y no invadidas por *Lophocladia lallemandii*

Resumen: Este estudio compara la estructura de la comunidad de macroinvertebrados móviles asociada a bosques mediterráneos de *Cystoseira* entre áreas invadidas por *Lophocladia lallemandii* y áreas no invadidas. Se identificaron un total de 150 táxones: 42 Polychaeta, 78 Arthropoda, 26 Mollusca, 4 Echinodermata. La comunidad epifaunal difirió entre áreas invadidas por *Lophocladia lallemandii* y áreas no invadidas cuando la Rhodophyta introducida alcanzó valores máximos de cobertura y biomasa, mientras que no presentó diferencias entre condiciones en otros períodos del año. Estas diferencias fueron principalmente debidas a una mayor abundancia de anfípodos, isópodos y poliquetos en áreas invadidas, y de moluscos y decápodos en áreas no invadidas, mientras que la riqueza y abundancia total de organismos no presentaron diferencias significativas entre condiciones. Los efectos de la invasión de *Lophocladia lallemandii* sobre las comunidades asociadas a *Cystoseira* parecen estar restringidos al período de crecimiento vegetativo del alga, siendo reversibles durante el período de pausa de crecimiento.

Palabras clave: invasiones biológicas; *Cystoseira crinita*; *Lophocladia lallemandii*; mar Mediterráneo; epifauna móvil.

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INTRODUCTION

Introduced seaweeds are responsible for severe worldwide biological invasions, with important effects on native macroalgal and animal assemblages (Piazzi et al. 2001, Buschbaum et al. 2006, Schaffelke and Hewitt 2007, McKinnon et al. 2009, Byers et al. 2010, Pacciardi et al. 2011). Effects of invasion may be particularly serious when habitat-forming species are involved, as each change in population of these organisms may have severe effects on associated assemblages (Gribben et al. 2009). Macroalgae are important habitat-forming organisms in temperate coastal systems, providing a suitable habitat for many epiphytes and mobile invertebrates (Edgar and Moore 1986, Taylor and Cole 1994, Cacabelos et al. 2010) and influencing the structure and the biodiversity of coastal systems (Tanaka and Leite 2003, Bates and Dewreede 2007, Wikström and Kautsky 2007).

In the Mediterranean Sea, species of genus *Cystoseira* are the most important habitat-forming species in shallow rocky bottoms (Ballesteros 1990a, b), where they play a key role in determining patterns of diversity (Sales and Ballesteros 2009). The erect structure of *Cystoseira* thalli, like those of other canopy species, can limit the spread of most invasive seaweeds, constituting a mechanical barrier against the invasion (Bulleri et al. 2010). However, invaders such as the Rhodophyta *Lophocladia lallemandii* (Montagne) F. Schmitz (Bedini et al. 2011) seem to be facilitated by the presence of *Cystoseira* beds. This species is widespread in tropical and subtropical waters and was probably introduced into the Mediterranean Sea through the Suez Canal (Boudouresque and Verlaque 2002). Until now, in the Mediterranean Sea, invasive events by *L. lallemandii* have only been described in the Balearic Islands (Patzner, 1998, Cebrian and Ballesteros 2010, Marbà et al. 2014) and in the Tuscan Archipelago (Bedini et al. 2011). In both areas, the alga is able to reach high values of percentage cover and biomass (Bedini et al. 2011) on rocky bottoms and in seagrass meadows (Ballesteros et al. 2007, Sureda et al. 2008, Marbà et al. 2014). *Cystoseira* beds are particularly subjected to invasion (Cebrian and Ballesteros 2007, Bedini et al. 2011), as thalli of these algae may offer a valuable substrate for *L. lallemandii* anchoring (Bedini et al. 2011). Negative effects of *L. lallemandii* invasion have been described for sessile invertebrates in meadows of the seagrass *Posidonia oceanica* (L.) Delile (Cabanellas-Reboredo et al. 2010, Deudero et al. 2010), while no information is available about effects of invasion on mobile macro-invertebrates.

The present study aimed to compare the structure of mobile epifaunal assemblages associated with *Cystoseira* beds between areas invaded and not invaded by *Lophocladia lallemandii*. The following hypotheses were tested: i) epifaunal assemblages associated with *Cystoseira* beds invaded by *L. lallemandii* differ in species composition and abundance from those colonizing non-invaded beds, ii) temporal patterns of assemblages vary between conditions, iii) differences between conditions are greater during the period of maximum vegetative growth of *L. lallemandii*.

MATERIALS AND METHODS

The study was carried out around the Island of Pianosa, in the Tuscan Archipelago National Park (northwestern Mediterranean Sea) at 5 m depth (Fig. 1). *Lophocladia lallemandii* started to spread around the island in 2008, and in 2010 it colonized with variable coverage a stretch of about 10 km between 2 and 10 m depth (Bedini et al. 2011). The alga begins to grow in July, reaches its maximum abundance in November and completely disappears between January and June (Bedini et al. 2011). All around the island, the rocky bottom between 4 m and 8 m of depth is colonized by *Cystoseira* spp. assemblages (mostly *C. crinita* Duby and *C. brachycarpa* var. *balearica* (Savageau) Giaccone). In invaded *C. crinita* beds, the biomass of *L. lallemandii* in November was about 0.2 kg dw m^{-2} (Bedini et al. 2011).

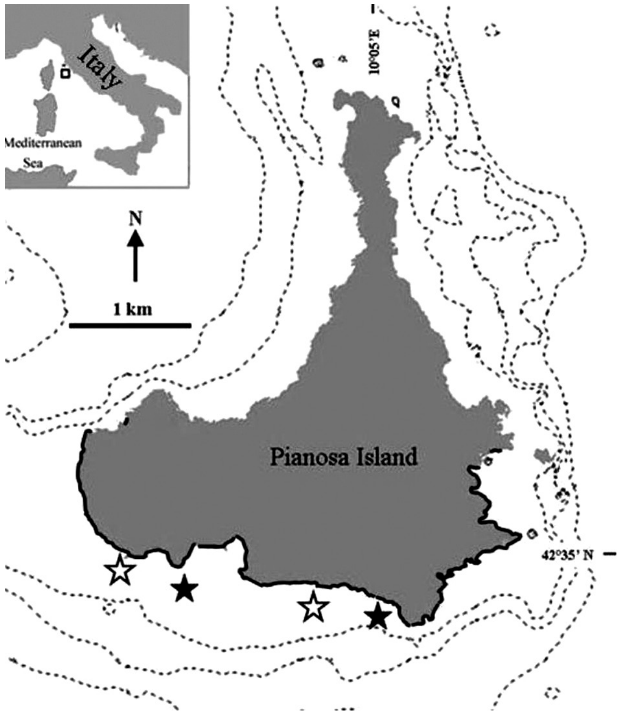

Fig. 1. – Map of the study site. Black lines indicate zones colonized by *Lophocladia lallemandii*. White stars, invaded areas; black stars, non-invaded areas.

Four areas of about 100 m^2 were selected in *C. crinita* beds along the southern coast of the island, two of them invaded by *L. lallemandii* and two non-invaded; areas were randomly chosen among those available for each condition (Fig. 1). On four dates during a one-year period (May 2010, August 2010, November 2010, May 2011), three samples were collected in each area. Samples were constituted by all organisms present within an area of 400 cm^2. All mobile macro-invertebrates present in each sample were identified and the abundance of each species was expressed as number of individuals m^{-2}. Epifaunal assemblages were analyzed by Permutational Analysis of Variances (PERMANOVA, Anderson 2001). A three-way model was used with Condition (Invaded vs. Non-invaded) as a fixed factor, Date (4 levels) as a random factor crossed with Condition and Area (2 levels) as a random factor nested in Condition. Data were log(x+1) transformed before calculation of the Bray-Curtis index of dissimilarity. The Monte-Carlo procedure was used when the number of permutations was low. A two-dimensional multidimensional scaling (n-MDS) was used for a graphical representation of results. The SIMPER routine was performed to establish which taxa most contributed to the dissimilarity between conditions and dates.

The number of taxa per sample and the abundance of organisms were detected by analyses of variance (ANOVA), with the same factors and levels used for

Table 1. – List and abundance of taxa (mean number of organisms m^{-2}). I, invaded assemblages; N-I, non-invaded assemblages.

	May 2010		Aug. 2010		Nov. 2010		May 2011	
	I	N-I	I	N-I	I	N-I	I	N-I
MOLLUSCA								
Polyplacophora								
Acanthochitona fascicularis (Linnaeus, 1767)	7.5	0.0	7.5	0.0	5.0	0.0	0.0	0.0
Gastropoda								
*Alvania discors (*Allan, 1818)	0.0	7.5	0.0	0.0	0.0	0.0	17.5	5.0
Alvania lineata Risso, 1826	30.0	25.0	25.0	17.5	5.0	0.0	30.0	0.0
Alvania mamillata Risso, 1826	0.0	5.0	7.5	0.0	0.0	0.0	0.0	0.0
Alvania subcrenulata (Bucquoy, Dautzenberg & Dollfus, 1884)	0.0	5.0	0.0	0.0	5.0	0.0	0.0	0.0
Aplysia punctata (Cuvier, 1803)	0.0	0.0	0.0	0.0	0.0	0.0	7.5	5.0
Barleeia unifasciata (Montagu, 1803)	430.0	82.5	45.0	205.0	0.0	50.0	362.5	55.0
Bittium latreillii (Montagu, 1803)	37.5	28.0	107.5	242.5	55.0	55.0	30.0	32.5
Bittium reticulatum (Payraudeau, 1826)	12.5	12.5	5.0	0.0	12.5	0.0	7.5	17.5
Calmella cavolini (Vérany, 1846)	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Columbella rustica (Linnaeus, 1758)	5.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0
Conus mediterraneus Hwass in Bruguière, 1792	5.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0
Gibbula varia (Linnaeus, 1758)	0.0	0.0	0.0	0.0	5.0	0.0	5.0	0.0
Granulina marginata (Bivona, 1832)	0.0	0.0	0.0	0.0	7.5	0.0	0.0	0.0
Hancokia uncinata (Linnaeus, 1758)	0.0	0.0	0.0	0.0	0.0	0.0	12.5	0.0
Jujubinus exasperatus (Pennant, 1777)	0.0	12.5	0.0	0.0	0.0	0.0	5.0	0.0
Jujubinus striatus (Linnaeus, 1758)	0.0	5.0	0.0	0.0	0.0	0.0	5.0	0.0
Marshallora adversa (Linnaeus, 1758)	0.0	0.0	0.0	0.0	0.0	17.5	0.0	0.0
Nassarius pygmaeus (Lamarck, 1822)	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pollia dorbignyi (Payraudeau, 1826)	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0
Rissoa lia (Monterosato, 1884)	0.0	7.5	0.0	0.0	0.0	0.0	0.0	5.0
Rissoa variabilis (Von Mühlfeldt, 1824)	12.5	17.5	5.0	50.0	20.0	32.5	0.0	0.0
Rissoa ventricosa Desmarest, 1814	37.5	62.5	37.5	212.5	7.5	50.0	5.0	45.0
Rissoa violacea Desmarest, 1814	0.0	0.0	0.0	0.0	0.0	0.0	17.5	0.0
Tricolia pullus pullus (Linnaeus, 1758)	5.0	0.0	5.0	0.0	7.5	0.0	0.0	0.0
Tricolia speciosa (Mühlfeld, 1824)	0.0	5.0	0.0	5.0	0.0	7.5	0.0	0.0
Vexillum (Pusiolina) tricolor (Gmelin, 1791)	0.0	0.0	5.0	0.0	5.0	0.0	0.0	0.0
ANNELIDA								
Polychaeta								
Crhysopetalum debile (Grube, 1855)	0.0	0.0	0.0	5.0	5.0	17.5	0.0	0.0
Dodecaceria concharum Örsted, 1843	7.5	5.0	0.0	0.0	5.0	0.0	0.0	0.0
Eunice harassii Audouin & Milne-Edwards, 1834	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0
Eunice pennata (O. F. Müller, 1776)	7.5	0.0	0.0	0.0	0.0	5.0	5.0	0.0
Eunice vittata (Delle Chiaje, 1828)	7.5	0.0	0.0	5.0	0.0	0.0	0.0	0.0
Euphrosine foliosa Audouin & Milne-Edwards, 1833	5.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0
Eupolymnia nebulosa Montagu, 1818	5.0	0.0	5.0	0.0	5.0	0.0	0.0	0.0
Haplosyllis spongicola (Grube, 1855)	0.0	5.0	0.0	0.0	0.0	0.0	0.0	5.0
Harmothoe spinifera (Ehlers, 1864)	0.0	0.0	5.0	5.0	0.0	0.0	0.0	0.0
Hydroides pseudouncinatus Zibrowius, 1968	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrineris coccinea (Renier, 1804)	7.5	5.0	0.0	0.0	0.0	5.0	0.0	0.0
Lysidice collaris Grube, 1870	0.0	0.0	7.5	0.0	0.0	0.0	5.0	0.0
Lysidice ninetta Audouin & Milne-Edwards, 1833	0.0	7.5	5.0	7.5	0.0	0.0	7.5	0.0
Marphysa belli (Audouin & Milne-Edwards, 1833)	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Megalomma vesciculosum (Montagu, 1815)	5.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0
Mysta picta (Quatrefages, 1865)	5.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5
Neanthes agulhana (Day, 1963)	0.0	0.0	7.5	0.0	17.5	0.0	0.0	0.0
Nematonereis hebes Verril, 1900	17.5	0.0	5.0	0.0	0.0	0.0	0.0	5.0
Nereis perivisceralis Claparède, 1868	5.0	0.0	5.0	0.0	0.0	0.0	0.0	5.0
Nereis rava Ehlers, 1864	5.0	5.0	0.0	0.0	0.0	0.0	0.0	7.5
Notomastus latericeus Sars, 1951	0.0	0.0	7.5	5.0	0.0	0.0	0.0	0.0
Palolo siciliensis (Grube, 1840)	12.5	5.0	5.0	32.5	0.0	5.0	5.0	0.0
Perinereis cultrifera (Grube, 1840)	12.5	0.0	0.0	5.0	5.0	0.0	0.0	0.0
Pionosyllis lamelligera Saint Joseph, 1887	0.0	0.0	0.0	5.0	0.0	0.0	5.0	0.0
Platynereis coccinea (Delle Chiaje, 1822)	7.5	0.0	0.0	0.0	32.5	5.0	0.0	7.5
Platynereis dumerilii (Audouin & Milne-Edwards, 1833)	30.0	5.0	95.0	57.5	142.5	17.5	7.5	5.0
Polyophthalmus pictus (Dujardin, 1839)	220.0	37.5	12.5	5.0	7.5	0.0	57.5	45.0
Pterocirrus macroceros Grube, 1860)	0.0	0.0	5.0	12.5	0.0	5.0	0.0	0.0
Spirobranchus polytrema Philippi, 1844	0.0	30.0	0.0	0.0	0.0	5.0	0.0	0.0
Subadyte pellucida (Ehlers, 1864)	0.0	0.0	0.0	0.0	0.0	0.0	5.0	5.0
Syllis armillaris (O. F. Müller, 1776)	20.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0
Syllis corallicola Verril, 1900	5.0	0.0	0.0	0.0	0.0	0.0	5.0	5.0
Syllis ferrani Alòs & San Martin, 1987	0.0	0.0	7.5	5.0	0.0	0.0	7.5	0.0
Syllis gerlachi (Hartmann-Schröder, 1960)	0.0	0.0	17.5	17.5	0.0	0.0	5.0	0.0
Syllis gracilis Grube, 1840	5.0	0.0	0.0	0.0	0.0	0.0	7.5	0.0
Syllis hyalina Grube, 1863	17.5	0.0	0.0	0.0	37.5	7.5	0.0	5.0
Syllis kronhi Ehlers, 1864	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syllis prolifera Krohn, 1852	17.5	0.0	7.5	7.5	20.0	0.0	0.0	0.0
Syllis variegata Grube, 1860	7.5	0.0	0.0	0.0	0.0	0.0	5.0	0.0
Syllis westheidei San Martìn, 1984	0.0	0.0	7.5	5.0	0.0	0.0	0.0	0.0
Trypanosyllis zebra (Grube, 1840)	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vermiliopsis striaticeps (Grube, 1862)	5.0	0.0	7.5	5.0	0.0	0.0	0.0	0.0
ARTHROPODA								
Crustacea								
Decapoda								
Acanthonyx lunulatus (Risso, 1816)	25.0	0.0	112.5	12.5	17.5	7.5	37.5	0.0
Alpheus dentipes Guèrin, 1832	0.0	0.0	32.5	7.5	5.0	0.0	17.5	0.0
Athanas nitescens (Leach, 1813)	5.0	0.0	50.0	0.0	5.0	0.0	0.0	0.0
Calcinus tubularis (Linnaeus, 1767)	12.5	0.0	105.0	120.0	20.0	57.5	0.0	12.5

Table 1 (cont,). – List and abundance of taxa (mean number of organisms m^{-2}). I, invaded assemblages; N-I, non-invaded assemblages.

	May 2010		Aug. 2010		Nov. 2010		May 2011	
	I	N-I	I	N-I	I	N-I	I	N-I
Cestopagurus timidus (Roux, 1830)	17.5	50.0	142.5	132.5	30.0	67.5	45.0	20.0
Clibanarius erythropus (Latreille, 1818)	0.0	17.5	0.0	0.0	0.0	0.0	17.5	25.0
Eualus cranchii (Leach, 1817)	0.0	0.0	12.5	5.0	0.0	0.0	0.0	0.0
Galathea strigosa (Linnaeus, 1761)	0.0	0.0	50.0	7.5	0.0	0.0	0.0	0.0
Hippolyte inermis Leach, 1815	0.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0
Hippolyte longirostris (Czerniavsky, 1868)	0.0	0.0	12.5	32.5	17.5	37.5	0.0	0.0
Hippolyte varians Leach, 1814	0.0	0.0	25.0	0.0	32.5	20.0	0.0	7.5
Pandalina brevirostris (Rathke, 1843)	0.0	0.0	0.0	0.0	0.0	0.0	17.5	7.5
Pagurus anachoretus Risso, 1827	7.5	30.0	20.0	5.0	17.5	5.0	0.0	7.5
Pilumnus hirtellus (Linnaeus, 1761)	0.0	5.0	20.0	0.0	0.0	0.0	0.0	0.0
Pisa tetraodon (Pennant, 1777)	0.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0
Processa edulis (Risso, 1816)	0.0	0.0	0.0	0.0	7.5	0.0	0.0	0.0
Synalpheus gambarelloides (Nardo, 1847)	0.0	5.0	0.0	0.0	12.5	0.0	0.0	0.0
Leptochelia savignyi (Kroyer, 1842)	0.0	0.0	5.0	12.5	0.0	0.0	0.0	0.0
Tanais dulongii (Audouin, 1826)	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda								
Anthura gracilis (Montagu, 1808)	0.0	0.0	5.0	0.0	5.0	0.0	0.0	0.0
Cymodoce truncata Leach, 1814	5.0	0.0	30.0	12.5	0.0	0.0	5.0	30.0
Dynamene bidentata (Adams, 1800)	0.0	5.0	5.0	17.5	7.5	0.0	12.5	12.5
Dynamene edwardsi (Lucas, 1849)	0.0	5.0	17.5	25.0	0.0	0.0	0.0	5.0
Eurydice pulchra Leach, 1815	0.0	7.5	32.5	12.5	5.0	30.0	0.0	5.0
Eurydice truncata (Norman, 1868)	0.0	12.5	0.0	0.0	0.0	0.0	0.0	0.0
Idotea granulosa Rathke, 1843	12.5	17.5	7.5	12.5	57.5	17.5	32.5	7.5
Sphaeroma serratum (Fabricius, 1787)	0.0	0.0	5.0	0.0	5.0	0.0	0.0	0.0
Amphipoda								
Ampelisca rubella A. Costa, 1864	0.0	0.0	0.0	17.5	0.0	0.0	0.0	0.0
Amphilochus neapolitanus Della Valle, 1893	55.0	12.5	12.5	17.5	0.0	0.0	175.0	155.0
Ampithoe ramondi Audouin, 1826	107.5	75.0	37.5	12.5	80.0	7.5	117.5	45.0
Apherusa chiereghinii Giordani - Soika, 1849	0.0	5.0	0.0	0.0	12.5	0.0	175.0	220.0
Apolochus picadurus (J. L. Bardard, 1962)	0.0	0.0	0.0	0.0	0.0	20.0	0.0	0.0
Caprella acanthifera Leach, 1814	117.5	95.0	25.0	37.5	57.5	0.0	7.5	0.0
Caprella cavediniae Krapp-Schickel & Vader, 1998	0.0	5.0	0.0	0.0	0.0	0.0	42.5	237.5
Caprella equilibra Say, 1818	0.0	55.0	5.0	0.0	0.0	0.0	0.0	0.0
Caprella grandimana (Mayer, 1882)	7.5	0.0	17.5	5.0	5.0	5.0	312.5	57.5
Caprella lilliput Krapp-Schickel & Ruffo, 1987	0.0	0.0	7.5	7.5	5.0	0.0	5.0	0.0
Caprella liparotensis Haller, 1879	0.0	0.0	0.0	0.0	0.0	0.0	5.0	5.0
Caprella rapax Mayer, 1890	0.0	0.0	0.0	0.0	0.0	0.0	17.5	0.0
Corophium sp.	0.0	17.5	0.0	0.0	0.0	0.0	0.0	0.0
Dexamine spiniventris (Costa, 1853)	117.5	5.0	30.0	25.0	37.5	0.0	257.5	45.0
Dexamine spinosa (Montagu, 1813)	120.0	5.0	30.0	17.5	0.0	0.0	0.0	0.0
Elasmopus pocillimanus (Bate, 1862)	67.5	5.0	37.5	0.0	0.0	0.0	82.5	12.5
Ericthonius argenteus Krapp-Schickel, 1993	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0
Erichthonius punctatus (Bate, 1857)	0.0	5.0	82.5	0.0	0.0	0.0	0.0	0.0
Eusiroides dellavallei Chevreux, 1899	7.5	0.0	0.0	0.0	0.0	0.0	5.0	0.0
Gammarella fucicola (Leach, 1814)	0.0	0.0	5.0	0.0	7.5	0.0	0.0	0.0
Hyale schmidti (Heller, 1866)	157.5	112.5	0.0	0.0	0.0	0.0	82.5	155.0
Leucothoe dentitelson (Chevreux, 1925)	0.0	0.0	7.5	5.0	0.0	0.0	0.0	0.0
Leucothoe venetiarum Giordani-Soika, 1950	0.0	7.5	0.0	0.0	0.0	0.0	5.0	25.0
Lysianassa costae (Milne-Edwards, 1830)	5.0	5.0	20.0	5.0	5.0	0.0	0.0	0.0
Lysianassina longicornis Lucas, 1849	0.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0
Maera ariadne Krapp, Marti & Ruffo, 1996	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microdeutopus algicola Della Valle, 1893	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0
Micropythia carinata (Bate, 1862)	17.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Peltocoxa mediterranea Schiecke, 1977	0.0	0.0	0.0	0.0	0.0	0.0	7.5	12.5
Phtisica marina Slabber, 1769	130.0	75.0	17.5	0.0	5.0	5.0	150.0	150.0
Podocerus variegatus Leach, 1814	5.0	0.0	0.0	0.0	0.0	5.0	37.5	7.5
Protohyale schmidtii Schiecke, 1977	0.0	0.0	0.0	0.0	0.0	0.0	162.5	30.0
Pseudoprotella phasma Montagu, 1804	37.5	0.0	0.0	0.0	0.0	0.0	12.5	0.0
Quadrimaera ariadne (Krapp, Marti & Ruffo, 1996)	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0
Quadrimaera inaequipes (A. Costa, 1851)	12.5	5.0	62.5	62.5	7.5	0.0	0.0	0.0
Stenothoe mandragora Krapp-Schickel, 1996	5.0	0.0	0.0	0.0	0.0	0.0	20.0	30.0
Stenothoe tergestina (Nebeski, 1881)	5.0	20.0	0.0	0.0	0.0	0.0	50.0	132.5
Siphonoecetes neapolitanus Schiecke, 1979	0.0	0.0	12.5	5.0	0.0	0.0	0.0	0.0
Pycnogonida								
Achelia echinata Hodge, 1864	7.5	5.0	0.0	0.0	0.0	0.0	5.0	0.0
Anoplodactylus pygmaeus (Hodge, 1864)	5.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0
Callipallene emaciata (Dohrn, 1881)	12.5	7.5	5.0	5.0	0.0	0.0	0.0	20.0
Nymphon gracile Leach, 1814	7.5	7.5	5.0	0.0	0.0	0.0	0.0	0.0
ECHINODERMATA								
Ophiuroidea								
Amphipholis squamata (Delle Chiaje, 1828)	0.0	20.0	137.5	30.0	42.5	0.0	7.5	0.0
Amphiura chiajei Forbes, 1843	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ophiotrix fragilis (Abildgaard, in O. F. Müller, 1789)	5.0	0.0	12.5	7.5	0.0	0.0	7.5	7.5
Echinoidea								
Psammechinus microtuberculatus (Blainville, 1825)	0.0	5.0	0.0	0.0	5.0	0.0	0.0	0.0

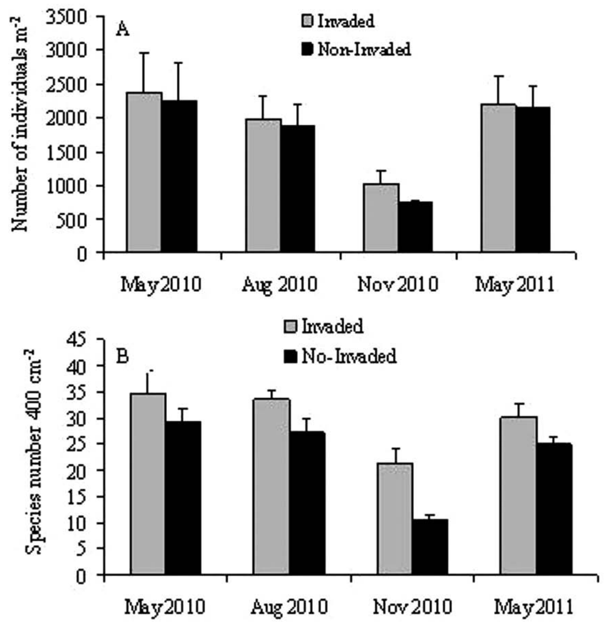

Fig. 2. – Abundance (A) and number of species (B) of invaded and non-invaded epifaunal assemblages associated with *Cystoseira crinita* beds.

multivariate analyses; Cochran's C-test was utilised before each analysis to check for homogeneity of variance and data were transformed when necessary (Underwood 1997).

RESULTS

A total of 150 taxa were identified: 42 Polychaeta, 78 Arthropoda, 26 Mollusca and 4 Echinodermata (Table 1).

ANOVA analyses detected a significant difference among dates for the abundance of organisms ($F=80.7$, $p=0.003$) and the mean number of taxa per sample ($F=20.6$, $p=0.001$), while differences between conditions were not significant ($F=2.6$, $p=0.120$ and $F=44.6$, $p=0.071$ respectively). Both variables were higher on spring dates than on the others (Fig. 2).

PERMANOVA detected a significant interaction between Date and Condition (Table 2). The pairwise

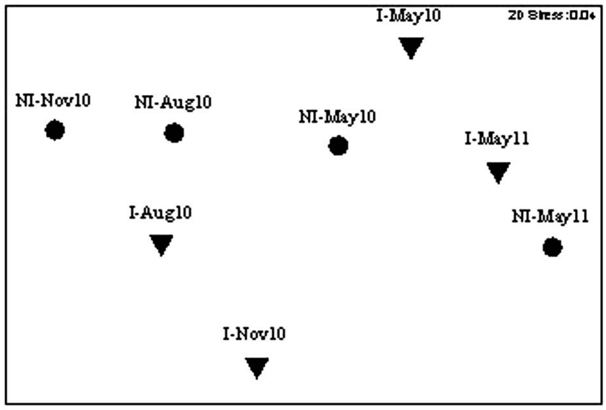

Fig. 3. – Multidimensional scaling on epifaunal assemblages associated with *Cystoseira crinita* beds. I, invaded; N-I, non-invaded.

test showed that differences between conditions were significant in November 2010 but not on the other sampling dates (Table 2). In invaded condition, May 2010 and May 2011 differed from August and November 2010; in non-invaded condition, November 2010 differed from the other dates. MDS showed a greater disjunction between invaded and non-invaded assemblages in November 2010 than in the other sampling dates (Fig. 3).

The SIMPER test showed that the main differences between assemblages in November 2010 were the greater abundance of amphipods (*Caprella acanthifera, Ampithoe ramondi, Dexamine spiniventris*), isopods (*Idotea granulosa*) and polychaetes (*Platynereis dumerilii*) in invaded areas and the greater abundance of molluscs (*Rissoa variabilis, Barleeia unifasciata*) and decapods (*Calcinus tubularis, Hippolyte longirostris, Cestopagurus timidus*) in non-invaded areas (Table 3).

The main differences between spring sampling dates (May 2010 and May 2011) and autumn ones (November 2010) were a higher abundance of organisms in spring, especially the molluscs *Barleeia unifasciata* and *Bittium latreillii* and the amphipods *Hyale schmidti, Ampithoe ramondi, Phtsisica marina* and *Caprella* spp.; only a few taxa were more abundant in autumn, including the decapods *Cestopagurus timidus* and *Calcinus tubularis* (Table 3).

Table 2. – Results of PERMANOVA analysis on epifaunal assemblages. Significant effects are in bold. MC, Monte-Carlo procedure.

Source	df	MS	Pseudo-F	P(perm)	perms
Date=D	3	15552.0	80.40	**0.001**	999
Condition=C	1	7643.7	14.21	0.125	999
Area(C)=A(C)	2	2047.2	10.58	0.388	999
D×C	3	4692.5	2.42	**0.002**	997
D×A(C)	6	1934.3	10.58	0.340	999
Residual	32	1827.9			
Total	47				

PAIRWISE TEST (C×D) Condition	P(MC)	Date	P(MC) Non-invaded	P(MC) Invaded
May 2010	0.119	May 10, Aug 10	0.068	**0.036**
August 2010	0.056	May 10, Nov 10	**0.008**	**0.036**
November 2010	**0.007**	May 10, May 11	0.077	0.093
May 2011	0.175	Aug 10, Nov 10	**0.004**	0.059
		Aug 10, May 11	**0.019**	**0.044**
		Nov 10, May 11	**0.005**	**0.014**

Table 3. – Results of SIMPER test showing the contribution of taxa to determining differences in assemblages between invaded and non-invaded areas in November 2010 and between May and November in non-invaded areas

Taxa November 2010	Abundance Invaded	Abundance Non-Invaded	Contribution %
Ampithoe ramondi	79.3	8.3	5.39
Cestopagurus timidus	29.3	66.8	5.32
Caprella acanthifera	58.3	0.0	4.57
Barleeia unifasciata	0.0	50.0	4.46
Calcinus tubularis	20.8	58.3	4.46
Idotea granulosa	58.3	16.8	4.35
Elasmopus pocillimanus	54.3	0.0	3.81
Platynereis dumerilii	142.8	18.3	3.63
Amphipholis squamata	41.8	0.0	3.27
Dexamine spiniventris	37.5	0.0	3.12
Rissoa variabilis	20.8	33.3	2.91
Hippolyte longirostris	18.0	36.8	2.78
Non-Invaded	May 2010	Nov. 2010	
Bittium latreillii	179.3	54.3	8.01
Hyale schmidti	112.5	0.0	7.06
Caprella acanthifera	95.0	0.0	5.08
Barleeia unifasciata	83.3	50.0	4.68
Ampithoe ramondi	75.0	8.5	3.99
Phtisica marina	75.0	4.3	3.89
Cestopagurus timidus	50.0	66.8	3.64
Calcinus tubularis	0.0	58.3	3.56
Caprella equilibra	54.3	0.0	3.52
Hippolyte longirostris	0.0	37.5	2.37
Non-Invaded	May 2011	Nov. 2010	
Caprella cavediniae	0.0	237.5	21.8
Apherusa chiereghinii	0.0	220.8	8.51
Phtisica marina	4.3	150.0	4.19
Stenothoe tergestina	0.0	133.3	3.54
Hyale schmidti	0.0	154.3	3.07
Cestopagurus timidus	66.8	20.8	2.47
Calcinus tubularis	58.3	12.5	2.31

DISCUSSION

Results of the study described the structure of epifaunal assemblages associated with *Cystoseira crinita* beds and highlighted differences between areas invaded by *Lophocladia lalemandii* and non-invaded areas related to the vegetative cycle of Rhodophyta.

Epifaunal assemblages associated with *C. crinita* were characterized by high abundance and diversity, compared with those described for other seaweed habitats (Gestoso et al. 2012, Janiak et al. 2012, Engelen et al. 2013). Macroalgal assemblages associated with Mediterranean *Cystoseira* beds are well known (Boudouresque 1972, Sales and Ballesteros 2010), while epifaunal assemblages have been less investigated and knowledge is limited to particular taxa (Arrontes and Anadon 1990, Chemello and Milazzo 2002, Fraschetti et al. 2002). The present study, analysing the whole epifaunal assemblages, confirms the important ecological role of *Cystoseira* beds in Mediterranean coastal systems. *Cystoseira* thalli, like those of other structurally complex algae (Tanaka and Leite 2003, Wikström and Kautsky 2007), may create a high number of microhabitats, hosting organisms with different requirements (Russo 1990, Gee and Warwick 1994, Taylor 1998). Moreover, *Cystoseira* beds may offer an effective refuge from predators and abundant food availability (Buschmann 1990, Holmlund et al. 1990, Martin-Smith 1993).

The sampling design of the study was not suitable for assessing the temporal dynamics of the assemblages. However, in non-invaded areas, epifaunal assemblages associated with *C. crinita* showed great differences between sampling dates, suggesting the occurrence of seasonal patterns which should be investigated through further studies. Seasonal variations in epifaunal assemblages associated with *Cystoseira* spp. as a consequence of taxa life cycles and modifications in seaweed structure have already been described (Fraschetti et al. 2002, Gozler et al. 2010). In fact, *Cystoseira* are perennial species with seasonal cycles of vegetative growth: they reach their maximum size in spring-summer period, while in autumn they lose secondary branches, changing their habitus (Sales and Ballesteros 2012). Temporal changes of epifaunal associated with *Cystoseira* spp. can also be caused by changes of macroalgal epiphyte assemblages. In fact, *Cystoseira* species host an abundant assemblage of macroalgae, mostly constituted by seasonal filamentous species (Ballesteros et al. 2009, Sales and Ballesteros 2010), which may change greatly throughout the year following the growth cycles of the main taxa.

The seasonal development of *L. lallemandii* overlaps this scenario. In fact, the study results showed that epifaunal assemblages associated with *Cystoseira crinita* beds differed between areas invaded and not invaded by *Lophocladia lallemandii* in November, when the invasive species reached maximum values of cover and biomass (Bedini et al. 2011), while assemblages showed no differences between conditions in other periods of the year.

The main effects of the presence of *L. lallemandii* were an increase in amphipods and polychaetes and a decrease in decapods and molluscs. Species more linked to the architecture of *Cystoseira* thalli may be damaged by substrate modification; in fact, many epifaunal organisms are related to particular macroalgae and may be strongly influenced by the presence of invasive species (Viejo 1999, Gestoso et al. 2010). On the other hand, polychaetes are not specifically facilitated by the morphology of canopy seaweeds, and food preference and/or different substrate requirements may well cause their increase in invaded areas; in fact, several polychaete species may be facilitated by turfs created by *L. lallemandii*, where sediment and organic matter could be trapped. Caprellid amphipods need cylindrical substrates with a small diameter to be encircled by pereopods in order to avoid being dislodged by water movements (Aoki and Kikuchi 1990), and the presence of *L. lallemandii* can increase the substrate available for anchoring. Moreover, herbivore amphipods, ampithoids in particular, may also be influenced by the increase in food availability in invaded areas (Duffy 1990, Duffy and Hay 2000, Poore et al. 2008).

The results show that the effects of *L. lallemandii* colonization on mobile organisms are related more to changes in species composition than to changes in patterns of diversity. This finding agrees with those described for other introduced seaweeds, suggesting that, while macroalgal invasions strongly affect diversity of sessile assemblages (Ribera and Boudouresque

1995, Piazzi et al. 2001, Schaffelke and Hewitt 2007, Baldacconi and Corriero 2009, Zuljevic and Nikolic 2008), the effects of invasions on mobile organisms are more related to changes in the structure of assemblages (Vázquez-Luis et al. 2009, Gestoso et al. 2012, Janiak et al. 2012, Pacciardi et al. 2011, Engelen et al. 2013).

Differences between invaded and non-invaded beds were not evident five months after the disappearance of *L. lallemandii*. The effects of invasion on *Cystoseira*-associated assemblages seem to be limited to the period of vegetative growth of the alga and reversible during the period of its vegetative rest. Recovery of assemblages could be related both to the intrinsic characteristics of organisms and to the lack of damage to *C. crinita* thalli. Macro-invertebrate assemblages are able to respond rapidly to various kinds of impacts (Teixeira et al. 2009), but they are also able to recover their original structure quickly after disturbance because of the short life cycles of the organisms (Lu and Shio-Sun Wu 2007, Pacciardi et al. 2011). Moreover, recovery followed the return of the habitat to its original structure. In fact, until now, no evidence of *Cystoseira* regression has been observed in invaded areas of Pianosa Island (Bedini et al. 2011). Although *L. lallemandii* completely cover *Cystoseira* thalli during the period of spread, several months without the invasive alga seem to be enough to avoid severe damage to *Cystoseira* beds.

The effects of *L. lallemandii* invasion at Pianosa Island seem to be less severe than those described in the Balearic Islands. However, the colonization of *L. lallemandii* in the Tuscan Archipelago has recently started and more severe effects could be hypothesized after longer periods of colonization on both *Cystoseira* beds and its associated assemblages, indicating the importance of monitoring the spread of the invasive alga.

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