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SYNERGISM BETWEEN DIFFERENT ASPECTS OF GLOBAL CHANGE: BIOLOGICAL INVASIONS AND EUTROPHICATION IN CORALLIGENOUS HABITATS

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GENERAL INTRODUCTION

1. SYNERGISM BETWEEN DIFFERENT ASPECTS OF GLOBAL CHANGE: BIOLOGICAL INVASIONS AND ENVIRONMENTAL DISTURBANCE

Since the Rio Convention, global change and biodiversity are two central concerns in both political and scientific debates. In addition to climatic changes, the global environment is undergoing modifications brought about by humans increasing use of the environment, and as a result of a number of interacting components which can be directly or indirectly due to human activities. Thus, global environmental change is a complex phenomenon comprising multiple events which alter the structure and function of ecological systems, with possible occurrence of serious cascade effects. As a result, biodiversity issues are at stake not only because of the extinction of endangered species, but because of new equilibria in the communities resulting from human-induced changes (Occhipinti-Ambrogi & Savini 2003).

In this context, there is a need for study of synergism at a global scale between different environmental processes (Vitousek 1994; Huenneke 1997). Among these processes, biological invasion is recognized as an important element of global change and a major driver of ecosystem modification (Vitousek et al. 1996, 1997). However, other human induced impacts, such as changes in the atmospheric composition, alteration of biogeochemical cycles, fragmentation of habitats and erosion of biodiversity, can affect species distribution and resources dynamics in terrestrial and aquatic systems, potentially interacting with biological invasions (Dukes & Mooney 1999; Harris & Tyrrel 2001). Eutrophication represents one of these human-induced global changes, as it is a growing problem in most of the aquatic habitats all over the world (Nixon 1995; Livingston 2001; Howarth & Marino 2006) and it is considered one of the main causes for deterioration of coastal water quality and loss of ecosystems complexity (Soltan et al. 2001; Arevalo et al., 2007).

1.1 Introduced species and success of biological invasions

Biological invasions have been recognised as an expression of global change (Vitousek et al. 1996; Bright 1999) as they are altering the biodiversity of nearly all the environments (Robinson & Dickerson 1987; Soule 1990; Hobbs & Mooney 1998; Levine 2000) and are often related to climatic and other changes in the globe (Bianchi & Morri 1993; Bianchi 1997; Dukes & Mooney 1999; Duarte et al. 1999).

Since the problem of introduced species is recognized world wide, in the framework of the Convention on Biodiversity (CBD/COP6, 2002) the Conference of Parts defined: **i) Introduced species:** species or taxa intentionally or accidentally introduced by human activity; **ii) Alien species**: species or taxa occurring beyond its natural range of distribution and dispersion; **iii) Invasive alien species:** alien species whose introduction and dispersion represents a threaten for ecosystems, habitats and organisms with an impact on economic and human health.

According to these international definitions, the introduced species are not all "aliens", while the alien species are not always "invasive" and they may have negligible or little effect; however they may also become invasive species and profoundly alter the host ecosystem, with serious ecological and economic consequences (Carlton 1989, 1996a; Ribera & Boudouresque 1995; Eno et al. 1997; Ivanov et al. 2000; Bax 2003).

The rate of biological introductions of marine macrophytes into new areas of the world has been increasing dramatically over the last few decades (Ribera & Boudouresque 1995). This is mainly due to an increase in ship traffic, aquaculture and other human activities, which multiply the opportunities for introduction (Carlton 1996b). In this context, Mediterranean is, at the world scale, the sea that harbours the greatest number of introduced macrophytes. Boudouresque & Verlaque (2002) listed 85 species meeting the criteria of being declared "introduced". They discuss the proportion of introduced macrophytes species that become invasive and conclude that about 9 species out of 85 are considered invasive, since they play a conspicuous role in the recipient ecosystem, becoming the dominant species or taking the place of keystone species; in some cases they are economically harmful. In general terms, it has been found, for several terrestrial ecosystems as well as for marine macrophytes in the Mediterranean Sea, that approximately 1 out of 10 introduced species (= established) becomes invasive in the new environment; this crude estimation is known as the 'tens rule' (Williamson 1993; Williamson & Fitter 1996; Boudouresque & Verlaque 2002a**).** However, factors determining whether introduction of a new species is successful and whether acclimation takes place in the new habitat are poorly understood.

Success will depend on the species' biological traits, adaptation strategies, dispersion vectors and characteristics of the host ecosystem (Ashton & Mitchell 1989; Simberloff 1989; Ribera & Boudouresque 1995; Goodwin et al. 1999). Bioinvasion studies are mostly focussed on the peculiar biological properties of the alien species successfully established in nonnative environments (see Kolar & Lodge 2001), while very few studies are carried out on the ecological mechanisms aiding invasion, as i.e. those related to the characteristics of the receiving ecosystem and to the effects of environmental disturbances.

The ecosystem characteristics that render communities or habitats vulnerable or resistant to biological introductions are currently the focus of much debate. Two of these characteristics, species richness and disturbance, have been extensively discussed (Simberloff 1989; Cohen & Carlton 1998; Occhipinti-Ambrogi 2000). The hypothesis known as Elton's 'biotic resistance hypothesis' (Elton 1958) assumes that a species-rich ecosystem will be more resistant to introductions than a species-poor one. Several researchers have found that there seems to be a negative correlation between species richness and the number of introduced species in a habitat (Loope & Mueller-Dombois 1989; Pimm 1989; Rejmánek 1989; Simberloff 1989; Lodge 1993; Ribera & Boudouresque 1995). This is usually explained by the fact that an ecosystem with many species represents a highly structured system with many complex inter-species interactions, such as competition, predation, mutualism, parasitism and disease. The higher the number of competitors, predators, parasites and diseases, the lower will be the availability of resources such as space, nutrients and light, and the possibility of successful establishment of introduced species (Stachowicz et al. 1999). However, the final picture often results more ambivalent, because a higher number of species will increase the diversity of biological resources and trophic niches potentially available to the introduced species. In other cases, the communities are vulnerable to biological introductions whatever the degree of species richness. Therefore, other models considered functional composition of assemblages more important than species diversity (Meiners et al. 2004; Arenas et al. 2006; Britton-Simmons 2006). Whatever the result, any environmental alteration which modifies structure of natural assemblages may in all cases reduce their resistance, facilitating the spread of alien species. For this reason, although the common properties of ecosystems affected by invasive species have been poorly investigated, invasibility of stressed ecosystems has been advocated in several papers, since Elton's classic book (Elton 1958; Occhipinti-Ambrogi & Savini 2003).

Environmental disturbances represent the second ecosystem characteristic that could play a major role in determining whether a community is rather vulnerable or resistant to species introductions (Hobbs 1989). The notion of stress (or disturbance) of the environment, and particularly for marine ecosystems, has been used extensively in the literature (Lewin 1983; Suchanek 1994; Leppakoski & Mihnea 1996; Bianchi et al. 1998) and it is generally used in a broad sense, assuming various types of disturbance both natural and man-induced. High levels of disturbance favour species introductions by temporarily disrupting or depleting native communities (Moyle & Light 1996), with an extent of community damage depending on the quality, frequency and degree of the disturbances. For example, some authors reported a positive correlation between the frequency of the disturbance and the success of an introduced species (Ashton & Mitchell 1989;

Rejmánek 1989; Case 1996; Moyle & Light 1996). The disturbances act differently within structured communities, either by increasing limiting resources (space, light and nutrients), or by determining the development of communities that are 'unsaturated' in terms of species numbers, or immature in terms of succession (communities poor in superior competitors). Moreover, effects of disturbance and resistance to stress of native communities will also depends on the existing successional stage of ecosystems undergoing the environmental stress (Irving et al. 2009).

Humans influence marine ecosystems in many ways: through nutrients and organic enrichment, pollution, physical habitat alterations and selective harm to plant and animal populations as i.e. overexplotation (McIntyre 1999; Bianchi & Morri 2000). All these different kinds of disturbances lead to greater vulnerability of the community with respect to species introductions (Hobbs 1989; Pimm 1989), consequently increasing probability of biological invasions success. In fact, environmental alterations may directly influence the spread of invasive species, by increasing its growth rate or reproductive ability, but they can also indirectly act, by decreasing communities or habitat resistance to the invasion through modifications of assemblage structure (Piola & Johnston 2008).

In this context, knowledge of the relationship between invasions by alien species and the degree of overall stress experienced by invaded marine systems, often caused by human intervention, became an essential goal for ecologists, as understanding of mechanisms aiding colonization of alien species is crucial both for assessment of threat posed by their spread and for planning control programs (Dukes & Mooney 1999; Harris & Tyrrell 2001). In fact, an organism capable of spreading in the absence of any primary facilitation mechanisms represents a major threat to the integrity of native assemblages and its management needs to directly target the organism itself; on the contrary, management of invasions by organisms requiring disturbance or other facilitating mechanisms to establish and persist includes several options that can indirectly act on the cause of disturbance rather than on the invader itself (Valentine et al. 2007).

1.2 Eutrophication and biological invasions in marine coastal systems

According to the OCSE definition (Organization for the Economic Cooperation and Development) eutrophication consists in " the nutrients enrichment of the natural waters which causes typical changes, such as increase of algal production and aquatic plants, impoverishment of fish resources, general degradation of natural waters quality and others effects reducing or precluding their use" (Marchetti 1993). In compliance with this definition, eutrophication is in general a complex process, always starting from an increase of nutrients load in the waters and evolving then in different way, depending on different factors related to the type of aquatic

ecosystem undergoing to nutrient enrichment. In fact, most part of the Mediterranean seawaters are characterized by scarce primary production and high transparency (>30m), so they are defined "oligotrophic" in natural condition, while seawater of the Adriatic sea and many marine and transitional coastal areas are defined "eutrophic" due to the relatively high levels of nutrient concentrations and primary production and low values of transparency. Nevertheless, in this last case it is often difficult to distinguish between a natural existing eutrophic condition, which is i.e. typical of the transitional waters, and a human-induced one, like that one of many harbours and estuarine zones, or many bays and marine coastal area affected by anthropic pressures. In fact, all these kinds of coastal habitats seat intense human activities which have by now more or less altered the original natural conditions of these habitats. Therefore, an eutrophic condition in general would be considered as symptom of a diseased ecosystem which final result could be more or less serious in connection with the natural nutrients background of the affected ecosystem.

Due to the increase of density populations developing along the coastlines habitats all over the word, increase of nutrient concentration in marine waters represents one of the main aspect of human-induced global changes (Vitousek 1994; Vitousek et al. 1997). Several human activities, such as overharvest of land, deforestation, fish farming, domestic and industrial sewage discharge, may directly or indirectly influence the nutrients inflow into the sea (Carpenter et al. 1998; McClelland & Valiela 1998; Pergent-Martini et al. 2006); thus, during the last decades nutritional input has been increased leading to widespread eutrophication of many coastal areas (Nixon 1995; Howarth & Marino 2006).

Effects of increase of nutrients availability on structure and functioning of marine ecosystems have been widely investigated (Morris & Keough 2003; Prado et al. 2008; Balata et al. 2008). In particular, both correlative and experimental studies carried out on rocky shores highlighted dramatic shifts of the structure of benthic assemblages following increasing gradients of nutrient concentration (Diez et al. 1999; Soltan et al. 2001; Gorgula & Connell 2004; Karez et al. 2004; Arevalo et al. 2007). In fact, nutrient availability is usually an important factor conditioning composition of seaweed assemblages (Teichberg et al. 2008), since nutrient enrichment may stimulate the spread of annual fast-growing algae and inhibit the growth of perennial species (Gorostiaga & Diez 1996; Diaz et al. 2002; Eriksson et al. 2002; Russell & Connell 2005; Worm & Lotze 2006; Kraufvelin 2007). Replacement of habitat-structuring species with ephemeral seaweeds occurring in eutrophic water lead to a reduction of ecosystem complexity and to a widespread biotic homogenization (Valiela et al. 1992; Morand & Briand 1996). Although this phenomenon has been widely investigated, most of studies has been carried out in intertidal, rocky pools or shallow subtidal habitats (Bokn et al. 2003; Kraufvelin et al. 2006; Masterson et al. 2008; Guerry et al.

2009; Atalah & Crowe 2010), while very few information are available about the effects of nutrient enrichment on deep subtidal communities, where abiotic conditions are more steady throughout the seasons (Witman & Dayton 2001). Since effects of human impacts may depend on the depth gradient (Korpinen et al. 2007; Piazzi & Balata 2010), any additional knowledge on this topic may be useful for coastal management, particularly for the most sensitive Mediterranean habitats as *Posidonia oceanica* and coralligenous habitat.

As far as relationship between eutrophication and biological invasions concerned, the increase of nutrient load is in general considered an anthropogenic factor enhancing dominance of non-native species in many natural systems (Hobbs & Huennecke 1992; Burke & Grime 1996). Nevertheless, effect of nutrient availability on the invasions has been examined mainly on terrestrial plants (Burke & Grime 1996; Gross et al. 2005; Leishman & Thomson 2005) while only a few experimental studies have been made on this topic in marine ecosystems, even if important synergetic effects have been highlighted by some authors (Steen 2003; Sánchez & Fernández 2006; Incera et al. 2009). Nutrient enrichment can aid the spread of introduced macroalgae through different mechanisms (Stimson et al. 2001; Torres et al. 2004). In fact, increase of nutrients concentrations in natural systems is detrimental to slow-growing plants which are adapted to nutrient-poor habitats and creates favourable conditions for faster-growing plants, such many invasive seaweeds. Thus, on the one hand, nutrients availability may directly enhance the growth of alien seaweeds and seagrasses facilitating their spread (Stimson et al. 2001; Torres et al. 2004; Lapointe et al. 2005); on the other hand, degradation of benthic systems caused by nutrients pollution can decrease resistance of native assemblage to invasions (Stachowicz et al. 1999). Therefore, the knowledge of synergetic mechanisms between nutrient enrichment and biological invasions represents an important goal for the ecologists in elaborating predictive models and planning conservation programs (Lapointe & Beldford 2010).

2. ALIENS SPECIES IN MEDITERRANEAN HABITATS: THE INVASION OF MACROALGA *CAULERPA RACEMOSA* VAR. *CYLINDRACEA*

The Mediterranean sea represents about 6% of the total world marine species, even though its surface is only 0.8% of the total surface of the oceans. An estimate of 8500 species of macroscopic marine organisms has been made for the Mediterranean (7200 metazoans and 1300 macrophytes) and this faunal richness is accompanied by a high level of endemic species (more than 25% in total). Areas of lower diversity are located in the Eastern Basin, in the Black Sea and in the Northern Adriatic (Fredj et al. 1992; Bianchi & Morr 2000).

The Mediterranean basin harbours around 600 introduced species representing 5% of the known flora and fauna (Boudouresque & Verlaque 2005; Boudouresque et al. 2005; Zenetos et al. 2005) and it harbours the greatest number of introduced macrophytes at the global level. The native Mediterranean fauna was mainly colonised by the Indian Ocean species, the so-called Lessepsian migrants (Por 1978), which have been entering through the Suez canal since its completion in 1869. It has been calculated that these species (over 300) now constitute nearly 5% of the global Mediterranean fauna and 13% of the species found in the southeastern Mediterranean, and this invasion is continuing (Galil 2000). Besides Lessepsian migrations, the main vectors for introductions in the Mediterranean are aquaculture (especially developed in the lagoons along the French coastline and the Italian Adriatic) and unintended transport (e.g. via ballast waters). The oyster transfer is considered the number one vector of macroalgae introduction in the Mediterranean Sea (Verlaque 2001) and this is probably also true for many animals. Nevertheless, it is not always easy to discriminate among different vectors, since specific investigations have not always been performed even in the case of the most remarkable invasions: for example, introduction of the invasive macroalga *Caulerpa taxifolia* was most likely started by the discharge from aquarium tanks used for decorative purposes. In other cases (i.e. the gasteropod *Rapana venosa*) vectors of introduction remains uncertain.

The Mediterranean sea can be also considered as one of the regions most severely affected by the biological invasions along with the Bay of San Francisco, the Baltic and the Black Sea (Klein & Verlaque 2008). The list of invasive species established by Zibrowius (1991) comprises of more than 160 species and many others have been added since then owing to occasional observations, even though a systematic survey has not yet been planned.

2.1 Introduced seaweeds in the Mediterranean basin

The Mediterranean sea harbours the greatest number of introduced seaweeds at the world scale; since the beginning of 20th century, this number has more or less doubled every 20 years (Ribera & Bouderesque 1995). More than 90 taxa of red, brown and green algae are probably introduced in the Mediterranean, even if they belong mainly to the Rhodophyta; the Indo Pacific Ocean is the main reserve of non-indigenous species (NIS) (Ribera Siguan 2002). In confirmation of the "tens rules" (see Chapter 1), about nine species out of 90 become "invasive", since they have negative impact on the recipient communities (Boudouresque & Verlaque 2002). Species of macroalgae have been responsible for some of the most dramatic invasions in the marine habitats (Verlaque 1994; Meinesz et al. 2001; Silva et al. 2002) and the most famous cases recorded for the Mediterranean coasts are due to following species:

- *Caulerpa taxifolia* (Vahl) C. Agardh, accidentally released from the Monaco Aquarium (North Western Mediterranean) quickly spread throughout all the Mediterranean basin (Meinesz & Hesse 1991);
- *Acrothamnion pressii* (Sonders) E.M. Wollaston (Indopacific origin) and *Womersleyella setacea* (Hollemberg) R.E. Norris (Pantropical origin). The first one is considered introducing via fouling (Cinelli & Sartoni 1969), while the second one via fouling and/or fisheries (Verlaque 1989);
- *Lophocladia lallemandii* (Montagne) F. Schmitz and *Stypopodium schimperi* (Buchinger ex Kutzing) (Klein & Verlaque 2008);
- *Asparagopsis armata* Harvey which is endemic of the southern hemisphere (Feldman & Feldman 1942) and the pantropical species *Asparagopsis taxiformis* (Delile) Trevisan (Barone et al. 2003; D'Archino et al. 2003; Flagella et al. 2003);
- *Codium fragile* var. *tomentosoides* (Goor) P.C. Silva and Atlantic species which introduction is related to transfer of oysters (Boudouresque 1994);
- *Sargassum muticum* (Yendo) Fensholt, *Undaria pinnatifida* (Harvey) Suringar and *Laminaria japonica* Areschoug which are all Japanese species occurring in the Mediterranean lagoons such as Venice Lagoon (Italy) (*S. muticum*, *U. pinnatifida*) (Curiel et al. 1998; Occhipinti-Ambrogi 2002), Thau Lagoons (France) (*S. muticum*, *U. pinnatifida, L. japonica*) (Belsher & Pommellec 1988; Verlaque 2001) and Mar Piccolo of Taranto (Italy) (*U.pinnatifida*) (Cecere et al. 2000). Their introduction seems to be related to the oysters transfer and, for *U. pinnatifida* and *L. japonica* also to the algal culture (Perez et al. 1984);

- *Caulerpa racemosa* (Forsskal) C. Agardh var *cylindracea* (Sonder) Verlaque, Huisman et Bouderesque (Verlaque et al. 2003) an Australian taxon which since its first record in Lybia (Nizzamudding 1991) it has rapidly spread in the basin.

However, factors determining the success of these introduced species in the Mediterranean sea remain unclear and models like the Elton's 'biotic resistance hypothesis'(see Chapter 1) are often not able to explain the phenomenon. In fact, the Mediterranean basin hosts the greatest number of introduced macrophytes, despite it is a hot spot for macrophyte species diversity (ε species diversity sensu Gray 2000) and this is not consistent with the assertion that high species diversity improves resistance to species introductions.

The Eastern Mediterranean basin has lower ε species diversity (sensu Gray 2000) than the Western basin and harbours relatively more introduced species, most of which originate from the Red Sea (Lessepsian species). The great success of Lessepsian species in the Eastern basin has been explained by the low native species diversity, resulting from the climatic crises repeatedly occurred in geological times (Por & Dimentman 1985) which have caused many niches to empty, leaving a place for the invasion of opportunistic allochtonous species (Giaccone & Di Martino 1997). However, the Eastern basin is probably more susceptible to biological invasions due to the intense maritime traffic from the Indian Ocean and higher occurrence of fish and shellfish farms (Galil & Zenetos 2002). In the Western Mediterranean, where there is an absence or quasi-absence of Lessepsian species, fewer vacant niches and higher diversity and inter-specific competition may prevent colonization; nevertheless, this part of the basin seems to be the main receptive region of exotic marine macrophytes. Therefore, other factors such as its high eco-diversity, the wider seawater temperature range (allowing the naturalization of species belonging to a wide biogeographical affinity) and greater demographic pressure (Ribera Siguan 2002) may play an important role. In confirmation of this, many pristine species-rich localities such as the Corsica Nature Reserve of Scandola (France), the Medes Islands (Spain) and the Gorgona Island are now strongly affected by certain alien species (Rodriguez Prieto et al. 1993; Sala & Boudouresque 1997; Piazzi & Cinelli 2001) and certain disturbed environments exhibit higher numbers of introduced taxa than undisturbed ones (Galil 2000). For example, in case of the sensitive habitats *Posidonia oceanica* (L.) Delile, it has been suggested that the success of 2 introduced *Caulerpa* species, *C. racemosa* and *C. taxifolia*, is linked to the degradation of the *Posidonia* meadow due to direct or indirect human influence (Occhipinti-Ambrogi & Savini 2003). In certain habitats that are exposed to human-made disturbances and which possess rather low species diversity, such as harbours and lagoons, the number of introduced species is higher than in undisturbed ones. However, all pathways of introduction converge in such habitats, so that the relationship between disturbance,

low species diversity and high number of introduced species may be an artefact due to the high rate of species importation (Ribera & Boudouresque 1995; Boudouresque & Verlaque 2002b).

Although all Mediterranean habitats are considered vulnerable to invasions (Lodge, 1993), some of them are suspected of being more sensitive than others (Wasson et al., 2005). According to Giaccone (2002), the Mediterranean habitats hierarchically more receptive to the introduced seaweeds species are: 1) photophilous infralittoral biocenosis, 2) lagoons and coastal habitats used for aquaculture, 3) harbour area, 3) coastal degraded habitats, 4) infralittoral sciaphilous biocenosis. Several studies are carried out on the effect of different macroalgal invaders in different Mediterranean habitats, mainly in the shallow rocky and *Posidonia oceanica* habitats (Piazzi & Balata 2009; de Villele & Verlaque 1995; Ceccherelli & Cinelli 1998; Ferrer et al. 1997; Piazzi et al. 2001) while very few studies are reported about macroalgal invasions in the deep rocky habitats, particularly in the coralligenous assemblages.

2.2 The *Caulerpa racemosa* var. *cylindracea* invasion

Among the main biological invasions in the Mediterranean Sea, the spread of aliens species of the genus *Caulerpa* and turf-forming Rhodophyta are considered particularly serious (Meinesz et al. 2001; Boudouresque & Verlaque 2002). The ecological and economic threats posed especially by the two Chlorophyta *Caulerpa racemosa* and *Caulerpa taxifolia* encouraged scientists to organise international campaigns of public awareness, research and prevention in Monaco, France, Italy, Spain, Croatia and Tunisia, the most colonised countries by these NIS (see: www.com.univ mrs.fr/gisposi/ and www.caulerpa.org). Following paragraph will describe the main biological and ecological traits of the invasive species *C. racemosa* which is the alien species object of this thesis.

2.2.1 Taxonomy

***Caulerpa racemosa* (Forsskal) J. Agardh** is a Chlorophyta of the order Bryopsidales belonging to the family Caulerpaceae; the genus *Caulerpa* includes approximately 85 species (Guiry & Guiry 2007). There is much confusion in the literature regarding the taxonomic classification of several *Caulerpa* species complexes (including the *C. racemosa* complex), within which different undetected species are certainly confused. The *C. racemosa* complex is distinguished from the flat feather-like *Caulerpa taxifolia* by spherical, club-shaped or mushroom- to disc-shaped branchlets (Klein & Verlaque 2008). A high number of infraspecific taxa (about 111) have been described inside the *C. racemosa* complex. However, high morphological plasticity induced by environmental parameters renders the validity of numerous taxa questionable (Ohba & Enomoto 1987; Prud'homme van Reine et al. 1996).

Three infra-specific taxa of *C. racemosa* have been identified in the Mediterranean Sea (Verlaque et al., 2000, 2003): a) *C. racemosa* var. *turbinata-uvifera*, an intermediate between var. *turbinata* (J.Agardh) Eubank and var. *uvifera* (C.Agardh) J.Agardh, corresponding to the first record in Tunisia and restricted to the eastern basin; b) *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse f. *requienii* (Montagne) Weber-van Bosse, recorded in the Levantine basin in 1951 and remained stable since its first record; c) the "invasive variety" of *C. racemosa* recorded for the first time in Lybia in 1991; it was first considered closed to the *C.racemosa* var. *occidentalis* (J.Agardh) Borgesen. The identity and origin of this new introduced taxa remained obscure for one decade. First it was supposed that *C. racemosa* was a Lessepsian migrant from the Red Sea (Alongi et al. 1993; Giaccone & Di Martino 1995a). However, morphological examination and bibliographical analysis ruled out the idea of a lessepsian migration while supporting the hypothesis of the species having been introduced by means of other vectors (Verlaque et al. 2000). Molecular data confirmed the morphological findings and suggested a hybrid origin for the invasive variety between the var. *turbinata-uvifera* and an unknown tropical strain (Durand et al. 2002). Nevertheless, Verlaque et al. (2003) disproved this hypothesis and demonstrated that the invasive event resulted from a recent introduction from Australia. Thus, the invasive variety was identified as a poorly known taxon named ***Caulerpa cylindracea*** **Sonder** (1845) which is endemic from the region between Perth and Hopetoun in South-western Australia (Harvey 1858; Womersley 1984; Fama` et al. 2000; Verlaque et al. 2003). A morphological and genetic study classified this taxon as ***Caulerpa racemosa*** **var.** ***cylindracea*** **(Sonder) Verlaque, Huisman & Boudouresque** (hereafter only *C. racemosa*) (Verlaque et al. 2003). The identity of specimens from Croatia, Cyprus, France, Greece, Italy, Turkey and the Canary Islands has been proved by genetic studies (Fama` et al. 2000; Verlaque et al. 2000, 2003; Nuber et al. 2007). High intra-population genetic variability has been observed in the recently introduced *C. racemosa* (Fama` et al. 2000, 2001; Jousson et al. 2001).

2.2.2 Morphology and reproduction

The *Caulerpa* species are coenocytic algae which have uniaxial siphonous thallus mostly divided into a creeping axis (stolons) with rhizoids and erect shoots (fronds) either nude, leaf-like or with grape- or feather-like ramuli. *C. racemosa* is charachterized by erect fronds up to 11 cm (exceptionally 19 cm) high bearing un-crowded vesiculate ramuli that are radially or distichously arranged (Appendix-Figures 1 and 2) and whose morphology is taxonomically relevant. Fronds are slightly inflated above the attachment to the stolon which is fixed to the substrate by thin short rhizoids (Verlaque et al. 2003). Morphometric data of *C. racemosa* in the Mediterranean Sea may vary according to region, depth and season (Klein & Verlaque 2008).

Like many other species, *C. racemosa* is capable of reproducing sexually and vegetatively. Sexual reproduction is holocarpic, the entire cytoplasm of the cell forms anisogametes which are liberated simultaneously, resulting in the subsequent death of the individual. *C. racemosa* like *Caulerpa taxifolia* is monoecious (Goldstein & Morall 1970; Panayotidis & Zuljevic 2001). The gamete release process is preceded by the appearance of small papillae and the transformation of the cytoplasm into a light green and brownish orange network. Approximately 14 min before sunrise gametes are released within a few minutes forming a green cloud (Panayotidis & Zuljevic 2001) and after gamete release, the emptied thallus decomposes rapidly within a few hours. The zygote develops into a protonema-like plant which forms creeping filaments with erect shoot. While some light is shed on the reproduction processes, the cues triggering sexual reproduction remain unclear (Klein & Verlaque 2008).

The asexual reproduction may occur in the forms of growth pattern, fragmentation and formation of propagules. The particular growth pattern of *Caulerpa* species, where one end of the ramified stolon decomposes while the apices keep growing, results in rapid multiplication of individuals. Fragmentation of the thallus can be caused by disturbances (water movements, grazing, human activities). The resulting fragments are able to survive several days of transport and may re-establish on a suitable substrate (Ceccherelli & Piazzi 2001a). Drifting *C. racemosa* fragments have frequently been observed in the water column in Italy and seem to be a highly effective multiplication mechanism especially in summer (Ceccherelli et al. 2000; Ceccherelli & Piazzi 2001a). Attachment of these *C. racemosa* fragments to the substratum occurs within a few days (Carruthers et al. 1993). Propagule formation has been observed in the laboratory (Renoncourt & Meinesz 2002) and it consisted in detached ramuli producing chlorophyllous filaments growing after only 5 days into a new individual.

2.2.3 Distribution, spread and seasonal dynamics

C. racemosa var. *cylindracea* is a native species of the South Western Australia, between Perth and Hopetoun (Womersley 2003; Collings et al. 2004), from which it was been introduced to Adelaide in 2001 (Appendix-Figure 3). In its native range, *C. racemosa* occurs in intermixed assemblages with other algae, without forming monospecific meadows (Carruthers et al. 1993; Verlaque et al. 2003).

C. racemosa was observed for the first time in the Mediterranean Sea in Libya in 1990 (Nizamuddin 1991), but vectors of primary introduction into the Mediterranean Sea remains unknown; maybe they are ship traffic (ballast water, ship hull fouling) and aquarium activities.

After its first record, *C.racemosa* was subsequently signalled in Italy (Alongi et al. 1993), Greece (Panayotidis & Montesanto 1994), Albania (Di Martino & Giaccone 1995), Cyprus (Hadjichristophorou et al. 1997), France (Jousson et al. 1998), Turkey (Cirik, 1999), Malta (Stevens 1999), Spain (Ballesteros et al. 1999), Tunisia (Belkhiria 1999), Croatia (Zuljevic´ et al. 2003), and Algeria (Ould-Ahmed & Meinesz 2007) probably due to the quickly action of dispersion vectors such as shipping (ballast water, anchor gear), fishing (dredging, trawling, bottom nets and traps) and/or currents (Piazzi et al. 1997; Gambi & Terlizzi 1998; Serio & Pizzuto 1998; Relini et al. 2001; Verlaque et al. 2003, 2004; Zuljevic et al. 2004; Ruitton et al. 2005a). Only 17 years after its first observation, *C. racemosa* has colonized 12 countries and all major islands in the Mediterranean Sea as well as the Canary Islands in the Atlantic Ocean (Fama` et al. 2000; Verlaque et al. 2004) (Appendix-Figure 4). It seems from the literature that country most heavily affected is Italy (500 km of coastline), followed by the Balearic Islands (120 km), France (83 km) and Croatia (15 km) (Piazzi et al. 2005a), even if this estimation must be considered with caution due to the lack of standardized recording methods.

In most of the invaded Mediterranean areas, population of *C.racemosa* remains stable since non decrease in colonized surface has been reported after 17 years (Klein & Verlaque 2008), but only a seasonality regression of the *C. racemosa* stolon and erect axis length, growth rate, cover and biomass was detected. In fact, in the Mediterranean habitats *C.racemosa* generally show a pattern of maximum growth between June and December (with peaks in September-November) followed by a winter regression varying from different Mediterranean areas, habitats and depths. In contrast, in southern Italy, *C. racemosa* does not show a clear winter regression (Giaccone & Di Martino 1995b).

2.2.4 Ecology

In its native range in south-western Australia, *C. racemosa* is a common and opportunistic species growing intermixed with other algae from the intertidal down to only 6 m depth on reef flats and in intertidal pools (Womersley 1984; Carruthers et al. 1993). In contrast, in the Mediterranean Sea, it occurs in wide and dense monospecific meadows and thrives under a large array of environmental conditions. In fact, it is found on all kinds of soft and hard substrata such as in tide pools, on pebbles, rock, dead *Posidonia oceanica* matte, sand, mud, detritic and coralligenous assemblages in depths ranging from 0 to 70 m, with highest abundance between 0 and 30 m (Verlaque et al. 2003; Piazzi et al. 2005a; Ruitton et al. 2005a).

Temperature of water in its native habitat range from 14.0 to 16.0 °C in winter and 22.5 °C in summer (Verlaque et al. 2003), while in the Mediterranean Sea, *C. racemosa* is exposed to a wider

temperature range down to 8 °C in Croatia (Zuljevic´ 2005) and up to an average of 28 °C in the Eastern basin (Cyprus, Libya, Turkey). Salinity ranges from 35.27 to 37.00 in south-western Australian waters and around 38.50 in Mediterranean waters, but *C. racemosa* was found in two Mediterranean coastal lagoons, Mar Piccolo and Mar Grande di Taranto (Mastrototaro et al. 2004), where salinity ranges from 34.3 to 37.7 (Alabiso et al. 1997). In the Mediterranean Sea, observation of deep populations (up to 70 m of depth) attests to the high tolerance of *C. racemosa* to low light conditions. The invasive alga is capable of performing photoacclimation, which takes place both at increasing depth and during a seasonal cycle. In fact, the number of reaction centres can be changed according to irradiance levels to maintain constant photosynthetic efficiency and photosynthetic efficiency itself can be increased under low irradiance levels while keeping the number of reaction centres constant (Raniello et al. 2004, 2006). The effect of water motion on *C. racemosa* is unclear. The species has been found on exposed shores as well as in sheltered areas with the exception of unstable soft-bottom substrates. However, on wave-exposed coasts the *C. racemosa* meadows may be damaged by sand scour (unpubl. data). It seems that *C. racemosa* is relatively resistant to burial by sediments (Piazzi et al. 2005b).

The species is found in polluted as well as relatively pristine areas (Ballesteros et al. 1999; Zuljevic´ et al. 2004; Ruitton et al. 2005a; Mifsud & Lanfranco 2007), so its wide spread would seem independent of environmental disturbance. Nevertheless, the increased occurrence of *C. racemosa* in the proximity of large cities and industrial, cargo, passenger, fishing and recreational boating harbours was often observed suggesting possible ecological mechanisms facilitating invasion in the impacted sites, even if clear affinity for polluted areas was never been demonstrated. Anyway, these observations attest the tolerance of *C. racemosa* to high levels of pollution which is partially demonstrated by biochemical studies: in fact, in *C. racemosa* higher levels of enzyme activity (SOD, CAT) have been observed compared to Mediterranean macroalgae, thus indicating higher capability to cope with environmental stress (Cavas &Yurdakoc 2005).

C.racemosa appear to be both resistant and resilient to the herbivores grazing action thanks to the production of secondary metabolites which are probably involved also in competition with other species: in fact, antiproliferative and apoptotic effects of *C. racemosa* crude extracts and Caulerpenyne have been shown on different cell lines (Cavas et al. 2006); in particular, Caulerpenyne directly applied onto the leaves of the seagrass *Cymodocea nodosa*, triggered alterations in photosynthesis (Raniello et al. 2007). Caulerpenyne production varies seasonally and between different parts of the thallus. Despite chemical defences produced by *C. racemosa*, several herbivores are encountered in the Mediterranean meadows. The fish species observed to graze on *C. racemosa* were *Boops boops* (Linnaeus, 1758), *Pagellus acarne* (Risso, 1827) and *Sarpa salpa*

(Linnaeus 1758) (Nizamuddin, 1991; Ruitton et al., 2006) and the lessepsian species *Siganus luridus* (Ruppell 1829) in the central and eastern Mediterranean Sea (Lundberg et al. 1999; Azzurro et al. 2004); the two sea urchins *Paracentrotus lividus* (Lamarck 1816) and *Sphaerechinus granularis* (Lamarck 1816) (Ruitton et al. 2006) and several herbivorous molluscs consume *C. racemosa*: *Aplysia* sp., *Ascobulla fragilis* (Jeffreys 1856), *Bittium latreillei* (Payraudeau 1826), *Elysia tomentosa* (Jensen 1997), *Lobiger serradifalci* (Calcara 1840), *Oxynoe olivacea* (Rafinesque 1814) (Gianguzza et al. 2001, 2002; Yokes & Rudman 2004; Cavas & Yurdakoc 2005; Djellouli et al. 2006).

2.3 Impact of *Caulerpa racemosa* var. *cylindracea* on Mediterranean habitats

The *C.racemosa* invasion represents the most severe invasive event ever known in the Mediterranean Sea in terms of quickness of spread, invaded surface and impact on ecosystems (Piazzi et al. 2005a; Klein & Verlaque 2008). Thanks to its stoloniferous structure, the invasive alga was being able to develop on all kind of substrata, forming permanent populations in all kinds of habitats and strongly interfering with the native assemblages (Meisenesz et al. 1993; Piazzi et al. 2001, 2005b; Piazzi & Balata 2008; Klein & Verlaque 2008; Infantes et al. 2011).

Particular concerns are awakened for the most sensitive habitats: in fact, marine ecosystems which are essential for biodiversity conservation, such as seagrass meadows and coralligenous habitat (sensu Ballesteros 2006), have been invaded by *C. racemosa* with consequent loss of the original assemblages structure and biodiversity (Ceccherelli & Campo 2002; Piazzi et al. 2007a; Antolic et al. 2008). Studies carried out in different invaded habitats highlighted the loss of α diversity (as both number and relative abundance of species) and β diversity (as variability in species composition and abundance among habitats or along gradients, Gray 2000), which may led to a biotic homogenization with deep consequences for structure and functioning of ecosystems (Piazzi & Balata 2008; Airoldi et al. 2008; Olden & Poff 2003). These effects may be amplified due to the capacity of *C.racemosa* to modify the structure of habitats, making the effects of colonization more persistent (Wikstrom & Kautsky 2004; Hastings et al. 2007). In fact, on the colonized substrates *C. racemosa* may form compact multilayered mats up to 15 cm thick which trap sediment thereby possibly contributing to the siltation of the assemblages (Pandolfo & Chemello 1995; Piazzi et al. 1997, 2007a,b; Argyrou et al. 1999; Zuljevic´ et al. 2003). Piazzi et al. (2007) have demonstrated that *C. racemosa*, by entrapping particles through the complex network of stolons, can result in an up to sevenfold increase in accumulated sediments. Thus, the effect of *C. racemosa* colonization and sedimentation stress are similar, indicating that the impact on macroalgae assemblages could be mainly caused by accumulation and burial by sediments induced by the mat

(Piazzi et al. 2005b). As a results, in the invaded areas it was observed the decrease in the total number of species and total macroalgae cover. All layers were concerned, with the encrusting layer being particularly reduced on rocky substrate.

As far as seagrasses are concerned, *C. racemosa* and *C. taxifolia* are outcompeting the endemic Mediterranean seagrass *P. oceanica* (de Villele & Verlaque 1995; Ceccherelli & Cinelli 1998), for which a reduced leaf length and leaf area index was found in presence of *C. racemosa* together with a higher turnover rate at the same time (Dumay et al. 2002b). In the *Cymodocea nodosa* (Ucria) Ascherson meadows a decreased of shoot density was observed in the presence of *C. racemosa* (Ceccherelli & Campo 2002).

2.3.1 Caulerpa racemosa as driver or passenger of ecological changes?

The general role of biological invasions in driving ecological changes is recognized by several studies which document the dramatic effects of invaders on the biodiversity and functioning of recipient ecosystems (Mack et al. 2000). The role of "driver" of ecological changes played by an invader is strengthened when it is recognized, like *C.racemosa*, as an "ecosystem engineers" or "foundations species" (Wright & Jones 2006; Bruno et al. 2003) because of its ability to modify the abiotic environment and influencing the community organization (Crooks 2002). In fact, possible consequences of the *C. racemosa* invasion event include modifications of physical and chemical conditions (water movement, sediment deposition, substrate characteristics) and the underwater landscape, as well as profound modifications of benthic assemblages. Due to its impact mainly on habitat architecture and sediments, and to the differentiation of extensive meadows in the Mediterranean Sea, *C. racemosa* is considered an habitat modifier (sensu Wallentinus & Nyberg 2007) and a new keystone species (=ecosystem engineers) (sensu Crooks 2002) (Pacciardi et al. 2011).

Nevertheless, although a clear relationship between success of *C.racemosa* invasion and degradation of habitats was never been demonstrated, its ability to become a dominant component of macroalgal assemblages seems greater in the degraded than in pristine environments (Piazzi & Ceccherelli 2006; Bulleri et al. 2009), suggesting more a role of "passenger" played by the invader which is successful in becoming established or in stepping up to the invasive status within communities that have been altered by human perturbations.

So, assessing if *C. racemosa* is the main cause of ecological changes (according to the driver model) or an opportunistic species (passenger model) that takes advantage of degraded environmental conditions is key to understanding pathways and impacts of biological invasions (Bulleri et al. 2010).

3. MEDITERRANEAN SENSITIVE HABITATS: CORALLIGENOUS ASSEMBLAGES

In the Mediterranean Sea, subtidal systems host three main habitats on hard bottoms: shallow rocky habitat, deep rocky habitat and habitat provided by dead matte of seagrass *Posidonia oceanica* (L.) Delile. Shallow rocky assemblages are typically dominated by macroalgae mostly belonging to Ochrophyta. Deep rocky subtidal habitat is characterised by a secondary substrate constituted by calcareous structures edified by algae belonging to Corallinales (Ballesteros 2006). ‘‘Matte’’ indicates a structure provided by rhizomes of *P. oceanica* and trapped sediments which may be several meters high; when the plant dies, matte structures persist, constituting a secondary bottom. Biotic-edified habitat characterizing the deep rocky habitats, together with meadows of the endemic seagrass *Posidonia oceanica*, are recognized as unique macrophytes dominated habitats, as they are the main ‘hot spot’ of species diversity in the Mediterranean (Barbera et al. 2003; Green & Short 2003; Ballesteros 2006). Unfortunately, these sensitive and unique habitats are threatened by high levels of pollution (sewage, dumping), anchoring, fishing pressure (dredging, bottom trawling), biological invasions and other anthropogenic disturbances (artificial structures, aquaculture, etc.) (De Grave & Whitaker 1999; Hall-Spencer & Moore 2000; Airoldi & Beck 2007). In this context, knowledge of the effects of different anthropic pressures and synergism between environmental disturbances in the most sensitive Mediterranean habitats became a fundamental goal in planning programmes for conservation of biodiversity.

3.1 The coralligenous habitat

The word ‘coralligenous’ (*coralligène* in French) was first used by Marion (1883) to describe the hard bottoms that fishermen from Marseilles called *broundo* and which are found at a depth of between 30 and 70 m, below seagrass meadows of *Posidonia oceanica* and above coastal muddy bottoms. *Coralligène* means ‘producer of coral’ and is related to the abundance of red coral (*Corallium rubrum*) found on this type of bottom.

In general, there is no real consensus among scientists studying benthic communities in the Mediterranean Sea about what a coralligenous habitat is. Ballesteros (2006) define coralligenous concretions as “the unique calcareous formations of biogenic origin in Mediterranean benthic environments, which are produced by the accumulation of calcareous encrusting algae growing in dim light conditions”. Algae and invertebrates growing in environments with low light levels are called sciaphilic in opposition to photophilic, that is, growing at high light levels. All plants and animals thriving in coralligenous habitats are, thus, sciaphilic. Although more extensive in the

circalittoral zone, coralligenous habitats can also develop in the infralittoral zone, provided that light is dim enough to allow growth of the calcareous algae that produce the calcareous framework. Therefore, the main criterion used to define the coralligenous habitat is the presence of a bioherm of coralline algae grown at low irradiance levels and in relatively calm waters. This bioherm is always very complex in structure and, in fact, allows the development of several kinds of communities (Laborel 1961; Laubier 1966), including those dominated by living algae (upper part of the concretions), suspension feeders (lower part of the concretions, wall cavities and overhangs), borers (inside the concretions) and even soft-bottom fauna (in the sediment deposited in cavities and holes). Therefore, the coralligenous habitat should be considered more as a submarine landscape or community puzzle rather than a single community.

3.1.1 Geographical and depth distribution

Coralligenous buildups are common all around the Mediterranean coasts, with the possible exception of those of Lebanon and Israel (Laborel 1987). According to Laborel (1961), the best developed formations are those found in the Aegean Sea, although the most widely studied banks are those of the Northwestern Mediterranean.

The minimal depth for the formation of coralligenous frameworks depends on the amount of irradiance reaching the sea bottom. On vertical slopes of most of the Western Mediterranean areas, this minimal depth reaches 20m, but it is much lower in other zones, where coralligenous communities are able to grow in shallower waters (12 m) because of the high turbidity of the water. This minimal depth is displaced to deeper waters in insular areas where water transparency is very high (Ballesteros & Zabala 1993). However, coralligenous frameworks can appear in very shallow waters if light conditions are dim enough to allow a significant development of coralline algae (Laborel 1987; Sartoretto 1994) and they may even occur in the clearest waters, where they can be found at a depth of only 10 m in a cave entrance (Marti et al. 2004).

Depth intervals for the distribution of coralligenous outcrops depends on geographical area and geomorphological features of the coastline. In general, coralligenous assemblages of the Western Mediterranean develop between 20 and 60m (Ballesteros 1992); nevertheless, in particularly clear waters, it colonize hard substrate between 45 and 100m (Ballesteros et al. 1993). In the Eastern Mediterranean it generally developed between 70 and 100m (Laborel 1961).

3.1.2 Environmental factors

Light is probably the most important environmental factor with respect to the distribution of benthic organisms along the rocky bottoms of the continental shelf (Ballesteros 1992; Marti et al. 2004, 2005). It is also very important for the development and growth of coralligenous frameworks, as its main builders are macroalgae which need enough light to grow but which cannot withstand high levels of irradiance (Peres & Picard 1964; Laubier 1966). According to Ballesteros (1992), coralligenous communities are able to develop at irradiances ranging from 1.3 MJ m^{-2} yr^{-1} to 50–100 MJ m–2 yr^{-1}, that is, between 0.05% and 3% of the surface irradiance. However, light levels reaching different microenvironments of coralligenous communities can differ by at least two orders of magnitude. Light levels reaching small holes and cavities of coralligenous banks must be almost zero, and similar to light levels reaching the bathyal zone or the innermost part of caves.

Coralligenous communities seem to be adapted to very low **nutrient** concentrations in sea water, as increased nutrient availability greatly affects the specific composition, inhibits coralligenous construction, and increases destruction rates (Hong 1980). In the absence of human disturbance, dissolved nutrients in sea water at coralligenous depths follow the annual pattern described for coastal oligothrophic Mediterranean waters, with the highest values in winter and the lowest in summer. The mean annual water nitrate concentration near the coralligenous concretions is around 0.6 μmol l^{-1}, with peaks of 1.5 μmol l^{-1} in winter and undetectable levels in summer (Ballesteros 1992). Phosphate concentrations are much lower and are always below 0.2 μmol l^{-1} (Ballesteros 1992; Ballesteros & Zabala 1993; Garrabou 1997).

As regard **hydrodynamic** and phisico-chemical characteristics of seawater, although flowing currents predominate at depths where coralligenous communities develop (Riedl 1966), this habitat is typical of relatively calm water, where the year-round average of water motion is at least one order of magnitude lower than water motion at a depth of 2 m (Garrabou 1997). **Salinity** ranges between 37 and 38 (Laubier 1966; Pascual & Flos 1984) while as far as **temperature** is concerned, most of the organisms living in coralligenous communities are able to support the normal seasonal values range characteristic of Mediterranean waters, which can vary between the annual temperature range of 10–23˚C, depending on the season, depth and geographical area (Laubier 1966; Pascual & Flos 1984; Ballesteros 1992; Ballesteros & Zabala 1993). However, some organisms living in coralligenous assemblages from deep waters seem to be highly stenothermal, as they are never found in shallow waters.

3.1.3 Structure and biodiversity

Coralligenous habitat is the final result of the two opposite actions of builders and bioeroders, which create a very complex structure of different morphology and in which several microhabitats can be distinguished.

The morphology and inner structure of coralligenous frameworks depends greatly on depth, topography, and the nature of prevailing algal builders (Laborel 1961). Two main morphologies can be distinguished (Peres & Picard 1964; Laborel 1987): banks and rims. Banks are flat frameworks with a variable thickness that ranges from 0.5 to several (3–4) m. They are mainly built over more or less horizontal substrata, and have a very cavernous structure (numerous holes, Laborel 1987). Rims develop in the outer part of marine caves and on vertical cliffs, usually in shallower waters than banks. The thickness of rims is also variable and ranges from 20–25 cm to >2 m; thickness increases from shallow to deep waters (Laborel 1987).

Coralline algae are the main coralligenous builders (Laborel 1961; Laubier 1966; Sartoretto 1996). According to Sartoretto et al. (1996), *Mesophyllum alternans* is the main algal building species for both ancient and recent coralligenous constructions in the northwestern Mediterranean, producing flat or slightly rounded banks or rims with a foliaceous structure. *M. alternans* is a highly tolerant species in terms of light, temperature and hydrodynamism, and is currently the dominant species in shallow waters. Other important building Corallinales are *Mesophyllum macroblastum, Lithothamnio philippi* and *Lithophyllum stictaeformis*. In some areas, *Peyssonnelia rosa-marina* and *P. polymorpha* may also be the dominant species, and form a very cavernous, highly bioeroded coralligenous framework. In deep water, other corallines like *Lithophyllum frondosum*, *L. cabiochae*, *Neogoniolithon mamillosum* become dominant builders (Appendix-Figures 5a-d).

Animal builders contributing to develop and consolidate the framework created by the calcareous algae are several bryozoans, polychaetes (serpulids), corals and sponges, which account for 24% of the total species number. The most abundant animal group are the bryozoans (*Pentapora fascialis*, *Myriapora truncata*), accounting for 62% of species, followed by the serpulid polychaetes (*Serpula vermicularis, Spirorbis* spp) with 23.4%. Minor contributors are the cnidarians (4%) (*Leptopsammia pruvoti*), molluscs (4%), sponges (4%), crustaceans (1.6%) and foraminiferans (0.8%) (*Miniacina miniacea*).

Bioeroders are fauna which erode calcareous concretions, in particular the excavating sponge *Cliona viridis*, the bivalve *Lithophaga lithophaga* and several annelids. The eroding species account for only around 1% of the total species number.

The final result of the builders and eroders of coralligenous concretions is a very complex structure, in which several microhabitats can be distinguished. Environmental factors (e.g., light, water movement and sedimentation rates) can vary by one to two orders of magnitude in parts of the same concretion situated as close as one metre from each other. This great environmental heterogeneity allows several different assemblages to coexist in a reduced space.

Algae, both encrusting corallines and green algae, usually dominate in horizontal to subhorizontal surfaces, although their abundance decreases with depth or in dim light. Phycologists have distinguished two main communities according to the light levels reaching coralligenous frameworks. In shallower waters banks, *Mesophyllum alternans* usually dominates in the basal layer and *Halimeda tuna* in the upper stratum, with an important coverage of other algae like *Peyssonnelia* spp. and *Flabellia petiolata* (Appendix-Figures 6a, b). This plant association is named *Lithophyllo-Halimedetum tunae*, and has been described in detail by Ballesteros (1991). Biomass of macroalgal assemblages ranges between 1200 and 2100 g dry weight (dw) m^{-2}, percent cover from 180–400% and the number of species is very high (average of 76 species in 1024 cm^2). This association develops at irradiances ranging from around to 3 and 0.4% of the surface irradiance.
In deeper waters or lower irradiances, the density of *Halimeda tuna* decreases and other calcareous algae become dominant (*Lithophyllum frondosum*, *Neogoniolithon mamillosum*, *Peyssonnelia rosa-marina*). Other common algae are members of the family Delesseriaceae and other laminar red algae (*Kallymenia*, *Meredithia*, *Gloiocladia, Sebdenia*, *Rhodophyllis*, *Predaea*), as well as the encrusting green alga *Palmophyllum crassum* (Appendix-Figures 7a-d). These assemblages correspond to the *Rodriguezelletum strafforellii* of Augier & Boudouresque (1975). Algal biomass averages 1600 g m^{-2} and percent cover 122%, mostly corresponding to encrusting algae and, around 90%, corresponding to corallines; the number of species is low (38 species in 1600 cm^2 or lower) (Ballesteros 1992).

Animal assemblages of these two plant associations can differ greatly from one to the other, as well as between sites and geographical areas. The abundance of suspension feeders mainly depends on average current intensity and availability of food (plankton, POC, DOC). In the richest zones (e.g., Gulf of Lions, Marseilles area) gorgonians can dominate the community, but in very oligotrophic waters (e.g., Balearic Islands, eastern Mediterranean), sponges, bryozoans and small hexacorals are the dominant suspension feeders. According to Hong (1982) four different categories of invertebrates can be distinguished with respect to their position and ecological significance in the coralligenous structure: the above mentioned 1) animal building and 2) eroding species, 3) cryptofauna colonising the small holes and crevices of the coralligenous structure (around 7% of the species, including different molluscs, crustaceans and polychaetes), 4) epifauna (living over the

concretions) and endofauna (living inside the sediments retained by the buildup), which represent a great number of species (nearly 67%). Macrozoobenthos species mainly characterizing coralligenous biocoenoses are: porifera *Petrosia ficiformis* and *Axinella* spp.; anthozoa *Paramuricea clavata, Eunicella cavolinii*, *E. singularis*, *Parazoanthus axinellae*, *Leptopsammia pruvoti*, *Alcyonium acaule* and *Corallium rubrum*; bryozoa *Pentapora fascialis* and *Myriapora truncata*; tunicata *Halocynthia papillosa* and *Clavelina* spp.

Coralligenous assemblages are characterized by high richness, biomass and production (Cocito et al. 2001; Hong 1982; Laborel 1961; Laubier 1966; Luning 1990) (Appendix-Figure 8), with values comparable to tropical reef assemblages, so that it can be considered one of the most important and characteristic assemblages of the Mediterranean Sea (Bianchi 2001). Moreover, coralligenous communities constitute the most important 'hot spot' of species diversity in the Mediterranean, togheter with the *Posidonia oceanica* meadows (Boudouresque 2004a). However, there appear to be no precise estimates of the number of species that thrive in the coralligenous assemblages. In fact, it is very difficult to mention all the species found to date in coralligenous communities, as the existing taxonomic literature is huge and contains many synonyms; this makes it impossible for a nonspecialist in most of the groups to come up with an accurate number of reported species. Estimates of the species richness found in coralligenous communities give a very conservative number of 1241 invertebrates, while Boudouresque (1973) has estimated that at least 315 species of macroalgae can thrive in Mediterranean sciaphilic communities (the coralligenous type being the most widespread). Instead, there are no estimates of the number of fishes that can be found in coralligenous communities, due to the high mobility of most species of this group, but estimates based on available literature regarding the biology of Mediterranean fishes (e.g., Whitehead et al. 1984–1986; Corbera et al. 1996; Mayol et al. 2000) range between 110 and 125 species. However, due to their rich fauna (Laubier 1966), complex structure (Peres & Picard 1964; Ros et al. 1985), and the paucity of studies dealing with coralligenous biodiversity, they probably harbour more species than any other Mediterranean community.

3.1.4 Disturbances

As others unique Mediterranean coastal habitats, coralligenous assemblages are threatened by several human induced impacts, such as changes in the atmospheric composition, alteration of biogeochemical cycles, fragmentation of habitats, erosion of biodiversity and biological invasions.

Large scale events related to the seawater temperature increase and global warming may be the main cause of some large-scale and other small-scale mass mortalities recorded during the past decade in the Mediterranean (Cerrano et al. 2000).

Degradation by wastewater seems to reduce faunal biodiversity along a gradient of multisource pollution, mainly affecting bryozoans, crustaceans and echinoderms; molluscs and polychaetes are largely unaffected (Hong 1980). Few data are available concerning the impact of various pollutants on the growth of coralline algae (Littler 1976), although it is known that orthophosphate ions inhibit calcification (Simkiss 1964). Hong (1980) observed that with increased pollution large thalli of *Mesophyllum alternans* are replaced by Peyssonneliaceae, which have a much lower building capacity (Sartoretto 1996). The abundances of the species responsible for accretion and those living in the coralligenous community decrease with the pollution gradient, both in terms of number and density of individuals; moreover, the species that act as bioeroders are more abundant in the polluted areas (Hong 1980). Thus, all the available evidence suggests that pollution accelerates the destruction of coralligenous assemblages and inhibits building activity. In marine coastal areas heavily polluted by both urban and industrial wastewater, water turbidity seems to be one of the main factor causing degradation and homogenisation of the phytobenthos. There is a slight decrease in the number of species (26 algal species sample^{-1}) when compared with similar sites and depths of unpolluted areas (30–38 algal species sample^{-1}) (Furnari et al. 1977; Battiato et al. 1979).

Degradation by fishing is mainly due to trawling, which is probably the most destructive fishing method that is causing degradation of large areas of coralligenous concretions (Boudouresque et al. 1990). Trawling not only causes direct physical damage by breaking down the coralligenous structure and rolling the coralligenous blocks, but also negatively affects photosynthetic production of encrusting and erect algae by increasing turbidity and sedimentation rates when applied to adjacent sedimentary bottoms (Palanques et al. 2001).

Degradation by divers activity is mainly caused by direct impact of divers on the largest invertebrates of the coralligenous community, which is one of the most popular sites for recreational diving in the Mediterranean (Boudouresque 2004b) due to its great variety of life and great visual appeal (Harmelin 1993).

Invasive species recently introduced in shallower habitats of the Mediterranean basin, seems to be very well adapted also to the coralligenous habitat. Probably the most dangerous alien species for the coralligenous community are the small red turf alga *Womersleyella setacea* and the green algae *Caulerpa taxifolia* and *C. racemosa* var. *cylindracea*. Although they were mainly found in relatively shallow waters (Meinesz & Hesse 1991), *Caulerpa taxifolia* has been recorded down to a

depth of 99 m (Belsher & Meinesz 1995) and in some areas (Cap Martin, France) it has totally invaded the coralligenous community (Meinesz 1999). Also *C. racemosa* var. *cylindracea* is quickly spreading in the Mediterranean (Piazzi et al. 2005) and it is also able to grow in deep waters where coralligenous assemblages develop (down to a depth of 70 m) (Piazzi et al. 2005a). Correlative studies highlighted several shift in the structure of assemblages (Piazzi et al. 2007b; Piazzi & Balata 2009), even if no experimental investigations have been performed to assess the effects of invasion and mechanisms involved.

3.2 Gaps in scientific knowledge

In terms of the current state of scientific knowledge of the coralligenous habitat, Ballesteros (2006) detect several gaps that make it rather difficult to make recommendations for protecting coralligenous assemblages and biodiversity joined it. In particular, he highlighted that effects of disturbances in this habitat are poorly understood and there are no data at all on the capacity of this environment to recover (with the exception of fish stocks after fishing prohibition). According to the author, the following issues would appear to be very important in the frame of the current increasing use of natural resources by mankind: a) impact of waste-water dumping, b) indirect impact of trawling, c) effects of alien species invasion, d) effect of large scale events.

4. OPEN ISSUES AND AIMS OF THE STUDY

The present project of research doctorate is set in the wider issue of possible synergetic effects among different aspects of global change in marine sensitive habitats. Biological invasions and eutrophication are the human-induced global changes considered: both single and mutual interaction effects on native communities are investigated by analysing the invasion event of alien seaweed *Caulerpa racemosa* var. *cylindracea* in coralligenous assemblages, which is one of the most sensitive habitats of the Mediterranean Sea and an important "hot spot" of biodiversity. So, starting from the topical subject of biological invasions by macroalgae, the study developed touching on various subjects, with the purpose of better investigate some of the issues still open in the current scientific debate.

4.1 Open issues

As for others bioinvasion studies, success of *C. racemosa* spread was been mainly researched in the peculiar biological properties of this alien species, while few studies are carried out on the ecological mechanisms aiding invasion, as i.e. those related to characteristics of the receiving ecosystem and effects of environmental disturbances. In this context, the most investigated habitats were been the subtidal shallow habitats and *Posidonia oceanica* meadows, while very little is known about the deep rocky habitats, such as coralligenous assemblages.

As to this general frame of scarce availability of information, the following particular open issues can be identified:

- Effect of nutrients pollution on biological invasions is poorly investigated in marine ecosystems, and no data are available about possible direct and indirect influence of eutrophication on the spread of *C. racemosa.* In fact, there are not studies about effect of nutrients enrichment on the invasive capability of *C. racemosa* and possible interaction effect between invasion and nutrients pollution on native macroalgal assemblages. Moreover, vulnerability to invasion was never related to human-induced disturbances in general, and no information are available about the role of nutrients in undermining the natural resistance of macroalgal assemblages to *C. racemosa* invasion.

- Impact of *C.racemosa* invasion was mainly studied in the subtidal shallower habitats, while little is known about macroalga invasion in the highly sensitive deep rocky habitats such as coralligenous assemblages.

- Consequences of changes of nutrient availability has been widely investigated in the intertidal, rocky pools and shallow subtidal habitats; instead, very few information are available about the effects on deep subtidal communities like coralligenous, specially in relation with the successional stages of assemblages.

4.2 Aims of the study

Given the above listed open issues, the general aims of the present research doctorate are to evaluate: **1)** the spread potential of *C. racemosa* in coralligenous habitats, **2)** impact of both *C. racemosa* and nutrient enrichment on the structure of macroalgal assemblages and **3)** possible synergetic effects between nutrient pollution and *C. racemosa* invasion on the native community.

Particular aims are to evaluate: **1)** the role played by nutrient pollution in **a)** the spread dynamic of *C. racemosa* and **b)** modifying vulnerability of coralligenous assemblages to *C. racemosa* invasion and **2)** the effects of the concurrent *C. racemosa* invasion and nutrient enrichment on macroalgal community.

To achieve these objectives, two manipulative field experiment were carried out in order to test following hypothesis: **i)** both nutrient enrichment and *C. racemosa* invasion can affect structure of macroalgal assemblages of the deep subtidal rocky bottom, **ii)** response of coralligenous macroalgae to nutrient enrichment changes according to the successional stage of the assemblages, **iii)** an increase of nutrient load can enhance the growth of *C. racemosa*, **iv)** the concurrent presence of these two stressors may lead to greater effects than the sum of the effects of each stressor acting alone, **v)** the natural resistance of coralligenous assemblages to *C. racemosa* invasion decreases under nutrients pollution.

5. EFFECTS OF NUTRIENT ENRICHMENT ON MACROALGAL CORALLIGENOUS ASSEMBLAGES

LUIGI PIAZZI, PAOLA GENNARO, DAVID BALATA

ABSTRACT

Effects of eutrophication on marine ecosystems have been widely studied, even if both the effects on deep subtidal rocky assemblages and response of different successional stages to nutrients impact are still not clear. In this context, the study aimed to evaluate the effects of nutrient enrichment on Mediterranean macroalgal assemblages associated with coralligenous habitat. A manipulative field experiment was carried out by supplying both mature and early successional stages of assemblages with nutrients. A total of 62 macroalgal species were identified. Multivariate and univariate analyses showed that the structure of both mature and early successional macroalgal assemblages of coralligenous significantly varied between areas treated with nutrients and not treated areas. Moreover, differences were stronger when macroalgal assemblages were in the early successional stage than in the mature one. Results highlighted the role played by nutrients in determining the structure of macroalgal coralligenous assemblages, furthermore suggesting possible synergetic effects with other kinds of disturbances.

KEY WORDS: Rocky subtidal, Coralligenous habitat, Nutrients Successional stages, Mediterranean Sea

5.1 Introduction

Increase of nutrient concentration in marine water represents one of the main aspect of human-induced global changes (Vitousek 1994; Vitousek et al. 1997). Several human activities, such as overharvest of land, deforestation, fish farming, domestic and industrial sewage discharge, may directly or indirectly influence the nutrients inflow into the sea (Carpenter et al. 1998; McClelland & Valiela 1998; Pergent-Martini et al. 2006). During the last decades nutritional input has been increased leading to widespread eutrophication of many coastal areas (Nixon 1995; Howarth & Marino 2006). Effects of increase of nutrients availability on structure and functioning of marine ecosystems have been widely investigated (Morris & Keough 2003; Prado et al. 2008; Balata et al. 2008). In particular, both correlative and experimental studies carried out on rocky shores highlighted dramatic shifts of the structure of benthic assemblages following increasing gradients of nutrient concentration (Diez et al. 1999; Soltan et al. 2001; Gorgula & Connell 2004; Karez et al. 2004; Arevalo et al. 2007). In fact, nutrient availability represents an important factor conditioning composition of seaweed assemblages (Teichberg et al. 2008), since nutrient enrichment may stimulate the spread of annual fast-growing algae and inhibit the growth of perennial species (Gorostiaga and Diez 1996; Diaz et al. 2002; Eriksson et al. 2002; Russell & Connell 2005; Worm & Lotze 2006; Kraufvelin 2007). Replacement of habitat-structuring species with ephemeral seaweeds occurring in eutrophic water lead to a reduction of ecosystem complexity and to a widespread biotic homogenization (Valiela et al. 1992; Morand & Briand 1996). Although this phenomenon has been widely investigated, most of studies has been carried out in intertidal, rocky pools or shallow subtidal (Bokn et al. 2003; Kraufvelin et al. 2006; Masterson et al. 2008; Guerry et al. 2009; Atalah & Crowe 2010), while very few information are available about the effects of nutrient enrichment on deep subtidal communities where abiotic conditions are more steady throughout the seasons (Witman & Dayton 2001). Nevertheless, effects of human impacts may depend on the depth gradient (Korpinen et al. 2007; Piazzi & Balata 2010), so any additional knowledge on this topic may be useful for coastal management. Moreover, resistance to stress depends on the successional stage of ecosystems (Irving et al. 2009), so different responses of mature and early successional stages to nutrient enrichment may give important information about the resistance capability of assemblages (Korpinen & Jormalainen 2008; Masterson et al. 2008). In the Mediterranean Sea, deep subtidal system is characterized by coralligenous habitat (Ballesteros 2006) consisting of calcareous structures mainly built by Rhodophyta belonging to Corallinales. Coralligenous habitat supports high biodiversity and it is considered the most important habitat of the Mediterranean coastal system together with seagrass beds (Cocito 2004; Ballesteros 2006). Correlative and experimental studies suggested that structure and biodiversity of coralligenous

assemblages can be strongly modified by several kinds of human-caused impacts (Hong 1983; Balata et al. 2005, 2007a; Piazzi et al. 2007); nevertheless, consequences of changes of nutrient availability have not been properly investigated, specially in relation with the successional stage of assemblages. Different successional stages of assemblages may co-exist in coralligenous systems as consequence of both natural and human induced disturbance. In fact, coralligenous habitat, as it was evidenced for other biogenic systems (Davis 1977), is subjected to several mechanical disturbances, such as anchoring or trawling, that may cause partial or total removal of organisms (Ballesteros 2006), creating a patchy distribution of different assemblages with different responses to pollutions. The study aimed at evaluating the effects of nutrient enrichment on macroalgal coralligenous assemblages. To achieve this objective, a manipulative field experiment was carried out by supplying both mature and early successional stages of assemblages with nutrients. The following hypotheses were tested: (i) increasing of nutrient load can affect structure of coralligenous assemblages and (ii) response of macroalgal assemblages to nutrient enrichment changes according to the successional stage of the assemblages.

5.2 Materials and Methods

The study was carried out in the western coast of Tuscany (43_2802400 N and 10_1904200 E, northwestern Mediterranean Sea), on a rocky bottom 24 m deep. Eight areas of about 25 m^2 wide and 10s of meters apart were selected and randomly assigned to the follow treatments: control mature assemblages, control early successional assemblages, nutrient-enriched mature assemblages and nutrient-enriched early successional assemblages. Mature successional assemblages consisted of the more superficial layer of coralligenous building, which is usually formed by living assemblages organized into a complex stratified structure with encrusting, turf and erect perennial species; early successional assemblages were assemblages developed over one year on a cleared substrate made up of calcareous dead thalli of encrusting Corallinales. In each area, four experimental plots of 400 cm^2 surface were chosen at random, several meters distant from each other. At the beginning of the study, in September 2009, all living organisms of the plots assigned to the early successional assemblages areas were scraped off the plots surface, including the living layer of encrusting Corallinales (Balata et al. 2007a). In nutrient-enriched areas, two nylon-mesh bags (1-mm mesh size) of 20 x 5 x 5 cm with 200 g of fertilising pellets (OSMOCOTE by Scotts) were placed along the two opposite sides of each plot and fixed to the substratum through nails (Balata et al. 2010). The chemical composition of pellets was 15 + 9 + 9, which is one of the combinations of nitrogen (15%, made up of 7% ammonia and 8% nitrate), phosphorous (9% in the

form of P_2O_5) and potassium (9% as KNO_3) commonly utilized for fertilizing terrestrial plants. Every 3 months, or rather before the complete dissolution of pellets, all experimental plots bags were replaced with new ones in order to maintain a constant water nutrient concentration throughout the study period. At the end of the study period, in September 2010, all organisms colonizing the plots were collected by a hammer and chisels. All macroalgal species were identified and abundance of each species was estimated as percentage cover by spreading out alga thalli and measuring percentage of plot surface occupied by the species (Ballesteros 1986). Multivariate analysis of variance based on permutations (PERMANOVA, Primer v6 computer program including the add-on package Permanova plus, Anderson et al. 2008) was used to examine differences in patterns of species composition and abundance between treatments. The analysis consisted in a 3-way model with Stage (mature assemblages vs. early successional assemblages) and nutrient (nutrient enriched vs. not enriched) as fixed and orthogonal factors, Area (2 levels) as random factor nested in the interaction Stage x Nutrient and four replicates for each Area. Although the differences between mature and early successional stages could be obvious, we decided to perform only one analysis instead two separated analyses for each stage in order to investigate the interactions between these two factors. PERMANOVA was conducted on Bray–Curtis dissimilarity matrix calculated from untransformed data. SIMPER analysis (Clarke 1993) was used to identify the percentage contribution of each species to the Bray– Curtis dissimilarity between conditions. A 2-dimensional nMDS (non-metric multidimensional scaling) was used as a graphical representation of the data. Values of total percentage cover and species number were analysed by 3-way ANOVA (GMAV 5 software, University of Sydney, Australia). Factors and levels considered in these analyses were the same described for the multivariate analysis. Cochran's C-test was used before each analysis to check for homogeneity of variance (Underwood 1997). Student Newman Keuls (SNK) test was used for *a posteriori* multiple comparisons of means.

5.3 Results

A total of 62 macroalgal species were identified (8 Chlorophyta, 8 Heterokontophyta and 46 Rhodophyta; Table 1, with nomenclatural authorities). Calcareous Corallinales completely covered the rocky bottom, forming a secondary substrate colonized by encrusting, turf and erect algae. Species of the genus Peyssonnelia were the most common encrusting forms, while *Womersleyella setacea*, *Heterosiphonia crispella*, *Eupogodon planus* and *Feldmannophycus raissiae* were widely present in the turf. The erect layer was mostly composed of *Flabellia petiolata*, *Laurencia chondroides* and *Tricleocarpa fragilis*. PERMANOVA detected significant interaction Stage x

Nutrient (Table 2); pair-wise test showed significant differences between treatments, even though differences between nutrient-enriched and controls treatments were higher in early successional assemblages than in mature ones (Table 2), as it was showed also by the nMDS ordinations (Fig. 1). The SIMPER test showed that in control treatments, mature and early successional assemblages had similar structure, being detected differences between two successional stages essentially due to the abundance value of the main species. Both mature and early successional assemblages treated with nutrients showed an increase of turf species, especially *W. setacea* and *Pseudochlorodesmis furcellata*, and some species of the erect layer such as *Halymenia floresia*. Moreover, in the mature assemblages, *Zanadinia typus* was less abundant in treated than in control plots and, in the early successional assemblages, *H. crispella* and *Colpomenia sinuosa* were more abundant in treated than in control plots. In nutrient-enriched plots, *H. floresia* and *C. sinuosa* were more abundant in early successional than in mature assemblages (Table 3). ANOVA performed on total percent cover detected significant interaction Stage x Nutrient, while differences in species number resulted not significant (Table 4). SNK test showed that values of percent cover in nutrient-enriched areas were higher than controls ones both for mature and early successional stage assemblages (Fig. 2).

5.4 Discussion

Results of the experiment showed that the structure of both mature and early successional stage of macroalgal coralligenous assemblages in the studied area significantly varied between nutrients treated and not treated areas. Moreover, detected differences were stronger when macroalgal assemblages were in the early successional stage than in the mature ones.

Changes in mature macroalgal assemblages were lower than those described for other habitats under nutrient enrichment regime (Karez et al. 2004; Kraufvelin 2007), as no severe shift in the assemblages structure occurred. On the contrary, heavy differences between treatments were observed in the early successional assemblages, confirming the higher resistance to stresses of well structured assemblages also for the Mediterranean coralligenous habitats. Severe shifts in structure of assemblages need longer periods due to the presence of perennial species (Kraufvelin et al. 2006). In fact, the spreads of ephemeral algae in itself is not enough to eliminate the structuring species of macroalgal assemblages. The community shift may occur after that age-related mortality remove perennial species if these latter are not replaced by juveniles due to competition by ephemeral algae (Kraufvelin et al. 2006). Increase in macroalgae abundance was the main effect of nutrient enrichment. The amount of algal biomass or cover is the result of balance between top-down and bottom-up forces acting on ecosystems (Masterson et al., 2008; Guerry et al. 2009; Atalah & Crowe 2010) and it may vary among habitats. The evaluation of top-down forces was not

the aim of the present study, yet effects related to nutrient enrichment cannot be separated from those of other forces acting on the system. However, in the Mediterranean deep subtidal habitats, grazing pressure is considered less important than in shallow habitats (Ballesteros 2006), thus its effects may be considered negligible compared to those of nutrients. Turf-forming species, flattened Rhodophyta and the Heterokontophyta *C. sinuosa* were the most increased taxa in treated areas. The spread of turfs under nutrient enrichment regime has been widely described both in correlative and experimental studies (Gorostiaga & Diez 1996; Diez et al. 1999; Diaz et al. 2002), as increasing load of nutrients in coastal water is considered the main cause of the shift from slow-growing macroalgae to fastgrowing turf-forming algae in benthic assemblages (Eriksson et al. 2002; Gorgula & Connell 2004). In fact, life-history and physiology of the latter species are better suited to nutrient overload owing to their fast growth rate, nutrient requirement and rapid uptake rates (Rosenberg & Ramus 1984; Hein et al. 1995; Pedersen & Borum 1996, 1997; Karez et al. 2004). However, species constituting turf showed different responses to nutrient availability: *W. setacea*, *H. crispella*, *P. furcellata*, *Polysiphonia* spp increased their abundance while *Ceramium* spp. or smaller-sized corticated Rhodophyta (*Eupogodon*, *Chondria*, *Feldmannophycus*) were unaffected by nutrients. Variability of the species nutrient responses reflects morphological and physiological characteristics of turf-forming algae. In general, algal species with higher surface- area/volume ratio tend to grow faster, require more nutrients and have higher nutrient uptake rates per time (Pedersen & Borum 1996; Taylor et al. 1998) than thicker algae with lower surface/ volume ratio. Thus, under high nutrient availability conditions, no-corticated and/or uniseriate filamentous species may be more facilitate than thin corticated algae with lower surface- area/volume ratio (Bokn et al. 2003; Karez et al. 2004). The shiphonous Udoteacea *P. furcellata* is considered one of the most tolerant species in the coralligenous assemblages (Balata et al. 2005, 2008). The introduced Rhodophyta *W. setacea* and Chlorophyta *P. furcellata* were the most increased species in treated plots. *W. setacea* is an invasive species already described as dominant species in areas characterized by severe stress regime such as high sedimentation rates (Airoldi 1998, 2003). The present study confirms the role of nutrients in aiding the spread of introduced macroalgal species (Sánchez & Fernández 2006; Incera et al, 2009). An increase of nutrients in natural systems can create favourable conditions for faster-growing plants, such as most of invasive seaweeds (Torres et al. 2004). Morphology of both *C. sinuosa* and flattened Rhodophyta is characterized by high surface-area/volume ratio such as no-corticated filamentous species; thus, their increase could be expected under nutrient enriched regime (Masterson et al. 2008; Teichberg et al. 2008). Encrusting Corallinales showed similar abundance in treated and control plots, also in the early successional assemblages, suggesting that Corallinales are not affected by high nutrient concentration. However, both the increase of

filamentous species and lost of structural species allow to hypothesize, on longer periods, a loss of functional diversity of assemblages and a shift towards a dominance of ephemeral seaweeds and crust. The present study demonstrated the role of nutrients in affecting macroalgal assemblages structure of coralligenous habitat in the studied area; moreover, it highlighted the occurrence of interactions with disturbances which may amplify the nutrients negative effects on assemblages. A complete removal of the living layer of Corallinales, as it was experimentally realized in the present study, is usually limited to small-scale events, but partial removal of organisms may commonly occur as consequence of several kinds of human disturbance, decreasing the resistance of assemblages to nutrient enrichment. Moreover, the study highlighted effects of nutrients similar to those observed for other stressors, such as sediment increase (Balata et al. 2005, 2007a,b) or invasion of introduced seaweeds (Piazzi et al. 2007; Piazzi & Balata 2009), suggesting that synergetic mechanisms may occur among these stressors leading to dramatic changes in deep subtidal rocky assemblages and to widespread homogenization of coralligenous habitats.

5.5 Tables and Figures

Table 1. List of identified taxa with values of mean percent cover per plot. C = controls, N = nutrient enriched; M = mature assemblages, ES = early successional assemblages

TAXA	N-ES	C-ES	N-M	C-M
Chlorophyta				
Cladophora echinus (Biasoletto) Kützing	0.37	0.38	0.65	0.65
Cladophora prolifera (Roth) Kützing	2.17	0	1.07	0.57
Codium bursa (Linnaeus) C. Agardh	0.15	0.06	0	0
Flabellia petiolata (Turra) Nizamuddin	4.97	4.02	48.50	47.25
Halimeda tuna (J. Ellis e*t* Solander) J.V. Lamouroux	0.12	0.13	2.00	4.12
Palmophyllum crassum (Naccari) Rabenhorst	0	0	2.25	0
Pseudochlorodesmis furcellata (Zanardini) Børgesen	23.62	2.46	4.22	0.67
Valonia macrophysa Kützing	0.35	0.18	0.07	0.10
Heterokontophyta				
Colpomenia sinuosa (Martens ex Roth) Derbès et Solier				
Cutleria chilosa (Falkenberg) P.C. Silva (sporophyte "*Aglaozonia*")	0.40	0	0	0
Dictyota linearis (C. Agardh) Greville	1.77	1.26	0.72	0.75
Halopteris filicina (Grateloup) Kützing	1.01	0.62	1.22	1.05
Nereia filiformis (J. Agardh) Zanardini	1.15	1.73	0	0.07
Sphacelaria cirrosa (P.H. Roth) C. Agardh	0.65	0.26	0	0
Sphacelaria plumula Zanardini	0.05	0	0.07	0.05
Zanardinia typus (Nardo) G. Furnari	0	1.00	1.00	8.82
Rhodophyta				
Acrodiscus vidovichii (Meneghini) Zanardini	0	0	1.35	1.02
Acrothamnion preissii (Sonder) Wollaston	0.27	0.16	1.27	0.12
Aglaothamnion tenuissimum (Bonnemaison) Feldmann-Mazoyer	0.32	0.10	0.25	0.17
Anthithamnion piliferum Cormaci *et* Furnari	0.40	0.47	0.45	0.65
Apoglossum ruscifolium (Turner) J. Agardh	0.02	0.07	0.20	0.15
Botryocladia botryoides (Wulfen) Feldmann	0.67	1.02	0.47	0.97
Ceramium bertholdii Funk	0.10	0.07	0	0.02
Ceramium diaphanum (Lighfoot) Roth	0.12	0.03	0.15	0.12
Ceramium flaccidum (Kützing) Ardissone	0.15	0.12	0	0.02
Ceramium codii (H. Richards) Feldmann-Mazoyer	0.40	0.26	0	0.15
Champia parvula (C. Agardh) Harvey	0.05	0.17	0.05	0.30
Chondria capillaris (Hudson) M.J. Wynne	0.37	2.32	0.05	0.27
Contarinia squamariae (Meneghini) Denizot	1.10	0.62	0.47	0.52
Crouania attenuata (C. Agardh) J. Agardh	0.55	0.26	0.3	0.45
Dasya ocellata (Grateloup) Harvey	0.12	0.22	0.67	0.12
Erythroglossum sandrianum (Kützing) Kylin	1.10	0.20	0.55	0.15
Eupogodon planus (C. Agardh) Kützing	3.27	3.15	1.30	1.77

Feldmannophycus rayssiae (Feldmann *et* Feldmann-Mazoyer)Augier *et* Boudouresque	1.20	1.00	1.82	0.50
Griffithsia schousboei Montagne	0.05	0.06	0	0
Jania adhaerens J. V. Lamouroux	0.80	0.22	3.67	0.95
Halydyction mirabile Zanardini	0	0.10	0	0
Halymenia floresia (Clemente and Rubio) C. Agardh	27.75	2.67	16.25	7.02
Heterosiphonia crispella (C. Agardh) M.J. Wynne	6.00	0.25	1.47	1.02
Hypoglossum hypoglossoides (Stackhouse) Collins *et* Harvey	0.17	0	0.25	0.10
Laurencia chondrioides Børgesen	23.12	23.62	44.12	46.25
Lomentaria chylocladiella Funk	0.15	0.07	0.05	0.15
Meredithia microphylla (J. Agardh) J. Agardh	2.30	1.25	4.15	3.50
Monosporus pedicellatus (J.E. Smith) Solier	0.57	0.22	0.25	0.12
Osmundea pelagosae (Schiffner) F.W. Nam	0.90	2.70	0.62	1.90
Peyssonnelia rubra (Greville) J. Agardh	24.20	23.22	37.32	39.50
Peyssonnelia squamaria (S.G. Gmelin) Decaisne	3.80	3.60	5.20	5.50
Phyllophora crispa (Hudson) P.S. Dixon	0.50	0	0	0
Plocamium cartilagineum (Linnaeus) P.S. Dixon	0.27	0	0.17	0.05
Polysiphonia elongata (Hudson) Sprengel	0.15	0	0	0
Polysiphonia furcellata (C. Agardh) Harvey	0.87	0.70	0.17	0.15
Polysiphonia perforans Cormaci, G. Furnari, Pizzuto *et* Serio	0.30	0.36	0.07	0.22
Pterothamnion plumula (Ellis) Nägeli	0.10	0.03	0.12	0.07
Rhodophyllis divaricata (Stackhouse) Papenfuss	0.55	0.06	0	0.10
Rodriguezella strafforelloi F. Schmitz	0.57	0.36	0.60	0.40
Sphaerococcus coronopifolius Stackhouse	1.67	0.06	0	0
Spyridia filamentosa (Wulfen) Harvey	0	0	0.05	0
Tricleocarpa fragilis (linnaeus) Huisman *et* R.A. Towsend	0.27	0.20	8.62	8.12
Womersleyella setacea (Hollenberg) R.E. Norris	42.12	4.35	91.75	15.00
Wrangelia penicillata (C. Agardh) C. Agardh	0.02	0.03	0	0.07

Table 2. Results of PERMANOVA analysis performed on species composition and abundance of coralligenous assemblages. Significant effects are reported in bold. C = controls, N = nutrient enriched; M = mature assemblages, ES = early successional assemblages

Source	df	MS	Pseudo-F	P(perm)
Stage = S	1	13601.0	43.57	**0.004**
Nutrient = N	1	10936.0	35.03	**0.008**
SxN	1	2132.5	6.83	**0.021**
Area(SxN)	4	312.1	1.07	0.383
Residual	24	290.8		
Total	31			

Pairwise tests SxN	$p_{(perm)}$		$p_{(perm)}$
ES: C,N	**0.018**	C: ES, M	**0.007**
M: C, N	**0.021**	N: ES, M	**0.001**

Table 3. Results of SIMPER test. C = controls, N = nutrient enriched; M = mature assemblages, ES = early successional assemblages

	Mean percent cover	Mean percent cover	Contribution %
Taxa	**C-M**	**C-ES**	**Av.diss.= 49.57**
Flabelia petiolata	47.25	4.03	30.97
Laurencia chondroides	46.25	25.33	14.4
Peyssonnelia spp	45	26.67	13.02
Womersleyella setacea	15	4.37	7.52
Tricheocarpa fragilis	8.13	0.2	5.67
Zanardina typus	8.83	1	5.56
Halymenia floresia	7.03	2.73	4.07
Halimeda tuna	4.13	0.13	2.89
	N-ES	**N-M**	**Av.diss.= 54.38**
Womersleyella setacea	42.13	91.75	18.76
Flabelia petiolata	4.98	48.5	16.53
Laurencia chondroides	19.38	44.13	9.61
Halymenia floresia	27.76	16.25	9.36
Pseudochlorodesmis furcellata	24.88	4.23	7.94
Peyssonnelia spp	28	42.13	6.49
Colpomenia sinuosa	16.13	0	6.11
Tricheocarpa fragilis	0.28	8.63	3.22
Heterosiphonia crispella	6	1.48	1.85
	C-M	**N-M**	**Av.diss.= 37.38**
Womersleyella setacea	15	91.75	43.38
Halymenia floresia	7.03	16.25	5.82
Zanardina typus	8.83	1	4.67
Pseudochlorodesmis furcellata	0.68	4.23	2.02
	N-ES	**C-ES**	**Av.diss.= 55.98**
Womersleyella setacea	42.13	4.37	23.73
Halymenia floresia	24.63	2.73	15.4
Pseudochlorodesmis furcellata	24.88	2.47	14.28
Colpomenia sinuosa	16.13	0	10.04
Heterosiphonia crispella	6	0.27	3.69
Osmundae pelagosae	0.9	3.6	2.11

Table 4. Results of ANOVA on total percent cover and species number per plot. C = controls, N = nutrient-enriched; M = mature assemblages, ES = early successional assemblages

		Percent cover			Species number		
Source	**DF**	**MS**	**F**	**P**	**MS**	**F**	**P**
Stage = S	1	83334.0	842.02	**0**	16.53	1.88	0.242
Nutrient = N	1	78903.7	797.26	**0**	42.78	4.87	0.091
Area(SxN)	4	98.9	0.20	0.938	8.78	0.58	0.677
SxN	1	1001.2	10.12	**0.033**	3.78	0.43	0.547
Residual	24	505.4			15.03		
Total	31						
Cochran's test		C = 0.348 (ns)			C = 0.3181 (ns)		
SNK (SxN):		M: N>C; ES: N>C N: M>ES; C: M>ES					

Figure 1. nMDS ordination on species composition and abundance of macroalgal assemblages of all replicate plots. White circles = control mature assemblages, black circles = control early successional assemblages, white triangles = nutrient-enriched mature assemblages, black triangles = nutrient-enriched early successional assemblages

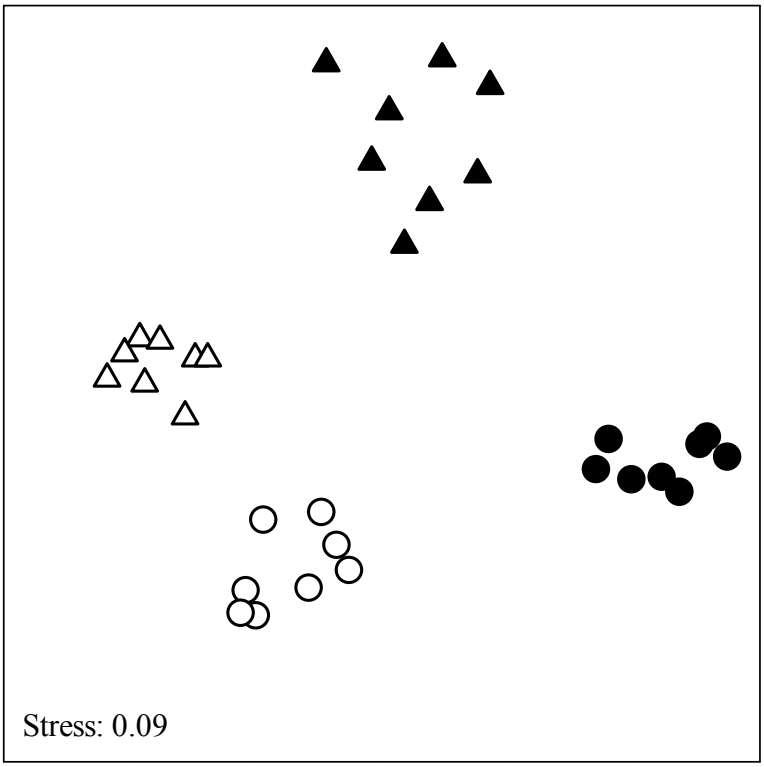
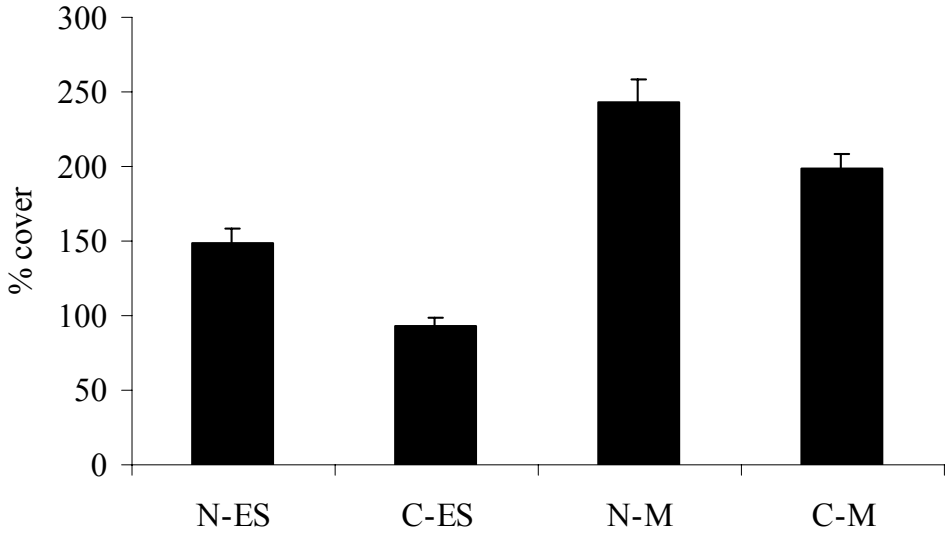
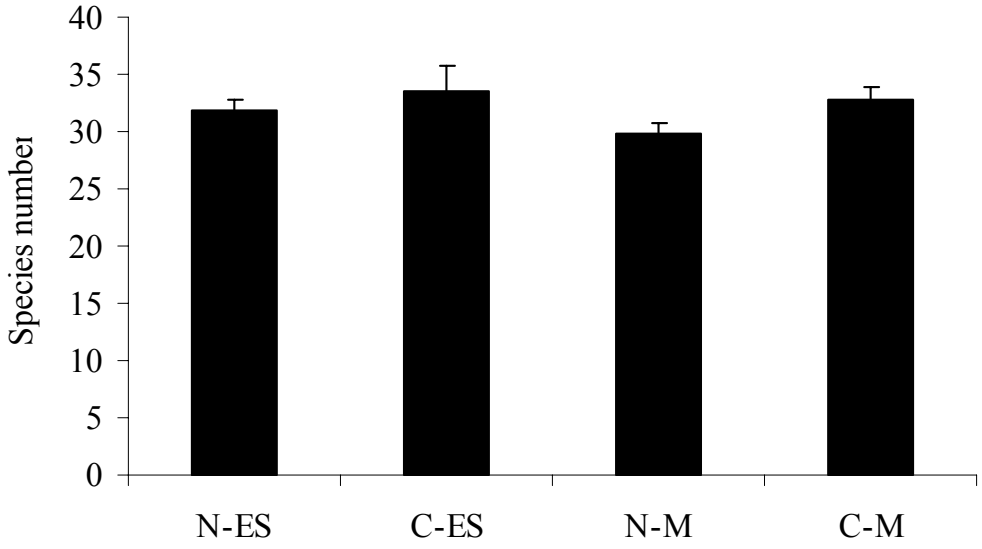


Figure 2. Values of percent cover (a) and species number (b) of macroalgal assemblages (mean ± SE, n = 8). C = controls, N = nutrient enriched; M = mature assemblages, ES = early successional assemblages.



a)



b)

6. SYNERGISM BETWEEN TWO ANTHROPIC IMPACTS: *CAULERPA RACEMOSA* VAR. *CYLINDRACEA* INVASION AND SEAWATER NUTRIENT ENRICHMENT

PAOLA GENNARO, LUIGI PIAZZI

ABSTRACT

Although eutrophication and biological invasions are recognized as important elements of global change, few studies have assessed how their synergism can affect structural and functional traits of marine ecosystems. The present study aimed to evaluate the effect of seawater nutrient enrichment on the spread of the introduced Chlorophyta *Caulerpa racemosa* var. *cylindracea* and the interactive effects of nutritional enrichment and *C. racemosa* invasion on the native macroalgal assemblages of a subtidal rocky bottom. To achieve these objectives, a manipulative field experiment was carried out at 24 m depth in the northwestern Mediterranean Sea by adding *C. racemosa* and supplying assemblages, nutrient enrichment, addition of *C. racemosa,* and both nutrient enrichment and addition the water column with nutrients. The following treatments were applied: non-manipulated of *C. racemosa* assemblages, nutrient enrichment, addition of *C. racemosa,* and both nutrient enrichment and addition of *C. racemosa*. Results showed that *C. racemosa* spread was enhanced by nutrient enrichment. Moreover, a significant interaction between nutritional increase and *C. racemosa* invasion was detected: the effects of *C. racemosa* invasion on native macroalgal assemblages were amplified by nutrient enrichment. Results suggested that synergism between effects of different anthropogenic impacts can have severe consequences on the integrity of marine ecosystems

KEY WORDS: Biological invasions, Nutrients, Rocky bottom, Macroalgal assemblages, Mediterranean Sea

6.1 Introduction

Global change represents a focal concern for ecologists (e.g. Grall & Chavaud 2002; Feely et al. 2004; Schiel et al. 2004; Harley et al. 2006; Martin & Gattuso 2009). In addition to climatic changes, the global environment is undergoing modification as a result of a number of interacting processes which are directly or indirectly due to human activities. Thus, global environmental change is a complex phenomenon comprising multiple events which alter the structure and function of ecological systems, with possible occurrence of serious cascade effects. In this context, there is a need for study of synergism at a global scale between different environmental processes (Vitousek 1994; Huenneke 1997). Among these processes, biological invasion is recognized as an important element of global change and a major driver of ecosystem modification (Vitousek et al. 1996, 1997). However, other human induced impacts, such as changes in the atmospheric composition, alteration of biogeochemical cycles, fragmentation of habitats and erosion of biodiversity, can affect species distribution and resources dynamics in terrestrial and aquatic systems, potentially interacting with biological invasions (Dukes & Mooney 1999; Harris & Tyrrel 2001). The increase of nutrient load, for example, is considered an anthropogenic factor enhancing the dominance of non-native species in many natural systems (Hobbs & Huenneke 1992; Burke & Grime 1996). The effect of nutrient availability on biological invasions has been examined mainly in terrestrial habitats (Burke & Grime 1996; Gross et al. 2005; Leishman & Thomson 2005); in contrast, only a few experimental studies have been carried out to investigate this phenomenon in marine ecosystems (but see Steen 2003; Sánchez & Fernández 2006; Incera et al. 2009). Eutrophication is a growing problem in the marine habitats of coastal waters all over the world (Nixon 1995; Livingston 2001; Howarth & Marino 2006) and is considered one of the main causes of deteriorating coastal water quality and loss of ecosystem complexity (Soltan et al. 2001; Arevalo et al. 2007). Biotic homogenization due to the proliferation of opportunistic species has been attributed mostly to high loading of nutrients derived from industrial and urban sewage effluents (Valiela et al. 1992; Morand & Briand 1996). Furthermore, nutrient enrichment can aid the spread of introduced macroalgae through different mechanisms (Stimson et al. 2001; Torres et al. 2004). Nutrient availability is usually an important factor in determining the species composition of seaweed assemblages (Teichberg et al. 2008). An increase in nutrients in natural systems is detrimental to slow-growing plants which are adapted to nutrient-poor habitats and creates favourable conditions for faster-growing plants, such as many invasive seaweeds. Moreover, the degradation of benthic systems caused by pollution can reduce the native assemblage's resistance to invasions (Stachowicz et al. 1999). Thus, knowledge of synergetic mechanisms between nutrient enrichment and invasions of introduced seaweeds can provide valuable insights, which will assist

ecologists in building predictive models and planning conservation programs (Lapointe & Beldford 2010). The Chlorophyta *Caulerpa racemosa* (Forsskål) C. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque (Verlaque et al. 2003) represents one of the most serious invasive species in the Mediterranean Sea (Klein & Verlaque 2008). The alga has rapidly colonized wide areas of the Mediterranean basin, forming permanent populations and interfering with the native assemblages (Piazzi et al. 2001, 2005b; Piazzi & Balata 2008; Klein & Verlaque 2008). Marine ecosystems which are essential for biodiversity conservation, such as seagrass meadows and coralligenous habitat (sensu Ballesteros 2006), have been invaded by *C. racemosa* with consequent loss of the original structure of assemblages (Ceccherelli & Campo 2002; Piazzi et al. 2007a; Antolic et al. 2008). The interaction of *Caulerpa racemosa* with other kinds of human impact has been investigated in relation to the increase of sediment deposition, showing important synergetic effects (Piazzi et al. 2005a, 2007b), but no data are available on the consequences of increased water nutrient load on *C. racemosa* invasion. However, several observations suggest that the spread of this invasive alga is related to different types of human pressures. For example, along the Mediterranean French coasts, *C. racemosa* cover is higher in marine areas close to harbours, and in areas affected by industrial and urban pollution, than in undisturbed areas (Klein et al. 2005). The same pattern is observed along the urbanized coasts of Tuscany, Italy, where the highest *C. racemosa* biomass values in the Mediterranean Sea have been recorded (Piazzi et al. 2001). Correlative and experimental studies highlight a positive influence of increasing nutrient availability on the spread of the co-generic invasive seaweed *Caulerpa taxifolia* (Vahl) C. Agardh (Chisholm et al. 1995, 1997; Ceccherelli & Cinelli 1997), suggesting similar effects on *C. racemosa*. The present study aimed to evaluate the role of seawater nutrients in the spread of *C. racemosa* and to detect possible interactive effects of nutrient enrichment and *C. racemosa* invasion on the native assemblages. To this end, a manipulative field experiment was carried out by adding *C. racemosa* and supplying water column with nutrients. The following hypothesis were tested: (1) an increase of nutrient load can enhance the growth of *C. racemosa*, (2) both nutrient enrichment and *C. racemosa* invasion may cause modifications in the structure of macroalgal assemblages of the subtidal rocky bottom, and (3) the concurrent presence of these 2 stressors may lead to greater effects than the sum of the effects of each stressor acting alone.

6.2 Materials and Methods

6.2.1 Study site and experimental design

The study was carried out on a rocky subtidal bottom 24 m deep located along the Tuscan coast south of Leghorn (43° 28' 24''N, 10° 19' 42'' E) where the substratum is colonized by coralligenous assemblages below 20 m depth. *Caulerpa racemosa* has been present at the study site since 1996, showing a patchy distribution extending from the surface to 40 m depth (Piazzi & Balata 2009). Field experiments took place from July to October 2009, which represents the main growth season of *Caulerpa racemosa* (Ruitton et al. 2005). The following treatments were considered: non-manipulated assemblages (hereafter indicated as control), nutrient enrichment (nutrient-enriched), addition of *C. racemosa* (invaded) and both nutrient enrichment and addition of *C. racemosa* (nutrient-enriched + invaded). For each treatment, 4 areas of about 100 m^2 and 10's of m apart were selected at random along 3 km of coastline. In each area, 3 replicate experimental plots of 400 cm^2 were located at random, several meters distant from each other.

6.2.2 Manipulative field experiment

In the areas assigned to invaded and nutrient-enriched + invaded treatments, 15 fragments of the invasive alga, 12 cm in length, were anchored in each plot using 2 wire bridges fixed to the substratum by means of 15 cm long nails. Alga fragments were collected in the adjacent patches inside the study site and attached within 1 h. At the beginning of the study, the mean cover of *Caulerpa racemosa* was about 70% of the experimental plot surface, thus comparable to that measured for naturally invaded assemblages in the same habitat (Piazzi & Balata 2008, 2009). In the areas assigned to nutrient-enriched and nutrient-enriched + invaded treatments, two 20 x 5 x 5 cm nylon mesh bags (1 mm mesh size), each containing 200 g fertilising pellets (Osmocote®, Scotts), were placed along the 2 opposite sides of each plot and fixed to the substratum with nails. The NPK composition of the pellets was 15-9-9, which is one of the combinations of nitrogen (15%, made up of 7% ammonia and 8% nitrate), phosphorus (9% in the form of P_2O_5) and potassium (9% as KNO_3) commonly utilized for fertilizing terrestrial plants. After 2 mo, before the complete dissolution of pellets, the bags were replaced with new ones in all treated experimental plots in order to maintain a constant water nutrient concentration throughout the study period. The quantity of fertiliser pellets per surface unit was higher than that used in similar experiments carried out previously on the same site so as to induce a response in macroalgal assemblages over a short time period (Balata et al. 2010).

To verify the efficiency of experimental manipulation, concentrations of seawater nutrients were measured after 1 mo from the beginning of the study in 2 areas selected at random among those with and without added nutrients. In each area, 2 replicate water samples were taken from each of the 3 experimental plots using 60 ml sterile syringes. Samples were immediately filtered (0.45 μm mesh size) and stored at –20°C pending laboratory nutrient analysis. Seawater concentrations of ammonia ($N\text{-}NH_4^+$), nitrite ($N\text{-}NO_2^-$), nitrate ($N\text{-}NO_3^-$) and phosphorus ($P\text{-}PO_4^{3-}$) were determined using a continuous-flow AA3 Auto- Analyzer (Bran-Luebbe) and expressed in μmol l^{-1}.
For each nutrient component, the statistical significance of concentration values was analyzed by 2-way analysis of variance (ANOVA) with Nutrient (nutrient-enriched vs. not enriched) as fixed factor and Area (2 levels) as random factor nested in Nutrient. The concentrations of ammonia, nitrate and phosphorus were significantly higher in nutrient-enriched plots (Table 1), confirming the effectiveness of the tested method for nutrient enrichment of the experimental plots. Differences between areas were significant only for nitrite concentration, which was not significantly different between nutrient-enriched and non-enriched plots.

6.2.3 Caulerpa racemosa growth

The maximum diameter (cm) of *Caulerpa racemosa* patches was measured every 40d throughout the study period. The growth rate per day was calculated as the difference in patch size between consecutive samplings divided for the number of days. At the end of this period, that is 4 mo after the start of the experiment, *C. racemosa* was removed from all treated plots and its abundance in each plot was evaluated in laboratory as biomass, total length of stolons and number of fronds. Biomass was expressed as g dry weight obtained after drying the material for 48 h at 60°C. Patch diameter and *Caulerpa racemosa* biomass, stolon length and the number of fronds were analysed by 2-way ANOVA with Nutrient (nutrient enriched vs. not enriched) as fixed factor and Area (4 levels) as random factor nested in Nutrient.

6.2.4 Macroalgal assemblages

At the end of the study period, experimental plots were sampled by scraping whole 400 cm^2 surface of the plots by means of a hammer and a chisel. Material collected for each plot was preserved in 4% formalin seawater. In the laboratory, all macroalgal species were identified and abundance of each species was estimated as percentage cover (percentage of plot surface occupied by the algal surface measured by spreading out the thalli; Ballesteros 1986). For each sample, total percentage cover was calculated by summing the percentage cover of all algae in the sample.

Percentage cover of turf, encrusting and erect layers was also calculated as the sums of the percentage cover of all the algae belonging to each layer (Piazzi et al. 2001). Diversity was evaluated as the number of species per plot and by the Shannon-Weaver index (H' = $-\sum$Ri/Rt lnRi/Rt, where Ri is the percentage cover of the species i and Rt is the total percentage cover). Multivariate analysis of variance based on permutations (PERMANOVA, Anderson 2001) was used to examine differences in patterns of composition and abundance of species between treatments. The analysis consisted in a 3-way model with Nutrient (nutrient enriched vs. not enriched) and Invasion (*Caulerpa racemosa* added vs. not added) as fixed and orthogonal factors, Area (4 levels) as random factor nested in the interaction Nutrient x Invasion and 3 replicates for each Area. PERMANOVA was conducted on the Bray- Curtis dissimilarity matrix (Bray & Curtis 1957), calculated from untransformed data. SIMPER analysis (Clarke 1993) was used to identify the percentage contribution of each species to the Bray-Curtis dissimilarity between conditions. A 2-dimensional non-metric multidimensional scaling (nMDS) was used to provide a graphical representation of the data. Values of total percentage cover, percentage cover of vegetation layers, species number and Shannon-Weaver index were analysed by 3-way ANOVA. Factors and levels considered in these analyses were the same described for the multivariate analysis. Cochran's C-test was used before each analysis to check for homogeneity of variance (Underwood 1997). Student Newman Keuls (SNK) test was used for *a posteriori* multiple comparison of means.

6.3 Results

6.3.1 Caulerpa racemosa growth

In the plots where *Caulerpa racemosa* were added, patches of the alga reached their maximum size in September, when their diameter measured 42.2 ± 2.3 cm (means ± SE, n = 12) in the invaded plots and 55.5 ± 1.7 cm in the nutrient-enriched + invaded plots. At the end of the study period (October 2009), patch diameter was 38.2 ± 3.6 cm and 51.1 ± 3.1 cm respectively in invaded plots and in nutrient-enriched + invaded plots (Fig. 1). The highest growth rate was registered between August and September, when it reached 0.49 ± 0.02 cm d^{-1} in invaded plots and 0.74 ± 0.02 cm d^{-1} in nutrient-enriched + invaded plots. *Caulerpa racemosa* biomass (15.2 ± 2.4 and 30.2 ± 3.4 gr dry wt m^{-2} respectively in invaded and nutrient-enriched + invaded plots), stolon length (691.9 ± 113.4 cm and 991.7 ± 98.4 cm) and number of fronds (115.4 ± 24.2 and 226.7 ± 20.7), were all lower in invaded plots than in nutrient-enriched + invaded plots. ANOVA detected significant differences between treatments for all the above mentioned variables; moreover, a significant variability among areas was detected for biomass, stolon length and number of fronds (Table 2).

6.3.2 Macroalgal assemblages

A total of 65 macroalgal species were identified (7 Chlorophyta, 7 Fucophyceae and 51 Rhodophyta; Table 3). In control areas, algal assemblages showed a well defined stratified structure. Calcareous Corallinales completely covered the rocky bottom, forming a secondary substrate colonized by encrusting, turf and erect algae. Species of the genus *Peyssonnelia* were the most common encrusting forms, while *Womersleyella setacea*, *Heterosiphonia crispella*, *Eupogodon planus* and *Feldmannophycus raissiae* were widely present in the turf. The erect layer was mostly composed of *Flabellia petiolata*, *Laurencia chondroides* and *Tricleocarpa fragilis*. PERMANOVA detected a significant interaction Nutrient x Invasion (Table 4); pair-wise test comparisons showed significant differences between treatments, which were clearly separated in the nMDS ordinations (Fig. 2). The SIMPER test showed that an increase of nutrient load caused the rise in percentage cover of turf species, especially *Womersleyella setacea*, and of some erect layer species such as *Meredithia microphylla* and *Laurencia chondroides*. In invaded plots, the percentage cover of encrusting taxa *Peyssonnelia* spp., *Zanardinia typus* and calcareous Corallinales and the erect species *Flabellia petiolata, Halimeda tuna, Laurencia chondrioides* and *Meredithia microphylla* decreased, while *Halopithys incurva*, *Womersleyella setacea* and *Clado phora prolifera* showed a high tolerance to *C. racemosa* colonization and increased percentage cover. Responses of macroalgal assemblages in the nutrient-enriched + invaded plots were similar to those in the invaded plots; however, in nutrient-enriched + invaded plots, there was a more pronounced decrease of sensitive taxa such as *Peyssonnelia* spp., *Zanardinia typus*, encrusting Corallinales, *Laurencia chondrioides* and *Flabellia petiolata*, while cover of *Womersleyella setacea* increased (Table 5).

In control plots, species number and total percentage cover were 33.3 ± 1.7 and 195.8 ± 8.9 respectively; lowest values for both these variables were found in the nutrient-enriched + invaded plots. Invaded plots showed intermediate values between control plots and nutrient enriched + invaded ones. Total percentage cover and percentage cover of turf layer showed the highest values in nutrient-enriched plots (238.9 ± 8.4) while percentage cover of encrusting and erect layers showed minimum values in nutrient-enriched + invaded plots (Fig. 3). ANOVA detected significant interaction between nutrient and invasion for total percentage cover, number of species, and percentage cover of all 3 algal layers. The SNK test showed that values of species number, total percentage cover and cover of erect and encrusting layers in invaded plots (both treatments) were significantly lower than in non-invaded plots, while the lowest values were detected in nutrient-enriched + invaded plots. The SNK test also showed that differences between nutrient-enriched plots (both treatments) and not enriched plots were not significant for species number or for cover

of erect and encrusting layers, while total percentage cover and cover of turf layer were significantly higher in nutrient-enriched than in not enriched plots; turf cover was also significantly higher in nutrient-enriched plots than in nutrient-enriched + invaded plots. The Shannon- Weaver index was higher in non-invaded plots than in invaded ones and in nutrient-enriched plots compared to not enriched ones (Table 6).

6.4 Discussion

The results of the present study show that *Caulerpa racemosa* growth was enhanced by nutrient enrichment. Moreover, the effects of invasion on native macroalgal assemblages were stronger where nutrients were added. The growth rates of *Caulerpa racemosa* observed in the present study, the values of biomass and the percentage cover in not nutrient-enriched plots were lower than those reported for shallower habitats in the same area (Piazzi & Cinelli 1999; Piazzi et al. 2001) and more similar to values reported for deeper populations along the French coasts (Ruitton et al. 2005), indicating the influence of depth in spread dynamics of the alga. Nutrient enrichment caused an increase in *C. racemosa* growth rate, resulting in higher values of biomass, stolon length, number of frond and patch size, which were clearly detected in spite of high variability among selected areas. These findings are in accordance with previous observations of the ecological characteristics of other *Caulerpa* species. The expansion of *C. prolifera* Forsskål (Lamouroux) along French coasts has been suggested to be related to the increase of domestic sewage pollution (Ollivier 1929) and thick mats of *C. verticillata* J. Agardh have been observed in sewage canals in Florida (Lapointe et al. 1994). The spread of introduced species, such as *C. taxifolia* in the Mediterranean Sea, *C. brachypus f. parvifolia* (Harvey) Cribb in Florida and *C. ollivierii* Dostál in the Bahamas is also considered to be enhanced by eutrophication (Chisholm et al. 1995; Lapointe et al. 2005; Lapointe & Beldford 2010). Results of the present study showed that invasion by *C. racemosa* may also be faster in eutrophic areas, suggesting that it could be favoured by an increase of pollution in the coastal water of the Mediterranean Sea. Effects of nutrient enrichment on the structure of macroalgal assemblages were lower than those described in other studies (Karez et al. 2004; Kraufvelin 2007) since no species disappeared as a consequence of nutrient enrichment, nor was there an increase in cover of typical species of polluted habitats. Probably the length of the experiment (about 4 mo) allowed observation of only the early phases of the eutrophication process in deep subtidal Mediterranean rocky assemblages. Nutrient enrichment caused an increase of macroalgal cover, mostly due to turf species, a pattern that has been widely described elsewhere (Gorostiaga & Diez 1996; Diaz et al. 2002; Gorgula & Connell 2004; Russell et al. 2005). Increasing nutrient levels in coastal waters are considered to be the principal cause of the

dominance of turf-forming species, which can spread more quickly under nutrient overload conditions than other seaweeds (Rosenberg & Ramus 1984; Hein et al. 1995; Pedersen & Borum 1996, 1997). The effects of addition of *Caulerpa racemosa* were similar to those described for naturally invaded deep subtidal Mediterranean assemblages (Piazzi et al. 2007a; Piazzi & Balata 2008, 2009), i.e. modification of the assemblage structure and reduced macroalgal cover and biodiversity. The addition of *Caulerpa racemosa* in combination with nutrient enrichment resulted in more extensive modification of the assemblage structure, compared to the other treatments, and a reduction in percent cover of sensitive species was observed. *C. racemosa* competes with benthic organisms by overgrowth of stolons (Piazzi et al. 2001; Kruzic et al. 2008; Baldacconi & Corriero 2009) and the enhanced abundance of *C. racemosa* caused by nutrient enrichment can amplify the effect of stolon cover on benthic assemblages. This effect can lead to severe consequences particularly in coralligenous habitats, which are highly sensitive to environmental alterations (Balata et al. 2005). The maintenance of this habitat is related to the balance between growth and death of calcareous organisms and a long recovery period is required following any damage, owing to the low growth rate of Corallinales, which are the main builders of this habitat in the Mediterranean region (Garrabou & Ballesteros 2000). Many sessile organisms can completely or partially recover during the vegetative rest period of *C. racemosa* (Piazzi & Ceccherelli 2006; Klein & Verlaque 2009), but this period in not sufficient to allow the recovery of encrusting Corallinales. The death of the latter due to *C. racemosa* cover could have serious consequences for the conservation of Mediterranean coastal habitats. Turf species showed lower values in plots where both stressors were present than in nutrient treated plots without the addition of *Caulerpa racemosa*. This finding confirms previous observations showing that turf species are more affected by *C. racemosa* than erect layer species, probably because the former are more susceptible to the alga's competitive mechanisms (Piazzi et al. 2001; Balata et al. 2005). However, despite the occurrence of antagonism between *C. racemosa* and turfs, the introduced turf-forming species *Womersleyella setacea* showed higher abundance in plots where both *C. racemosa* and nutrients were added than in control plots. In fact, *W. setacea* was one of the species that most increased their abundance following nutrient enrichment and was less affected by *C. racemosa* colonization than other turf-species. Thus, the final result of the interaction between nutrient enrichment and *C. racemosa* invasion was the shift from a well structured macroalgal assemblage to one strongly dominated by a small number of invasive species. This replacement process implies a simplification of the architectural complexity of macroalgal assemblages, due to a decrease in species richness and the reduction or disappearance of engineering species (such as encrusting Corallinales, Peyssonneliaceae, and erect Udoteaceae). Although the aim of the present study was not to evaluate

the role played by pollution in modifying vulnerability of macroalgal assemblages to invasion, biotic and environmental changes observed in the nutrient-enriched plots suggest that these may have lead to a further reduction in these assemblages' resistance to *Caulerpa racemosa*. In fact, the spread of invasive seaweeds is considered to be favoured not only by the high ecological fitness of the invaders but also by the characteristics of the receiving environment (Dunstan & Johnson 2007) and anthropogenic disturbance, causing changes in the resource availability, often leads to a higher incidence and abundance of invaders (Schaffelke & Hewitt 2007; Valentine et al. 2007). The amount of resource availability across the resource spectrum is another factor that determines the success or failure of a seaweed invasion (Dunstan & Johnson 2007). Thus, tolerance by *Caulerpa* species to changes in resource availability and the presence of degraded receiving habitats are both considered to promote colonization by these species (Occhipinti- Ambrogi & Savini 2003). For example, sediment traits of urban wastewater impacted seabed are described to enhance the competitiveness of *C. taxifolia* when it is in contact with Mediterranean seagrasses (Chisolm et al. 1995; Ceccherelli & Cinelli 1997). Changes in the structure of assemblages following nutrient enrichment and in particular the increase of *Womersleyella setacea*, suggest further positive feedback between impacts, as the presence of algal turfs can favor colonization by *C. racemosa* (Ceccherelli et al. 2002; Piazzi et al. 2003; Bulleri & Benedetti-Cecchi 2008). Different roles, as passenger or driver of ecosystem modifications (MacDougall & Turkington 2005), have been attributed to *C. racemosa* (Bulleri et al. 2010) and the importance of nutrient enrichment in this context could be an interesting topic for further investigation. Nutrient concentrations tested in the present study were higher than those usually measured in the Mediterranean coastal area affected by diffuse sources of pollution. Nevertheless, values of nutrient concentration comparable to those in our study were measured in some marine coastal areas subjected to major point sources of nutrient pollution, such as sewage effluents from intensive fish farming installations (Gennaro et al. 2006) and outfalls from domestic waste treatment plants (Arevalo et al. 2007). Given the long time response of macroalgal assemblages to diffuse eutrophication sources and the short vegetative period of *Caulerpa racemosa* (July to October), we had to stress the ecosystem by means of an experimental set-up that could induce a response in assemblages over a short time period that was comparable to that caused by chronic exposure to nutrient pollution. Further investigations could test the effects of changes in amount and temporal variability of nutrient levels; in fact, impacts are known to be dependent on both the intensity of stresses and their patterns of variations (Benedetti-Cecchi et al. 2006; Bertocci et al. 2007; Vaselli et al. 2008). Non-native macroalgal invasions are expected to increase in coming years (William & Smith 2007), as is land-based nutrient pollution in coastal waters (Howarth & Marino 2006). Our results agree with other findings (Ceccherelli &

Cinelli 1997; Steen 2003; Sánchez & Fernández 2006; Lapointe & Beldford 2010), indicating that the spread of some species of non- native macroalgae in the oligotrophic regions can be favored by nutrient enrichment. The role of eutrophication in aiding invasions of non-native macroalgae must be recognized and more experimental studies on this topic are needed in order to predict the con sequences of possible synergisms between these aspects of global change and to identify appropriate strategies to effectively manage the phenomenon in the future.

6.5 Tables and Figures

Table 1. Nutrient concentrations in plots with and without added nutrients (mean ± SE, n = 12) and results of ANOVA analysis between the 2 experimental conditions. Significant p-values are in **bold** type

Nutrients	Plots without added nutrients (µmol l^{-1})	Nutrient enriched plots (µmol l^{-1})	F	p
$N\text{-}NH_4^+$	1.7 ± 0.6	47.3±7.1	11.5	**0.006**
$N\text{-}NO_3$	0.7 ± 0.3	48.8 ± 12.3	18.8	**0.001**
$N\text{-}NO_2^-$	0.3 ± 0.1	3.3 ± 0.9	1.4	0.286
$P\text{-}PO_4^{3-}$	<0.001	9.1 ± 2.5	4.1	**0.003**

Table 2. *Caulerpa racemosa*. Results of nested ANOVA analysis performed on variables patch diameter, stolon length, biomass and number of fronds. Significant p-values are in bold type; ns: not significant.

Source	df	MS	F	p	Source	df	MS	F	p
Patch diameter					**Biomass**				
Nutrient = N	1	1568.16	42.70	**0.0006**	Nutrient = N	1	0.767	10.66	**0.017**
Area(N)	6	36.72	0.97	0.4756	Area(N)	6	0.072	5.15	**0.004**
Residual	16	37.83			Residual	16	0.014		
Total	23				Total	23			
Cochran's C = 0.453 (ns)					Cochran's C = 0.304 (ns)				
Stolon length					**Frond number**				
Nutrient = N	1	1315478	7.04	**0.037**	Nutrient = N	1	148444	23.91	**0.002**
Area(N)	6	186977.8	3.6	**0.018**	Area(N)	6	6207.41	3.85	**0.014**
Residual	16	51867.76			Residual	16	1614.28		
Total	23				Total	23			
Cochran's C = 0.396 (ns)					Cochran's C = 0.307 (ns)				

Table 3. Floristic list of samples collected in the treated and not treated experimental plots. c: control, n: nutrient-enriched, i: invaded, n+i: nutrient-enriched + invaded. Values of the mean percentage cover are reported for each treatment.

TAXA	c	n	i	n+i
Chlorophyta				
Cladophora echinus (Biasoletto) Kützing	0.3	0.5	0.3	0.0
Cladophora prolifera (Roth) Kützing	0.4	1.2	3.8	5.7
Flabellia petiolata (Turra) Nizamuddin	47.5	46.2	34.2	24.9
Halimeda tuna (J. Ellis e*t* Solander) J.V. Lamouroux	3.1	2.2	0.0	0.0
Palmophyllum crassum (Naccari) Rabenhorst	0.1	1.5	0.0	0.0
Pseudochlorodesmis furcellata (Zanardini) Børgesen	0.8	2.5	0.3	3.0
Valonia macrophysa Kützing	0.2	0.1	0.0	0.4
Ochrophyta				
Dictyopteris polypodioides (A.P. De Candolle) J.V. Lamouroux	0.4	0.1	0.0	0.0
Dictyota linearis (C. Agardh) Greville	0.7	0.8	0.5	0.5
Halopteris filicina (Grateloup) Kützing	0.8	1.0	3.2	4.4
Nereia filiformis (J. Agardh) Zanardini	0.2	0.1	0.1	0.0
Sphacelaria cirrosa (P.H. Roth) C. Agardh	0.0	0.1	0.0	0.0
Sphacelaria plumula Zanardini	0.1	0.1	0.1	0.0
Zanardinia typus (Nardo) G. Furnari	4.0	1.8	0.0	0.1
Rhodophyta				
Acrodiscus vidovichii (Meneghini) Zanardini	0.9	1.1	0.0	0.0
Acrosorium venulosum (Zanardini) Kylin	0.2	0.5	0.3	0.4
Acrothamnion preissii (Sonder) Wollaston	0.1	1.1	0.3	2.2
Aglaothamnion tenuissimum (Bonnemaison) Feldmann-Mazoyer	0.2	0.2	0.0	0.0
Amphiroa rubra (Philippi) Woelkerling	0.1	0.3	0.0	0.0
Anthithamnion piliferum Cormaci *et* Furnari	0.7	0.5	0.6	0.8
Apoglossum ruscifolium (Turner) J. Agardh	0.2	0.2	0.0	0.1
Botryocladia botryoides (Wulfen) Feldmann	1.1	0.4	0.5	0.3
Ceramium bertholdii Funk	0.0	0.0	0.0	0.0
Ceramium diaphanum (Lighfoot) Roth	0.1	0.1	0.0	0.0
Ceramium flaccidum (Kützing) Ardissone	0.0	0.0	0.0	0.0
Ceramium codii (H. Richards) Feldmann-Mazoyer	0.2	0.0	0.0	0.0
Champia parvula (C. Agardh) Harvey	0.4	0.1	0.2	0.1
Chondria capillaris (Hudson) M.J. Wynne	0.3	0.0	0.0	0.0
Contarinia squamariae (Meneghini) Denizot	0.7	0.4	0.0	0.0
Crouania attenuata (C. Agardh) J. Agardh	0.4	0.2	0.2	0.1
Dasya baillouviana (S.G. Gmelin) Montagne	0.1	0.5	0.2	0.6
Dasya ocellata (Grateloup) Harvey	0.0	0.0	0.0	0.0
Erythroglossum sandrianum (Kützing) Kylin	0.0	0.0	0.0	0.0
Eupogodon planus (C. Agardh) Kützing	1.9	1.1	0.7	0.6
Feldmannophycus rayssiae (Feldmann *et* Feldmann-	0.7	1.4	1.4	0.8

Mazoyer)Augier *et* Boudouresque				
Gelidium bipectinatum G. Furnari	0.0	0.0	0.0	0.2
Jania adhaerens J. V. Lamouroux	1.0	3.0	1.5	2.4
Halopithys incurva (Hudson) Batters	1.0	4.0	7.8	8.1
Halydyction mirabile Zanardini	0.0	0.4	0.0	0.0
Halymenia floresia (Clemente and Rubio) C. Agardh	0.0	0.0	0.1	0.0
Herposiphonia secunda (C. Agardh) Ambronn	0.0	0.0	0.0	0.0
Heterosiphonia crispella (C. Agardh) M.J. Wynne	1.1	1.3	0.8	1.1
Hypoglossum hypoglossoides (Stackhouse) Collins *et* Harvey	0.2	0.2	0.0	0.0
Laurencia chondrioides Børgesen	42.5	42.3	20.8	7.8
Lomentaria chylocladiella Funk	0.2	0.1	0.0	0.0
Meredithia microphylla (J. Agardh) J. Agardh	9.0	15.3	2.4	2.8
Monosporus pedicellatus (J.E. Smith) Solier	0.1	0.3	0.2	0.3
Osmundea pelagosae (Schiffner) F.W. Nam	2.4	0.6	0.0	0.0
Peyssonnelia rubra (Greville) J. Agardh	46.7	44.4	18.9	14.2
Peyssonnelia squamaria (S.G. Gmelin) Decaisne				
Phyllophora crispa (Hudson) P.S. Dixon	0.0	0.8	0.0	1.0
Plocamium cartilagineum (Linnaeus) P.S. Dixon	0.1	0.1	0.1	0.0
Polysiphonia elongata (Hudson) Sprengel	0.0	0.0	0.0	0.2
Polysiphonia furcellata (C. Agardh) Harvey	0.1	0.2	0.1	0.1
Polysiphonia perforans Cormaci, G. Furnari, Pizzuto *et* Serio	0.3	0.1	0.0	0.0
Pterothamnion plumula (Ellis) Nägeli	0.1	0.1	0.0	0.0
Rhodophyllis divaricata (Stackhouse) Papenfuss	0.2	0.0	0.0	0.0
Rodriguezella strafforelloi F. Schmitz	0.4	0.7	0.7	0.8
Sebdenia dicotoma Berthold	0.2	0.4	0.0	0.0
Spyridia filamentosa (Wulfen) Harvey	0.0	0.1	0.1	0.0
Tricleocarpa fragilis (linnaeus) Huisman *et* R.A. Towsend	13.2	9.6	7.0	3.7
Womersleyella setacea (Hollenberg) R.E. Norris	15.9	87.5	34.1	57.9
Wrangelia penicillata (C. Agardh) C. Agardh	0.2	0.0	0.0	0.0

Table 4. Results of PERMANOVA analysis on species composition and abundance of macroalgal assemblages in experimental plots and pairwise tests for interaction factor N x I (Nutrient x Invasion). N–: not nutrient-enriched (c, i: control vs. invaded); N+: nutrient-enriched (n, i: nutrient vs. nutrient+ invaded); I–: not invaded (c, n: control vs. nutrient-enriched); I+: invaded (i, n + i: invaded vs. nutrient-enriched + invaded). Significant p(perm) values are in **bold** type

Source	df	MS	pseudo-F	$p_{(perm)}$
N	1	3135.6	72.02	**0.001**
I	1	6811.7	156.46	**0.001**
N x I	1	609.8	14.00	**0.001**
Area (N x I)	4	43.5	0.57	0.835
Residual	40	75.9		
Total	47			

Pairwise tests (N x I)

	$p_{(perm)}$		$p_{(perm)}$
N- : c , i	**0.001**	I- : c, n	**0.001**
N+: n, n+i	**0.001**	I+: i, n+i	**0.001**

Table 5. Results of SIMPER test showing taxa contributing most to differences between experimental treatments. c: control, n: nutrient-enriched, i: invaded, n+i: nutrient-enriched + invaded. Values in bold in the right-hand column show the average dissimilarity between the 2 treatments in the columns to the left

TAXA	**Mean % cover**	**Mean % cover**	**Contribution %**
	c	**i**	**Average dissimilarity = 19.4**
Peyssonnelia spp.	45.42	18.92	19.31
Encrusting Corallinales	200	174.17	18.97
Laurencia chondroides	38.75	20.75	13.11
Flabellia petiolata	42.5	35.83	6.28
Meredithia microphylla	9.1	3.08	5.69
Halopithys incurva	1.83	7.82	5.18
Womersleyella setacea	18.42	24.08	4.36
Zanardina typus	4.02	1.33	3.01
Cladophora prolifera	0.38	3.77	2.48
Halimeda tuna	3.08	0	2.24

	c	n	Average dissimilarity = 18.48
Womersleyella setacea	18.42	87.5	42.81
Laurencia chondroides	38.75	42.33	7.04
Meredithia microphylla	9.1	15.33	6.07
Halopithys incurva	1.83	4	2.66
Jania adhaerens	0.97	3.03	1.47
Pseudochlorodesmis furcellata	0.83	2.53	1.1

	c	n + i	Average dissimilarity = 35.19
Encrusting Corallinales	200	135.42	27.62
Peyssonnelia spp.	45.42	14.17	13.29
Laurencia chondroides	38.75	8.18	13.01
Womersleyella setacea	18.42	48.75	12.95
Flabellia petiolata	42.5	25.75	7.17
Meredithia microphylla	9.1	2.77	3.36
Halopithys incurva	1.83	8.08	3.06
Tricheocarpa fragilis	10.25	4.93	2.7
Cladophora prolifera	0.38	5.67	2.26
Zanardina typus	4.02	0	1.72
Halimeda tuna	3.08	0	1.31

	i	n + i	Average dissimilarity = 22.84
Encrusting Corallinales	174.17	135.42	28.88
Womersleyella setacea	24.08	48.75	18.37
Laurencia chondroides	20.75	8.18	9.38
Flabellia petiolata	35.83	25.75	7.6
Tricheocarpa fragilis	11.17	4.93	4.86
Peyssonnelia spp.	18.92	14.17	3.82
Meredithia microphylla	3.08	2.77	2.41
Pseudochlorodesmis furcellata	0.33	2.95	1.95

Table 6. Results of ANOVA analysis on total Percent cover, percent cover of vegetation layers (Erect, Encrusting, Turf), Species number per sample and values of Shannon-Weaver index (H'). SNK test for interaction factor N x I (Nutrient x Invasion) = N(I): N x I comparisons for pairs of levels of factor "Nutrient"; I(N): N x I comparisons for pairs of levels of factor "Invasion"; c: control; n: nutrient-enriched; i: invaded; n+i: nutrient-enriched + invaded. SNK test for Nutrient factor = N-: not nutrient enriched plots (c and i); N+: nutrient enriched plots (n and n+i). SNK test for Invasion factor = I-: *C.racemosa* not added plots (c and n); I+: *C.racemosa* added plots (i and n+i).

Source	df	MS	F	p	Source	df	MS	F	p
Erect					**Percent cover**				
Nutrient = N	1	283.2	0.9	0.344	Nutrient = N	1	6627	31.7	**0.001**
Invasion = I	1	24201.1	82.8	**0**	Invasion = I	1	238854.1	1145.8	**0**
Area (NxI)	12	291.9	1.1	0.382	Area (NxI)	12	208.4	0.3	0.959
NxI	1	4700.5	16.1	**0.001**	NxI	1	47125.3	226.0	**0**
Residual	32	262.0			Residual	32	542.5		
Total	47				Total	47			
C = 0.191 (ns)					C=0.243 (ns)				
SNK test N x I	N(I)	c = n i > n+i	I(N)	c > i n > n+i	SNK test NxI	N(I)	c < n i > n+i	I(N)	c > i n > n+i
Encrusting					**Species number**				
Nutrient = N	1	11535.1	48.9	**0**	Nutrient = N	1	58.5	12.8	**0.003**
Invasion = I	1	58569.2	248.29	**0**	Invasion = I	1	910.0	199.4	**0**
Area (N x I)	12	235.8	1.44	0.198	Area (NxI)	12	4.5	1.6	0.141
NxI	1	1743.6	7.39	**0.018**	NxI	1	22.6	4.9	**0.045**
Residual	32	163.5			Residual	32	2.8		
Total	47				Total	47			
C = 0.174 (ns)					C=0.204 (ns)				
SNK test N x I	N(I)	c = n i > n+i	I(N)	c > i n > n+i	SNK test N x I	N(I)	c = n i > n+i	I(N)	c > i n > n+i
Turf					**H'**				
Nutrient = N	1	32489.6	445.9	**0**	Nutrient = N	1	0.157	18.1	**0.001**
Invasion = I	1	863.6	11.8	**0.004**	Invasion = I	1	0.124	14.3	**0.002**
Area (N x I)	12	72.8	0.4	0.906	Area (NxI)	12	0.008	0.7	0.693
NxI	1	6320.4	86.7	**0**	NxI	1	0.001	0.1	0.707
Residual	32	148.9			Residual	32	0.011		
Total	47				Total	47			
C = 0.241 (ns)					C=0.229 (ns)				
SNK test N x I	N(I)	c < n i< n+i	I(N)	c = i n > n+i	SNK test	N I	N- > N+ I- > I+		

Figure 1. *Caulerpa racemosa.* Diameter of patches (mean ± SE, n = 12) over the 4 mo of the experiment. i: invaded plots, n+i: nutrient enriched + invaded plot

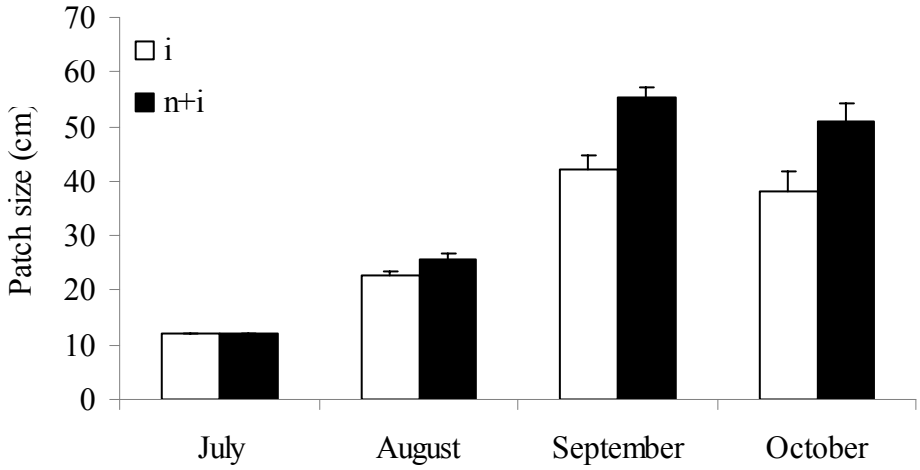


Figure 2. nMDS ordination of species composition and abundance of macroalgal assemblages of all replicate plots ◯ control, ● nutrient-enriched, Δ invaded, ▲ nutrient-enriched + invaded

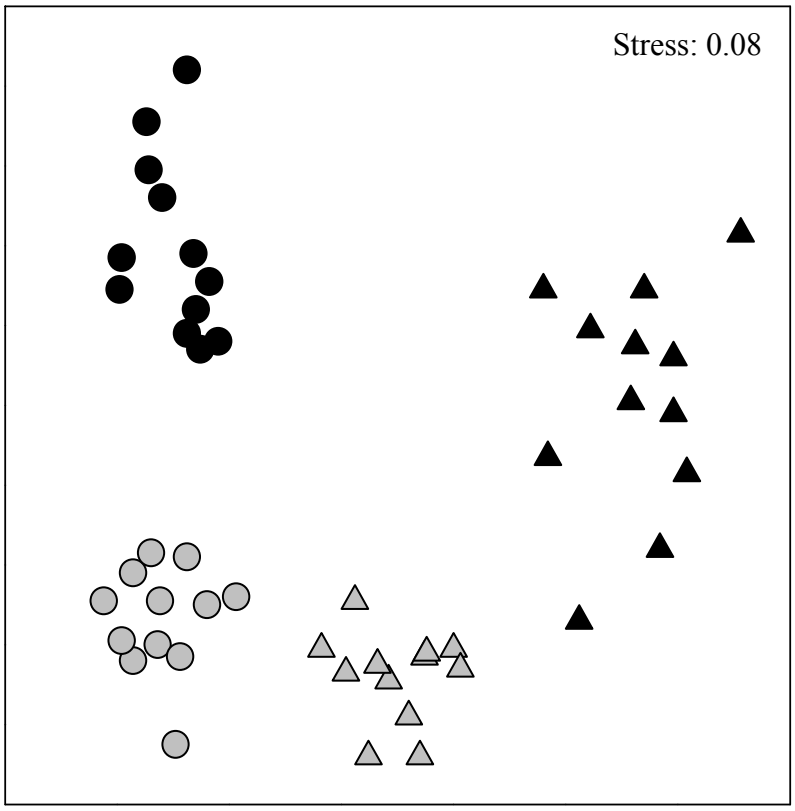
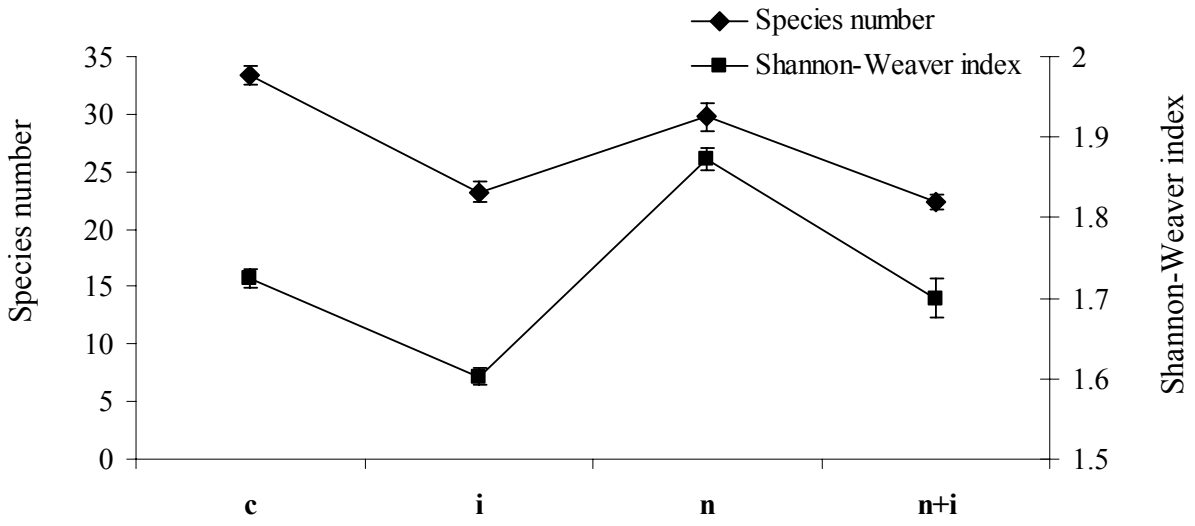
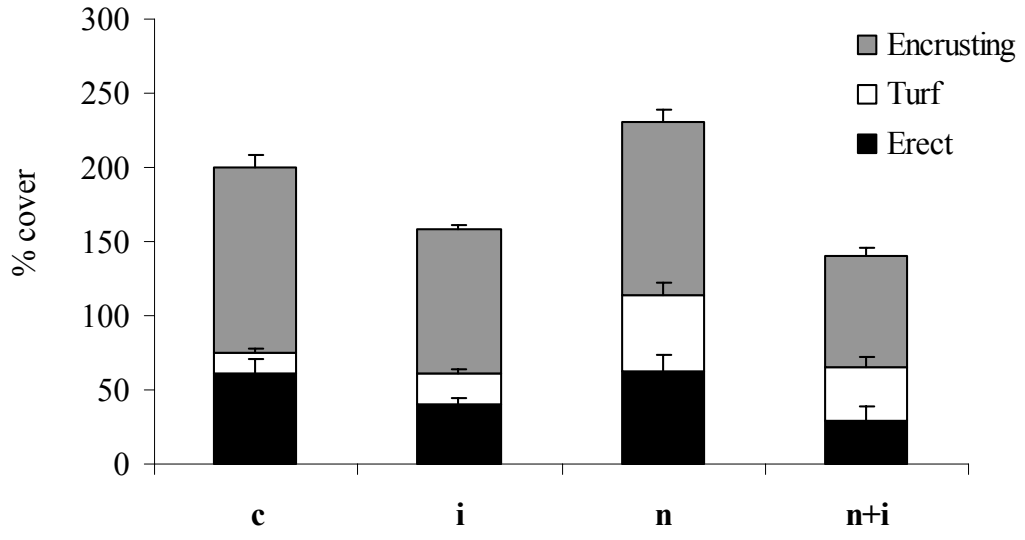


Figure 3. Vegetation cover of experimental plots (mean ± SE, n = 12). c: control, i: invaded, n: nutrient-enriched, n+i: nutrient-enriched + invaded. (a) Number of species and Shannon-Weaver index; (b) percentage cover of vegetation layers (encrusting, turf and erect)



a)



b)

7. THE ROLE OF NUTRIENTS IN SUCCESSFUL INVASION OF *CAULERPA RACEMOSA* VAR *CYLINDRACEA*

PAOLA GENNARO, LUIGI PIAZZI

ABSTRACT

Effects of nutrients dynamics on biological invasions have been less investigated in marine habitats. The present study aimed to evaluate the role of nutrients pollution in determining successful invasion of the introduced seaweed *Caulerpa racemosa* var. *cylindracea* in the Mediterranean subtidal rocky habitat. To this end, a manipulative field experiment has been carried out by supplying water column with nutrients for a one year period and afterwards by transplanting *C. racemosa* both in nutrients-enriched and in reference macroalgal assemblages. Results showed that extension and weightiness of *C. racemosa* invasion in the assemblages previously treated with nutrients were higher than in reference ones, highlighting that communities stressed by nutrients pollution are more vulnerable to invasion. Nutrients enrichment changed the structure of natural macroalgal assemblages mainly by encouraging growth of turf species, while no significant effects were detected for the erect and prostrate layers and for species number; this last result suggests that susceptibility of the community to invasion can depends more on morpho-functional identity of macroalgae rather than on diversity of assemblages. Changes in seawater nutrients availability may facilitate the spread of *C. racemosa*, by both enhancing its growth and eroding the natural resistance of macroalgal assemblages. Thus, maintenance of good water quality may play an important role in containing invasion by the introduced seaweed.

KEY WORDS: *Caulerpa racemosa* var. *cylindracea*, Mediterranean Sea, nutrients, resistance, successful invasion, subtidal rocky habitat

7.1 Introduction

Biological invasions is recognized as an important element of global change and a major driver of ecosystem modification (Vitousek et al. 1996, 1997), both in undisturbed and human disturbed marine habitats. Nevertheless, where other global-change elements impacted on marine ecosystems, severe synergetic effects between biological invasion and the other stressors may occur; in fact, many human-induced alterations of natural systems can generally affect species distribution and resource dynamics in terrestrial and aquatic systems, consequently interacting with biological invasions (Vitousek 1994; Huenneke 1997). Knowledge of the effects of environmental alterations on biological invasions is an essential goal for ecologists, as understanding of mechanisms aiding colonization of alien species is crucial both for assessment of threat posed by their spread and for planning control programs (Dukes & Mooney 1999; Harris & Tyrrell 2001). An organism capable of spreading in the absence of any primary facilitation mechanisms represents a major threat to the integrity of native assemblages and its management needs to directly target the organism itself; on the contrary, management of invasions by organisms requiring disturbance or other facilitating mechanisms to establish and persist includes several options that can indirectly act on the cause of disturbance rather than on the invader itself (Valentine et al. 2007).

Environmental alterations may directly influence the spread of invasive species, by increasing growth rate or reproductive ability, but they can also indirectly act, by decreasing habitat resistance to the invasion through modifications of assemblage structure (Piola & Johnston 2008). In fact, ecological properties of the recipient community can be crucial in determining successful invasion. The ability of communities to resist biological invasions may be related to different intrinsic characteristics which define the ecological stability of a community as resistance property (Londsale 1999; Prieur-Richard & Lavorel 2000; Dunstan & Johnson 2007). In many cases, communities resistance may be directly correlated to biodiversity, as highly diversified communities may be less susceptible to invasions (Levine 2000; Naeem et al. 2000; Stachowicz et al. 2002) owing to a more complete utilization of environmental and/or biological resources (Elton 1958). Other models considered functional composition of assemblages more important than species diversity (Meiners et al. 2004; Arenas et al. 2006; Britton-Simmons 2006). Whatever the result, any environmental alteration which modifies structure of natural assemblages may in both cases reduce their resistance facilitating the spread of alien species.

In marine coastal systems, the increase of nutrient availability represents a major alteration of environmental conditions and it is considered one of the main causes of ecosystems complexity degradation (Soltan et al. 2001; Arevalo et al. 2007). The effects of nutrients dynamics on biological invasions have been widely investigated on terrestrial plant communities (Burke & Grime 1996;

Gross et al. 2005; Leishman & Thomson 2005). On the contrary, in marine systems only few studies have been carried out on this topic, even if important synergetic effects have been highlighted by some authors (Steen 2003; Sánchez & Fernández 2006; Incera et al. 2009). Nutrients availability may enhance the growth of alien seaweeds and seagrasses facilitating their spread (Stimson et al. 2001; Torres et al. 2004; Lapointe et al. 2005). Moreover, high nutrient concentrations may lead to degradation of benthic systems so decreasing resistance of native assemblages to invasion (Stachowicz et al. 1999). Knowledge of interaction mechanisms occurring between nutrients and biological invasions represents a crucial information in planning necessary programs to control the spread of alien species (Lapointe & Beldford 2010).

Caulerpa racemosa (Forsskål) C. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque (*C. racemosa* from here after) is considered one of the most invasive introduced seaweeds in the Mediterranean Sea; it has rapidly and successfully colonized wide areas of this basin, forming permanent populations and strongly interfering with native species (Piazzi et al. 2001, 2005b; Klein & Verlaque 2008; Piazzi & Balata 2008). Some of biological and ecological factors affecting both alga spread and invasibility of the Mediterranean habitats have been investigated; results of these studies highlighted that *C. racemosa* invades specific habitats better than others (Katsanevakis et al. 2010) and that in the same specific habitat differently structured assemblages show different resistance to invasions (Ceccherelli et al. 2002; Bulleri et al. 2010). However, vulnerability of assemblages to *C. racemosa* invasion was never related to human-induced environmental changes. A few authors observed both a more distribute pattern of *C. racemosa* in marine areas which are subjected to high level of human pressure (Klein et al. 2005) and a higher tolerance of the invasive alga to high sedimentation rates compared to most of native seaweeds (Piazzi et al. 2005a, 2007). Moreover, important synergetic effects between *C. racemosa* and nutrient enrichment has been described in a recent study (Gennaro & Piazzi 2011) which have showed enhanced spread of *C. racemosa* under high nutrient regime of seawater, without yet investigating the involved mechanisms. In particular, no information are available about the role of nutrients in undermining natural resistance of native macroalgal assemblages to *C. racemosa* invasion.

The present study aimed to evaluate the role of nutrient pollution in determining successful invasion of *C. racemosa*. To this end, a manipulative field experiment has been carried out by chronically exposing macroalgal assemblages to high nutrients load and afterwards by transplanting *C. racemosa*. The following hypothesis were tested: (i) an increase of nutrients load may alter the structure of macroalgal assemblages of the subtidal rocky bottom, (ii) the resistance of native assemblages to *C. racemosa* invasion decreases under high nutrient concentration.

7.2 Materials and Methods

The study was carried out along the Tuscan coast to the south of Leghorn (43°28'24" N and 10°19'42" E) below 20 m depth. Manipulative field experiment took place from July 2009 to September 2010, on the subtidal rocky bottom 24 m deep, where substratum is colonized by coralligenous assemblages (*sensu* Ballesteros 2006). Macroalgal reference assemblages and nutrient-enriched assemblages were considered as treatments of the experimental design which was realized in two phases: first, macroalgal assemblages assigned to the nutrient-enriched treatment were chronically exposed to high nutrient concentrations for a one year period, in order to stress the ecosystem and to induce structural response of communities to the source of pollution; later, we tested the invasion capacity of *C. racemosa* both in references assemblages and in assemblages previously treated with nutrients. For each treatment, two areas were selected at random along 1 km of coastline and, within each area, 8 experimental units 400 cm^2 in size were chosen. In the areas assigned to nutrient enrichment, in July 2009 two 20x5x5 cm nylon-mesh bags (1-mm mesh size), each containing 200 gr of fertilising pellets (OSMOCOTE® Scotts), were placed along the two opposite sides of each experimental plot and fixed to the substratum with nails. The NPK chemical composition of pellets was 15+9+9, which is one of the combinations of nitrogen (15%), phosphorous (9%) and potassium (9%) commonly utilized for fertilizing terrestrial plants. Every three months beginning from July 2009, before the complete dissolution of pellets, the bags were replaced with new ones in all experimental plots in order to maintain a constant water nutrients concentration throughout the study period. The amount of fertilising pellets per surface unit was the same used in previous experiments carried out in the same area (Gennaro & Piazzi 2011). In July 2010, after one year from starting experiment, the mesh bags were removed and 4 of the 8 plots of each area were sampled by scraping all organisms through a hummer and a chisel, in order to analyzed the structure of macroalgal assemblages stressed by chronic exposure to nutrients. Collected material was preserved in 4% formalin seawater, all macroalgal species were identified in the laboratory and abundance of each species was estimated as percentage of plot surface occupied by the algal surface measured by spreading out the thalli (Ballesteros 1986). Seaweeds were divided into prostrate, turf and erect species and abundance of each vegetation layer was calculated as the sum of percentage cover of all species belonging to the same layer. Diversity of assemblages was evaluated as number of species per plot surface.

In the same month of July, which is the maximum vegetative growth period of *Caulerpa racemosa* (Ruitton et al. 2005), 15 fragments of the alga 12 cm in length were transplanted at the edge of each experimental unit, both in nutrient enriched and reference areas, using two wire bridges fixed to the substratum by means of 15 cm long nails. Two months after transplanting *C. racemosa* fragments,

the extension of *C. racemosa* invasion was measured as the maximum distance from the edge of plots reached by stolons and as biomass and total stolons length within each plot surface. The maximum distance reached by stolons was measured in situ by SCUBA diving, while biomass and total stolons length was measured in the laboratory after *C. racemosa* removing. Biomass was expressed as gr dry weight (gr_{dw}) obtained after drying the material for 48 h at 60°C.

Multivariate analysis of variance based on permutations (PERMANOVA, Anderson 2001) was used to examine differences in patterns of composition and abundance of species between treatments. The analysis consisted in a 2-way model with Nutrient (nutrient enriched vs. not nutrient enriched) as fixed a factor and Area (2 levels) as random factor nested in Nutrient and four replicates for each Area. PERMANOVA was conducted on Bray-Curtis dissimilarity matrix, calculated from untransformed data. SIMPER analysis (Clarke 1993) was used to identify the percentage contribution of each species to the Bray-Curtis dissimilarity between conditions.

Total percentage cover, mean species number per plot and percentage cover of vegetation layers were analyzed by 2-way ANOVA with the same factors and levels used in PERMANOVA analysis. Cochran's *C*-test was used before each analysis to check for homogeneity of variance (Underwood 1997).

The maximum distance reached by *C. racemosa* stolons, biomass and stolons length were analysed by 2-way ANOVA with the factor Condition (previous-treated vs. controls) as fixed factor and Area (2 levels) as random factor nested in Condition.

7.3 Results

A total of 53 macroalgal species were identified (6 Chlorophyta, 7 Heterokontophyta and 38 Rhodophyta). Calcareous Corallinales completely covered the rocky bottom, forming a secondary substrate colonized by prostrate, turf and erect algae. Species of the genus *Peyssonnelia* were the most common prostrate forms, while *Womersleyella setacea*, *Pseudochlorodesmis furcellata*, *Eupogodon planus* and *Feldmannophycus raissiae* were widely present in the turf. The erect layer was mostly composed of *Flabellia petiolata*, *Halimeda tuna*, *Laurencia chondroides, Meredithia microphylla* and *Tricleocarpa fragilis*. PERMANOVA detected significant differences between references and nutrient-enriched assemblages (Table 1). The SIMPER test showed that percentage cover of both turf species, especially *Womersleyella setacea* and *Pseudochlorodesmis furcellata*, and some species of the erect layer, such as *Meredithia microphylla*, increased in nutrient-enriched assemblages. On the contrary, *Zanardina typus* was less abundant in nutrient-enriched than in reference plots (Table 2). Total percentage cover and cover of turf were significantly higher ($F = 18.35$, $P = 0.042$ and $F = 74.16$, $P = 0.003$ respectively) in nutrient-enriched assemblages than in

references ones, while not significant differences between treatments were found for percentage cover of erect (F = 4.34, P = 0.179) and prostrate (F = 0.05, P = 0.88) layers and for the mean species number (F = 3.52, P = 0.193) (Fig.1a and 1b).

At the end of the study period (September 2010), the mean distance of *Caulerpa racemosa* stolons from the edge of the plots was 14.7 ± 1.2 cm (mean ± SE, n=8) in the references plots and 26.4 ± 1.3 cm in the previously nutrient-treated plots (Fig. 2a). *C. racemosa* biomass (0.029 ± 0.002 and 0.091 ± 0.007 gr $_{dw}$ 400 cm^{-2} in references and nutrient-treated plots respectively) and total stolons length (80.2 ± 8.3 cm and 197.2 ± 17.9 cm) were lower in references plots than in nutrient-treated plots (Fig. 2b and 2c). ANOVA detected significant differences between conditions for all the above mentioned variables (mean distance of *C. racemosa* stolons F =164.19, P = 0.002, biomass F = 304.52, P = 0.001, stolon length F = 13.96, P = 0.024). Differences between areas were also significant for stolons length (F = 4.62, P = 0.023).

7.4 Discussion

The present study highlighted that *Caulerpa racemosa* invasion was more serious under nutrients enriched regime, as the invaded surface, stolons length and alga biomass developed on the assemblages exposed to nutrients enrichment were higher than in not nutrients treated assemblages.

Changes in structure of macroalgal assemblages caused by nutrients were similar to those described in previous investigations carried out both in the same zone (Gennaro & Piazzi 2011) and in other geographical areas (Gorostiaga & Diez 1996; Diaz et al. 2002). The main structural change was an increase of percentage cover of turf, but also an increasing abundance of flattened Rhodophyta and decreasing of prostrate Heterokontophyta were observed as minor modifications. Growing abundance of turf species is a pattern widely described in several marine areas subjected to nutrients enrichment (Eriksson et al. 2002; Gorgula & Connel 2004). In fact, the chief species of turf layer are filamentous seaweeds, which generally grow better than other morphological forms under high nutritional availability due to their faster growth, high nutrients requirement and uptake rates per time (Pedersen & Borum 1997; Taylor et al. 1998).

The increase of turf in nutrients-enriched assemblages could explain their lower resistance to invasion: in fact, turf may facilitate the spread of *C. racemosa* by providing alga rhizoids with a suitable substrate for anchorage (Piazzi et al. 2003; Bulleri & Benedetti-Cecchi 2008). On the other hand, *C. racemosa* seems to suffer the presence of dense populations of canopy seaweeds (Bulleri et al. 2010). In the present study, no significant variations of abundance of erect species were observed; however, presence of turf, both on the rocky substrate and on the other seaweeds, may

allow *C. racemosa* stolons to easier overgrow erect species. Moreover, turf may indirectly facilitate *C. racemosa* spread, since it acts as a sediments trap (Airoldi 2003) which induce taking root of rhizotrophic species such as Caulerpales (Chisholm et al. 1996; Ceccherelli & Cinelli 1997).

In the present study, species number of receiving assemblages did not substantially vary, suggesting that there is not always a positive relation between biodiversity and resistance to invasion, as it was supported by some descriptive studies since Elton (1958). Results suggest that morpho-functional identity of seaweeds can be more important than diversity in determining resistance of macroalgal assemblages to *C. racemosa* invasion. This result agrees with other studies highlighting the key role played by species type or functional identity of macroalgae in influencing the invasibility of assemblages (Ceccherelli et al., 2002; Arenas et al. 2006; Dunstan & Johnson 2007).

C. racemosa is able to strongly modify the colonized habitats both on rocky substrates and soft bottoms, causing severe shift in the structure of benthic assemblages (Piazzi & Balata 2009; Pacciardi et al. 2011); thus, this species may be considered as driver of ecological changes (*sensu* MacDougall & Turkington 2005). However, both the present and previous studies (Bulleri et al. 2010) showed that *C. racemosa* spread is influenced by any environmental change which causes a shift from canopy dominated assemblages to turf dominated ones. Therefore, *C. racemosa* may be also considered an opportunistic species able to profit from degradation of structural complexity of assemblages. Changes in nutrient availability, in particular, may facilitate the spread of *C. racemosa*, by both enhancing its growth (Gennaro & Piazzi 2011) and eroding the natural resistance of macroalgal assemblages.

Control actions of *C. racemosa* invasion is considered particularly difficult, as the alga is able to colonize a lot of Mediterranean habitats and the effectiveness of direct actions like stolons eradication is very low (Ceccherelli & Piazzi 2005). However, results of this study suggest that conservation of natural assemblages complexity may partially prevent the spread of the invasive alga. Thus, maintenance of good water quality and preservation of natural habitat, together with control of dispersion vectors, may probably represent the only actions suitable to contain the invasion.

7.5 Tables and Figures

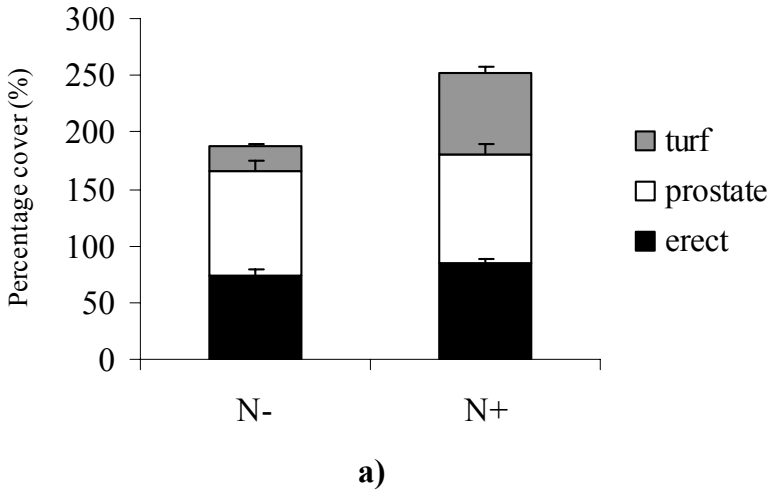
Table 1. Results of PERMANOVA analysis on species composition and abundance of macroalgal assemblages.

Source	df	MS	Pseudo-F	P(perm)	P(MC)
Nutrient = N	1	2308.9	7.47	0.333	**0.017**
Area(N)	2	309.1	1.21	0.321	0.305
Residual	12	254.8			
Total	15				

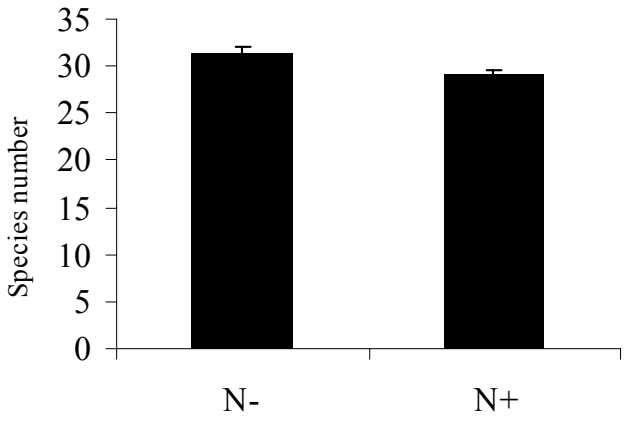
Table 2. Results of SIMPER test showing taxa that mostly contributed to determine differences between conditions

Taxa	Mean % cover	Mean % cover	Contribution (%)
	N-	N+	
Womersleyella setacea	8.13	40.25	23.19
Peyssonnelia spp.	88.88	93	20.06
Pseudochlorodesmis furcellata	2.95	15.25	9.07
Flabellia petiolata	35.25	28.5	8.05
Meredithia microphylla	2.45	13	7.7
Laurencia chondrioides	27.13	29.88	7.59
Halimeda tuna	2.13	1.68	1.8
Zanardinia typus	2.13	0	1.63
Heterosiphonia crispella	0.54	2.53	1.51

Figure 1. Macroalgae assemblages structure in the nutrient-enriched (N+) and not enriched (N-) experimental plots (mean ± SE, n=4). Total and macroalgae layers (turf, prostrate and erect) percent cover (a) and mean species number (b)

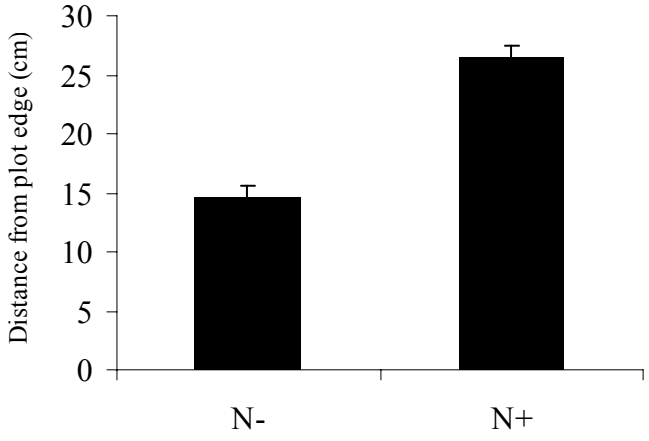


a)

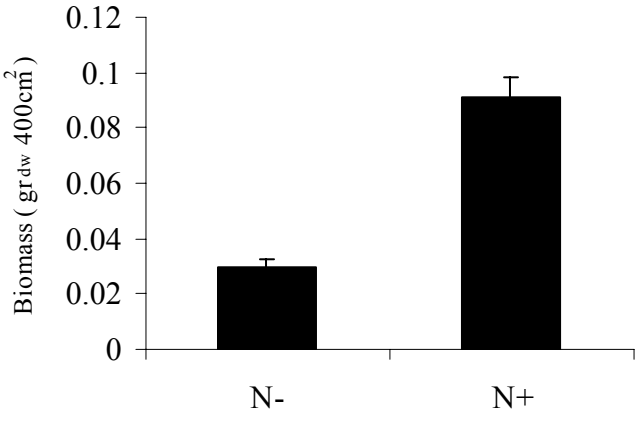


b)

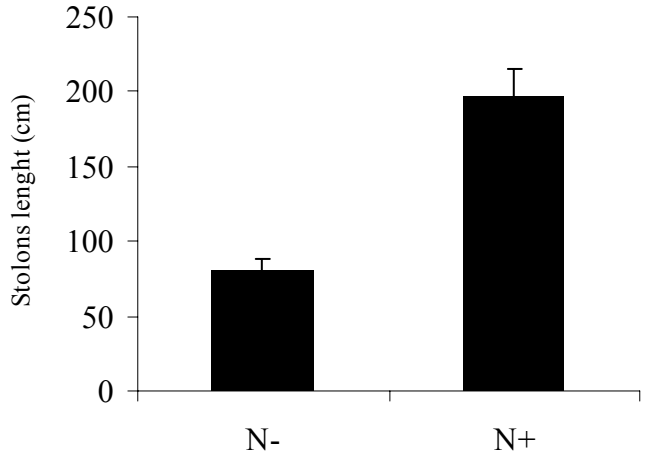
Figure 2. Values of invasion parameters measured in the nutrient-enriched (N+) and not enriched (N-) experimental plots (mean ± SE, n=8). Mean distance of *Caulerpa racemosa* stolons from the edge of the plot (a), biomass of *C.racemosa* expressed as gr dry weight per plots surface of 400cm^2 (b) and stolons length (c)


Distance from plot edge (cm)
30
25
20
15
10
5
0
N-
N+

a)


Biomass (gr dw 400cm2)
0.12
0.1
0.08
0.06
0.04
0.02
0
N-
N+

b)


Stolons lenght (cm)
250
200
150
100
50
0
N-
N+

c)

GENERAL DISCUSSION AND CONCLUSIONS

8. DISCUSSION

Effects of nutrient enrichment on coralligenous macroalgal assemblages were lower than those described in other studies (Karez et al. 2004; Kraufvelin 2007) since no species disappeared as a consequence of nutrient enrichment, nor was there an increase in cover of typical species of polluted habitats. Probably the length of the experiments (about 15 months in total) allowed observation of only the early phases of the eutrophication process in deep subtidal Mediterranean rocky assemblages. However, nutrient enrichment caused an increase of macroalgal cover, mostly due to turf species, which can spread more quickly under nutrient overload conditions than other seaweeds (Rosenberg & Ramus 1984; Hein et al. 1995; Pedersen & Borum 1996, 1997), according to a pattern that has been widely described elsewhere (Gorostiaga & Diez 1996; Diaz et al. 2002; Gorgula & Connell 2004; Russell et al. 2005). In consequences of this, structure of both mature and early successional stage of macroalgal coralligenous assemblages in the studied area significantly varied between nutrients treated and not treated areas. Moreover, detected differences were stronger when macroalgal assemblages were in the early successional stage than in the mature ones. Changes in mature macroalgal assemblages were lower than those described for other habitats under nutrient enrichment regime (Karez et al. 2004; Kraufvelin 2007), as no severe shift in the assemblages structure occurred. On the contrary, heavy differences between treatments were observed in the early successional assemblages, confirming the higher stress resistance of well structured assemblages also for the Mediterranean coralligenous habitats. Severe shifts in structure of assemblages need longer periods due to the presence of perennial species (Kraufvelin et al. 2006). In fact, the spread of ephemeral algae in itself is not enough to eliminate the structuring species of macroalgal assemblages. The community shift may occur after that age-related mortality remove perennial species if these latter are not replaced by juveniles due to competition by ephemeral algae (Kraufvelin et al. 2006). Increase in macroalgae abundance was the main effect of nutrient enrichment. The amount of algal biomass or cover is the result of balance between top-down and bottom-up forces acting on ecosystems (Masterson et al. 2008; Guerry et al. 2009; Atalah & Crowe 2010) and it may vary among habitats. The evaluation of top-down forces was not the aim of the present study, yet effects related to nutrient enrichment cannot be separated from those of other forces acting on the system. However, in the Mediterranean deep subtidal habitats, grazing pressure is considered less important than in shallow habitats (Ballesteros 2006), thus its effects may be considered negligible compared to those of nutrients. Turf-forming species *Pseudoclorodesmis furcellata* and *Heterosiophonia crispella*, flattened Rhodophyta *Halimenia floresia* and the

Heterokontophyta *Colpomenia sinuosa* (Appendix- Figures 9-10) were the most increased taxa in early successional treated areas, while the cover increase of *W. setacea* under high nutrient load was more enhanced in the mature treated plots. The spread of turfs under nutrient enrichment regime has been widely described both in correlative and experimental studies (Gorostiaga & Diez 1996; Diez et al. 1999; Diaz et al. 2002), as increasing load of nutrients in coastal water is considered the main cause of the shift from slow-growing macroalgae to fastgrowing turf-forming algae in benthic assemblages (Eriksson et al. 2002; Gorgula & Connell 2004). In fact, life-history and physiology of the latter species are better suited to nutrient overload owing to their fast growth rate, nutrient requirement and rapid uptake rates (Rosenberg & Ramus, 1984; Hein et al., 1995; Pedersen & Borum 1996, 1997; Karez et al. 2004). However, species constituting turf showed different responses to nutrient availability: *W. setacea*, *H. crispella*, *P. furcellata*, *Polysiphonia* spp increased their abundance while *Ceramium* spp. or smaller-sized corticated Rhodophyta (*Eupogodon*, *Chondria*, *Feldmannophycus*) were unaffected by nutrients. Variability of the species nutrient responses reflects morphological and physiological characteristics of turf-forming algae. In general, algal species with higher surface- area/volume ratio tend to grow faster, require more nutrients and have higher nutrient uptake rates per time (Pedersen & Borum 1996; Taylor et al. 1998) than thicker algae with lower surface/ volume ratio. Thus, under high nutrient availability conditions, no-corticated and/or uniseriate filamentous species may be more facilitate than thin corticated algae with lower surface- area/volume ratio (Bokn et al. 2003; Karez et al. 2004). The shiphonous Udoteacea *P. furcellata* is considered one of the most tolerant species in the coralligenous assemblages (Balata et al. 2005, 2008). The introduced Rhodophyta *W. setacea* and Chlorophyta *P. furcellata* were the most increased species in treated plots. *W. setacea* is an invasive species already described as dominant species in areas characterized by severe stress regime such as high sedimentation rates (Airoldi 1998, 2003). The present study confirms the role of nutrients in aiding the spread of introduced macroalgal species (Sánchez & Fernández 2006; Incera et al. 2009). An increase of nutrients in natural systems can create favourable conditions for faster-growing plants, such as most of invasive seaweeds (Torres et al. 2004). Morphology of both *C. sinuosa* and flattened Rhodophyta is characterized by high surface-area/volume ratio as well as no-corticated filamentous species; thus, their increase could be expected under nutrient enriched regime (Masterson et al. 2008; Teichberg et al. 2008). Encrusting Corallinales showed similar abundance in treated and control plots, also in the early successional assemblages, suggesting that Corallinales are not affected by high nutrient concentration. However, both the increase of filamentous species and lost of structural species allow to hypothesize, on longer periods, a loss of functional diversity of assemblages and a shift towards a dominance of ephemeral seaweeds and crust.

The present study demonstrated the role of nutrients in affecting macroalgal assemblages structure of coralligenous habitat in the studied area; moreover, it highlighted the occurrence of interactions with other disturbances, such as mechanical damages due to fishing and touristic activities which may amplify the nutrients negative effects on assemblages. A complete removal of the living layer of Corallinales, as it was experimentally realized in the present study, is usually limited to small-scale events, like i.e. anchorage practices linked to the yachting activities. Nevertheless, partial removal of organisms may commonly occur as consequence of several kinds of human disturbance, decreasing the resistance of assemblages to nutrient enrichment. Moreover, the study highlighted effects of nutrients similar to those observed for other stressors, such as sediment increase (Balata et al. 2005, 2007a,b) or invasion of introduced seaweeds (Piazzi et al. 2007; Piazzi & Balata 2009), suggesting that synergetic mechanisms may occur among these stressors leading to dramatic changes in deep subtidal rocky assemblages and to widespread homogenization of coralligenous habitats.

The present study provide interesting information about the spread potential of the invasive alga *C. racemosa* in the rocky deep subtidal habitas. Parameters expressing the morphological and physiological develop of *C. racemosa* in coralligenous habitats such as growth rates, values of biomass, percentage cover, stolon length and numbers of fronds were lower than those reported for shallower habitats in the same area (Piazzi & Cinelli 1999; Piazzi et al. 2001) and more similar to values reported for deeper populations along the French coasts (Ruitton et al. 2005a), indicating the influence of depth in spread dynamics of the alga. Results of experimental studies carried out in the shallow rocky bottoms and *Posidonia oceanica* dead mattes highlighted the great invasive ability and the strong competitive traits of *C. racemosa* in these habitats (see also Piazzi et al. 1997; Piazzi & Cinelli 1999; Ceccherelli et al. 2000), where the alien alga rapidly invaded both rock and dead matte substratum, completely covering the macroalgal assemblages and reaching abundance of 100%, biomass of 237.5 g dw m^{-2} on rock and up to 447 g dw m^{-2} on *Posidonia* matte and growth rate of 2 cm d^{-1}. Similar results were obtained for number of fronds, which reached very high values of 21000 m^{-2} in shallower habitats (-15 m depth) decreasing to 5000 m^{-2} at -22 m; De Biasi et al. (1999) observed a similar trend of decrease in the *C. racemosa* cover from 5–10 m to 15–20 m depth. These results confirmed that, despite its large tolerance of physical factors, *C. racemosa* growths better under conditions of high irradiance (Capiomont et al. 2005), while more sciafilous invasive species are better adapted to the deeper habitats. Consequently, colonization of *C. racemosa* was more serious in shallower habitats and this would be consistency with the general statement that most of the green alga species thrive in the more bright habitats of the infralittoral, due to their pigments endowment mainly formed by the chlorophyll complex. On the contrary,

species belong to Rhodophyta, like i.e. the invasive species *Womersleyella setacea*, can synthesize the more additional pigments (phycobilins) the more is the depth, so becoming capable to efficiently photosynthesize in the shadows conditions of deep marine habitats.

Despite results highlighted the depth effect on the growth and morphological traits of *C.racemosa*, the spread potential of the invasive alga, which can be generally expressed by the invasive patches width or patch diameter (Ceccherelli et al. 2002), results instead more high in coralligenos than in the shallower habitats. In fact, values of patch diameters observed in our study are nearly twice as much as values reported for shallow rocky habitats in the same area, indicating that the particular structure of native coralligenous assemblages probably allows a better horizontal spread rather than a more local overlap of stolons to form thick mattes. This results could be explained by a different allocation of the energy growth linked to the depth factor and/or to the different architectural structure of macroalgal asseblages between shallow and deep rocky habitats. In fact, shallower marine habitats are usually characterized by highly structuring erect species, like *Cystoseira* spp. or *P. oceanica* meadows, which formed a natural barrier against the horizontal spread of invasion, while erect species in coralligenous habitats are not so well structured, allowing the invasion to widen to more large bottom surfaces.

Nutrient enrichment caused an increase of *C. racemosa* growth rate, resulting in higher values of biomass, stolons length and number of fronds, which were clearly detected in spite of high variability among selected areas. Size of invasion patches was also increased by nutrient pollution, enhancing the spread potential of *C.racemosa* in coralligenous habitat of about 35%. These findings are in accordance with previous qualitative observations of the ecological traits of other *Caulerpa* species. The expansion of *C. prolifera* Forsskål (Lamouroux) along French coasts has been suggested to be related to the increase of domestic sewage pollution (Ollivier 1929) and thick mats of *C. verticillata* J. Agardh have been observed in sewage canals in Florida (Lapointe et al. 1994). The spread of introduced species, such as *C. taxifolia* in the Mediterranean Sea, *C. brachypus* f. *parvifolia* (Harvey) Cribb in Florida and *C. ollivierii* Dostál in the Bahamas is also considered to be enhanced by eutrophication (Chisholm et al. 1995; Lapointe et al. 2005; Lapointe & Beldford 2010). Results of the present study demonstrated that also invasion by *C. racemosa* may be faster in eutrophic areas, suggesting that it could be favoured by an increase of pollution in the coastal water of the Mediterranean Sea.

The effect of transplanting of *C.racemosa* on coralligenous assemblages were similar to those described for naturally invaded deep subtidal Mediterranean assemblages (Piazzi et al. 2007a; Piazzi & Balata 2008, 2009) and confirmed also a general pattern of reduction of biodiversity

observed for shallower rocky and *P.oceanica* dead matte habitats. A reduction of biodiversity is considered a common consequence of biological invasions (Abrams 1996; Bax et al. 2003; Walker & Kendrick 1998; Gray 1997) and similar patterns have been described separately for the colonisation of both *C. racemosa* and other alien invasive algae, such as *W. setacea* in Mediterranean habitats (Airoldi et al. 1995; Piazzi & Cinelli 2001, 2003; Piazzi et al. 2001, 2007a). In fact, the natural biodiversity of all Mediterranean benthic assemblages seems affected by invasions, as suggested by low values of the species number per sample usually reported for invaded assemblages of different habitats, especially in areas invaded by *C. racemosa* (Piazzi & Balata 2009). In all the studied habitats, lower diversity in invaded assemblages was related to the disappearance of several species, lower abundance of some structural species and dominance of few tolerant species. The species that usually mostly appeared sensitive to invasions were the erect species reproducing sexually, such as *Flabellia petiolata*, *Osmundaea pelagosae*, *Padina pavonica*, *Laurencia obtusa* and *Halimeda tuna*. This pattern was confirmed for the coralligenous assemblages of the present study, which lost the well defined structure of the not-colonized assemblages, due to strong reduction of the erect species *F.petiolata*, *H.tuna*, *Laurencia chondroides* and *Meredithia microphylla* (Appendix - Figures 6 and 11) and encrusting species *Peyssonnelia* spp., *Zanardinia typus* (Appendix - Figures 5 and 11) and calcareous *Corallinales*. The reduction of abundance of the erect and encrusting algae, which are structural species dominating the non invaded coralligenous habitat, seems to favour proliferation of the tolerant species *Halopithys incurva*, *Womersleyella setacea*, *Pseudochlorodesmis furcellata* and *Cladophora prolifera* (Appendix - Figures 9 and 11), which showed a high resistance to invasion. Some of the competitiveness mechanisms of *C.racemosa* acting in the coralligenous habitats are probably the same generally recognized for other Mediterranean habitats, that are its ability of quickly spread through vegetative growth (Ruitton et al. 2005b), easily covering other macroalgae; the effects of overgrowth on the invaded assemblages may be increased by the capability of this alga to stratify and trap sediments (Airoldi & Virgilio 1998; Piazzi et al. 2007b). Moreover, the persistence of its populations may limit the substrate available for settlement of spores, damaging the species reproducing sexually (Airoldi 1998). *C. racemosa* colonization appeared particularly threatening for encrusting algae, probably because the wide mats constituted by its stolons can avoid light penetration, can trap sediments and can create a reduced habitat that strongly affect the lower vegetation layers (Piazzi et al. 2007b). So, impact of *C.racemosa* on coralligenous macroalgae asseblages seems to be mainly due to the habitat modifier action of this alien species, which confirm the role of "driver" of ecological changes (*sensu* MacDougall & Turkington 2005, Chapter 2) played by this alga.

The observed increase of opportunistic species in the invaded plots allows to hypothesize also the possible develop of synergic mechanisms of facilitation among different invaders making the effect of *C.racemosa* invasion more persistent. In fact, replacement of ecological specialists by widespread generalists can cause a reduction in ecosystem resilience making the coralligenous assemblages more vulnerable to further biological invasions (Olden et al. 2004; Piazzi & Balata 2010). The lower habitat complexity resulting from reduction of the structural encrusting and erect species of coralligenous assemblages can facilitate other highly competitive invaders such as *W. setacea* (Stachowicz et al. 1999), the which develop can act as a positive feedback on the *C.racemosa* spread. In fact, it has been described that the invasion of alien *Caulerpales* may be enhanced in areas previous invaded by introduced filamentous species (Ceccherelli et al. 2002; Piazzi et al. 2003a). The presence of turf species such as *W.setacea* can promote colonisation of *C.racemosa* by physical modification of habitat. In fact, the dense network of ramification within turf forms a cohesive surface layer which mechanically catches drifting fragments of the invasive alga and, by trapping sediment, it could also enhance nutrient availability of the substratum (Piazzi et al. 2001).

The effects of *C. racemosa* invasion on native macroalgal assemblages were amplified by nutrients pollution, indicating the develop of synergetic action between biological invasion and nutrients disturbance. In fact, the concurrent presence of these two stressors resulted in a more extensive modification of the assemblage structure, compared to the other treatments, and a further reduction in percent cover of sensitive species (encrusting and erect algae) was observed. According to a widely described pattern (Gorostiaga & Diez 1996; Diaz et al. 2002; Gorgula & Connell 2004; Russell et al. 2005b), nutrient enrichment characterizing the first phase of euthrophication processes caused an increase of diversity, due to proliferation of the opportunistic turf species the which develop is usually restrained by the more competitive structuring species of the assemblages. Increasing nutrient levels in coastal waters are considered to be the principal cause of the dominance of turf-forming species, which can spread more quickly under nutrient overload conditions than other seaweeds (Rosenberg & Ramus 1984; Hein et al. 1995; Pedersen & Borum 1996, 1997). This pattern was confirmed in the present study, given that turf species *W. setacea* and *P.furcellata* increased their cover in the nutrient-enriched plots while most of erect and encrusting species seemed to be not influenced by nutrient enrichment, at least in the first phase of nutrient pollution. Thus, the drastic reduction of encrusting and erect species cover observed in the area subjected to both stressors indicated that synergetic effect on native assemblages was mainly due to the increasing growth of *C. racemosa* caused by nutrient pollution, which acted directly and indirectly by increasing abundance of turf layer, rather than to a direct negative effect of nutrient

enrichment on sensitive species. *C. racemosa* competes with benthic organisms by overgrowth of stolons (Piazzi et al. 2001; Kruzic et al. 2008; Baldacconi & Corriero 2009) and enhanced abundance of *C. racemosa* caused by nutrient enrichment can amplify the effect of stolons cover on benthic assemblages. This effect can lead to severe consequences particularly in coralligenous habitats, which are highly sensitive to environmental alterations (Balata et al. 2005). The maintenance of this habitat is related to the balance between growth and death of calcareous organisms and a long recovery period is required following any damage, owing to the low growth rate of Corallinales, which are the main builders of this habitat in the Mediterranean region (Garrabou & Ballesteros 2000; see Chapter 3). Many sessile organisms can completely or partially recover during the vegetative rest period of *C. racemosa* (Piazzi & Ceccherelli 2006; Klein & Verlaque 2009), but this period in not sufficient to allow the recovery of encrusting Corallinales. The death of the latter due to *C. racemosa* cover could have serious consequences for the conservation of Mediterranean coastal habitats.

Total turf cover showed lower values in plots where both stressors were present than in nutrient treated plots without addition of *C. racemosa*. This finding confirms previous observations showing that turf species are more affected by *C. racemosa* than some tolerant erect species, such as *H.incurva* and *C.prolifera*, probably because the former are more susceptible to the alga's competitive mechanisms (Piazzi et al. 2001; Piazzi& Balata 2008; Piazzi & Balata 2009). However, despite the occurrence of antagonism between *C. racemosa* and turfs, the introduced turf-forming species *W. setacea* showed higher abundance in plots where both *C. racemosa* and nutrients were added than in control plots. In fact, *W. setacea* was one of the species that most increased their abundance following nutrient enrichment and was less affected by *C. racemosa* colonization than other turf-species, such as *Ceramium* spp. This finding confirms that different morphological groups within turf-forming assemblages show different response to *C.racemosa* invasion and to environmental stress in general; in fact, different growth strategy may lead to different capability to thrive under stressed conditions. According to Balata et al. 2010, turf-species of Rhodophyta belonging to filamentous uniseriate and pluriseriate with erect thallus group, like *Ceramium* and *Polysiphonia*, decreased in stressed areas while filamentous uniseriate and pluriseriate forms with extensive prostrate filaments, like *Womersleyella* and *Lophosiphonia*, appeared tolerant and produced abundant assemblages under stressed conditions.

Thus, the final result of the interaction between nutrient enrichment and *C. racemosa* invasion was the shift from a well structured macroalgal assemblage to one strongly dominated by a small number of invasive species. This replacement process implies a simplification of the architectural complexity of macroalgal assemblages, due to the decrease in species richness and reduction or

disappearance of engineering species (such as encrusting Corallinales, Peyssonneliaceae, and erect Udoteaceae). These results suggested that synergism between effects of different anthropogenic impacts can have severe consequences on the integrity of marine ecosystems.

Biotic and environmental changes observed in nutrient-enriched plots in the first phase of eutrophication suggested that they may have modified vulnerability of macroalgal assemblages to invasion, leading to a further reduction in these assemblages' resistance to *Caulerpa racemosa*. In fact, the spread of invasive seaweeds is considered to be favoured not only by the high ecological fitness of the invaders, but also by the characteristics of the receiving environment (Dunstan & Johnson 2007) and anthropogenic disturbance, causing changes in the resource availability, often leads to a higher incidence and abundance of invaders (Schaffelke & Hewitt 2007; Valentine et al. 2007). The amount of resource availability across the resource spectrum is another factor that determines the success or failure of a seaweed invasion (Dunstan & Johnson 2007). Thus, tolerance by *Caulerpa* species to changes in resource availability and the presence of degraded receiving habitats are both considered to promote colonization by these species (Occhipinti-Ambrogi & Savini 2003). For example, sediment traits of urban wastewater impacted seabed are described to enhance the competitiveness of *C. taxifolia* when it is in contact with Mediterranean seagrasses (Chisolm et al. 1995; Ceccherelli & Cinelli 1997). Changes in the structure of assemblages following nutrient enrichment, and in particular the increase of *W. setacea*, suggested further positive feedback between impacts, as the presence of algal turfs can favour colonization by *C. racemosa* (Ceccherelli et al. 2002; Piazzi et al. 2003; Bulleri & Benedetti-Cecchi 2008).

Different roles, as passenger or driver of ecosystem modifications (MacDougall & Turkington 2005), have been attributed to *C. racemosa* (Bulleri et al. 2010) and the importance of nutrient enrichment in this context was hypothesized at the end of the first experiment and confirmed by the results of the second experiment, which clearly demonstrated that *C.racemosa* behaves like an opportunistic species that takes advantage of degraded environmental conditions. In fact, the *Caulerpa racemosa* invasion was more serious in coralligenous assemblages chronically exposed to nutrients enrichment for one year, as the invaded surface, stolons length and alga biomass developed on the nutrient stressed assemblages were higher than in not nutrients treated ones.

In spite of the more long exposure time, changes in structure of macroalgal assemblages caused by nutrients were similar to those described in the previous shorter experiment carried out in the same zone; moreover, they were comparable to previous investigations carried out in other geographical areas (Gorostiaga & Diez 1996; Diaz et al. 2002). The main structural change was an increase of percentage cover of turf, but also an increasing abundance of flattened Rhodophyta and decreasing of prostrate Heterokontophyta were observed as minor modifications. Growing

abundance of turf species is a pattern widely described in several marine areas subjected to nutrients enrichment (Eriksson et al. 2002; Gorgula & Connel 2004). In fact, the chief species of turf layer are filamentous seaweeds, which generally grow better than other morphological forms under high nutritional availability due to their faster growth, high nutrients requirement and uptake rates per time (Pedersen & Borum 1997; Taylor et al. 1998). The increase of turf in nutrients-enriched assemblages could explain their lower resistance to invasion: in fact, as it was previously discussed, presence of turf may facilitate the spread of *C. racemosa* by providing alga rhizoids with a suitable substrate for anchorage (Piazzi et al. 2003; Bulleri & Benedetti-Cecchi 2008). On the other hand, *C. racemosa* seems to suffer the presence of dense populations of canopy seaweeds (Bulleri et al. 2010). As it was observed in the first experiment, no significant variations of abundance of erect species were observed in the nutrient stressed assemblages, while turf species significantly increased their mean cover, enhancing vulnerability of assemblages to invasion. In fact, presence of turf, both on the rocky substrate and on the other seaweeds, may allow *C. racemosa* stolons to easier overgrow erect species. Moreover, as it was previously discussed, turf forming species may indirectly facilitate *C. racemosa* spread, since they acts as a sediments trap (Airoldi 2003) which induce taking root of rhizotrophic species such as Caulerpales (Chisholm et al. 1996; Ceccherelli & Cinelli 1997).

In the present study, species number of the receiving assemblages did not substantially vary, suggesting that there is not always a positive relation between biodiversity and resistance to invasion, as it was supported by some descriptive studies since Elton (1958). Results suggest that morpho-functional identity of seaweeds can be more important than diversity in determining resistance of macroalgal assemblages to *C. racemosa* invasion. This result agrees with other studies highlighting the key role played by species type or functional identity of macroalgae in influencing the invasibility of assemblages (Ceccherelli et al. 2002; Arenas et al. 2006; Dunstan & Johnson 2007). Therefore, impact evaluation of biological invasions should always consider not only the total number of species present in a particular habitat, but also the species identity and their ecological function (Piazzi & Balata 2008).

C. racemosa is able to strongly modify the colonized habitats both on rocky substrates and soft bottoms, causing severe shift in the structure of benthic assemblages (Piazzi & Balata 2009; Pacciardi et al. 2011); thus, this species may be considered as driver of ecological changes (*sensu* MacDougall & Turkington 2005). Driver species are also known as “ecosystem engineers” due to their ability to change the environment via their own physical structures (autogenic) or by transforming materials from one state to another by mechanical or other means (allogenic) (Jones et al. 1994, 1997). *C. racemosa* appears to demonstrate both type of mechanisms (Klein & Verlaque

2008). Autogenic mechanisms are related to its ability to modify the habitat forming dense mattes of stolons (Klein & Verlaque 2008) and to exert effects dependent on habitat characteristics: for instance, the presence of the stolon mattes formed by *C. racemosa* is able to reduce the habitat complexity of the rocky bottoms and hence their heterogeneity (Piazzi & Balata 2007). Allogenic mechanisms were mainly observed on rocky bottoms, where this alga represents an important trap for sediments, with consequent changes in the substrate characteristics (Piazzi et al. 2005b, 2007). However, both the present and previous studies (Bulleri et al. 2010) showed that *C. racemosa* spread is influenced by any environmental change which causes a shift from canopy dominated assemblages to turf dominated ones. Therefore, *C. racemosa* may be also considered a passenger of ecological changes because it behaves like an opportunistic species which profits from degradation of structural complexity of assemblages. Changes in nutrient availability, in particular, may facilitate the spread of *C. racemosa*, by both enhancing its growth and eroding the natural resistance of macroalgal assemblages.

9. CONCLUSIONS

Non-native macroalgal invasions are expected to increase in coming years (William & Smith 2007), as is the land-based nutrient pollution in coastal waters (Howarth & Marino 2006). Our results agree with other findings (Ceccherelli & Cinelli 1997; Steen 2003; Sánchez & Fernández 2006; Lapointe & Beldford 2010), indicating that the spread of some species of non- native macroalgae in the oligotrophic regions can be favored by nutrient enrichment. In fact, changes in seawater nutrients availability may facilitate the spread of *C. racemosa*, by both enhancing its growth and eroding the natural resistance of macroalgal assemblages. So, results of this study suggest that maintenance of both good water quality and natural assemblages complexity is an essential condition to partially prevent the spread of invasive algae; at least at the current state of knowledge, it probably represents the only effective strategy in containing invasions in progress. In fact, direct control actions of macroalgae invasions are considered particularly difficult, as the effectiveness of direct actions like eradication resulted very low (Ceccherelli & Piazzi 2005). Thus, reduction of wastewater discharges and programs of natural habitats conservation, together with control of dispersion vectors, may probably represent the only actions suitable to contain the biological invasions in the Mediterranean Sea.

The role of eutrophication in aiding invasions of non-native macroalgae must be recognized and more experimental studies on this topic are needed in order to predict consequences of possible synergisms between these aspects of global change and to identify appropriate strategies to effectively manage the phenomenon in the future. In this context, particular attention would be turned to the most sensitive habitats, such as *Posidonia oceanica* meadows and coralligenous assemblages, both representing a casket of biodiversity in the Mediterranean Sea. Studies carried out on *P.oceanica* habitats demonstrated that healthy meadows are more resistant to invasion and they also represent a natural barrier to colonisation defending nearby marine habitats. Therefore, some of the causes of tropical seaweeds invasions in the Mediterranean Sea should be researched also in the conservation status of *P. oceanica* meadows (Occhipinti-Ambrogi & Savini 2003). The present study demonstrated that preserving coralligenous habitats from nutrient pollution and mechanical damages could represent an important step in both control of biological invasions and conservation of biodiversity in the Mediterranean Sea. In fact, high richness, biomass and production, with values comparable to tropical reef assemblages, make coralligenous assemblages one of the most important and characteristic assemblages of the Mediterranean Sea (Bianchi 2001). Nevertheless, despite its complexity, coralligenous habitat is a fragile ecosystem, as its persistence is related to the maintenance at the natural level of the peculiar biotic and abiotic factors (Hong 1983).

Finally, the present study can give an important contribution to all the researches aimed at finding an answer to the question "Why invasive species like *C.racemosa* are so successful?". Synthesizing previous and current studies, we can conclude that successful of *C.racemosa* invasion in the Mediterranean sea can be explained only by the concurrent action of biological and ecological factors directly and indirectly acting on both the invasive species and the invaded native assemblages. The high ecological fitness of the invaders is surely the most important starting point for a successful invasion, which probably would not be brought to the end without the action of other factors. So, knowledge of structural and functional characteristic of the receiving ecosystem, as well as level of stress to which it is subjected, became fundamental information to predict future development of an invasive event. This means that each invasive event can evolve in a different way depending on species invader, type of invaded habitat and presence or not of anthropogenic pressures.

For this reason, in order to understand, control and eventually prevent the spread of biological invasions, it is very important to develop an integrated approach aimed to clarify the species intrinsic biological peculiarities (growth and dispersion rate, reproduction and adaptive strategies, environmental stress tolerance) on one hand and its effects on the invaded habitats together with the ecological mechanisms determining success of invasion (receiving ecosystem traits and effects of environmental disturbances) on the other hand.

APPENDIX

Figure 1. Thallus of the invasive *Caulerpa racemosa* from the Gulf of Marseille (30 m). Herbarium specimen, J. Klein. (Klein & Verlaque 2008).

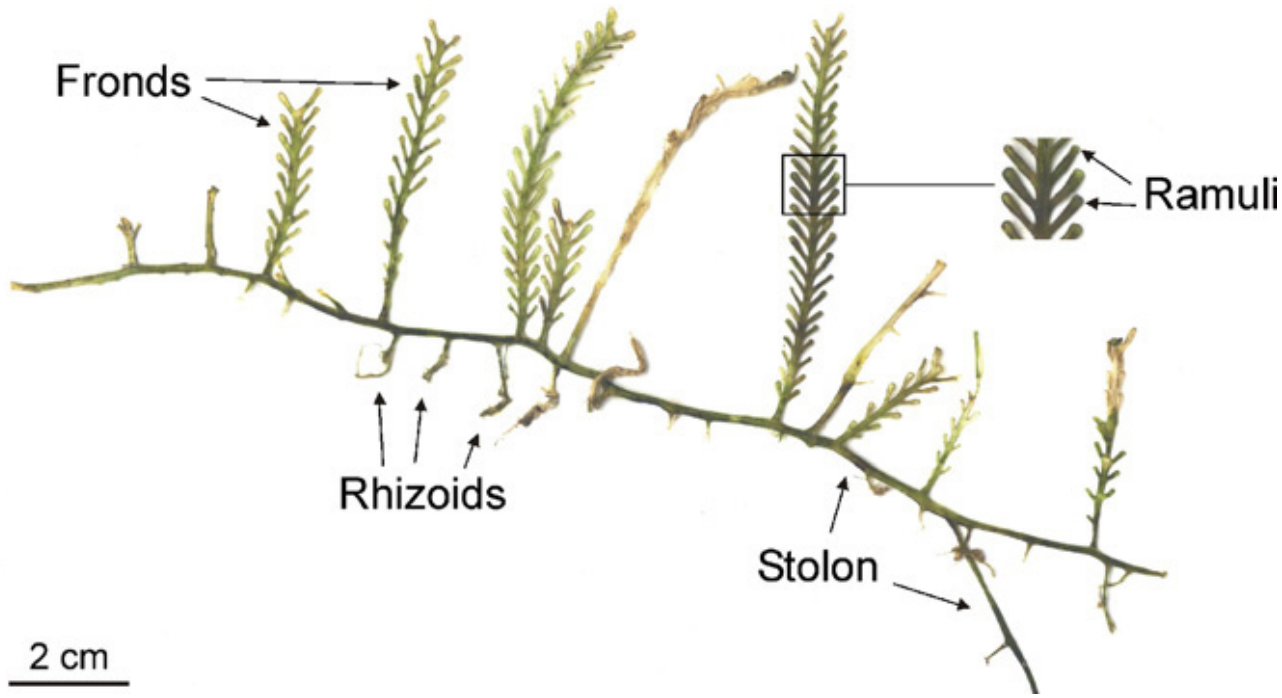


Figure 2. *Caulerpa racemosa* var. *cylindracea*

Figure 3. Map indicating the native range of *Caulerpa racemosa* var. *cylindracea* in south-western Australia (grey surface) and its introduction in Adelaide (• + arrowhead) (from Verlaque et al. 2003; amended in Klein & Verlaque 2008).

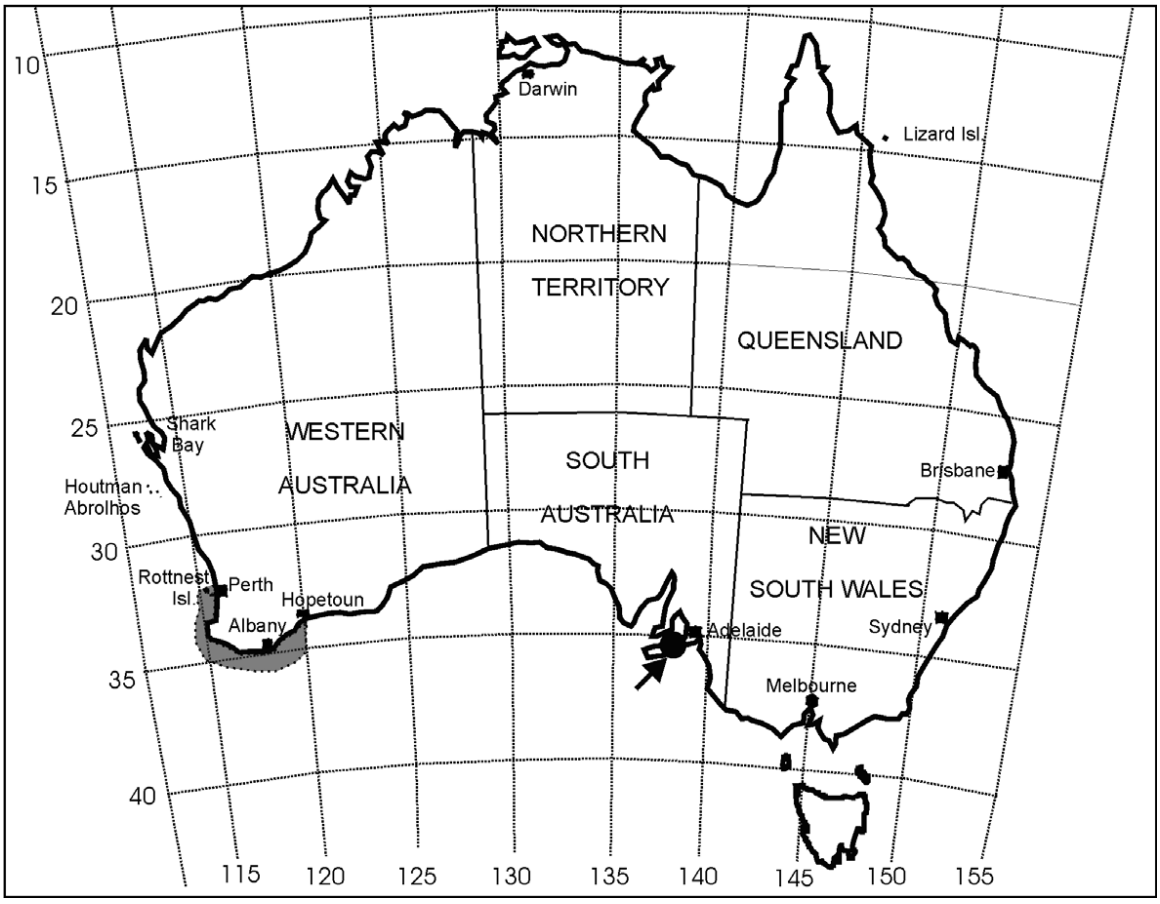


Figure 4. First sighting of *Caulerpa racemosa* var. *cylindracea* in Libya in 1991 (• + arrowhead) and subsequently observed colonies (•) in the Mediterranean Sea and the Canary Islands (from Verlaque et al. 2004; Piazzi et al. 2005a, amended in Klein & Verlaque 2008).

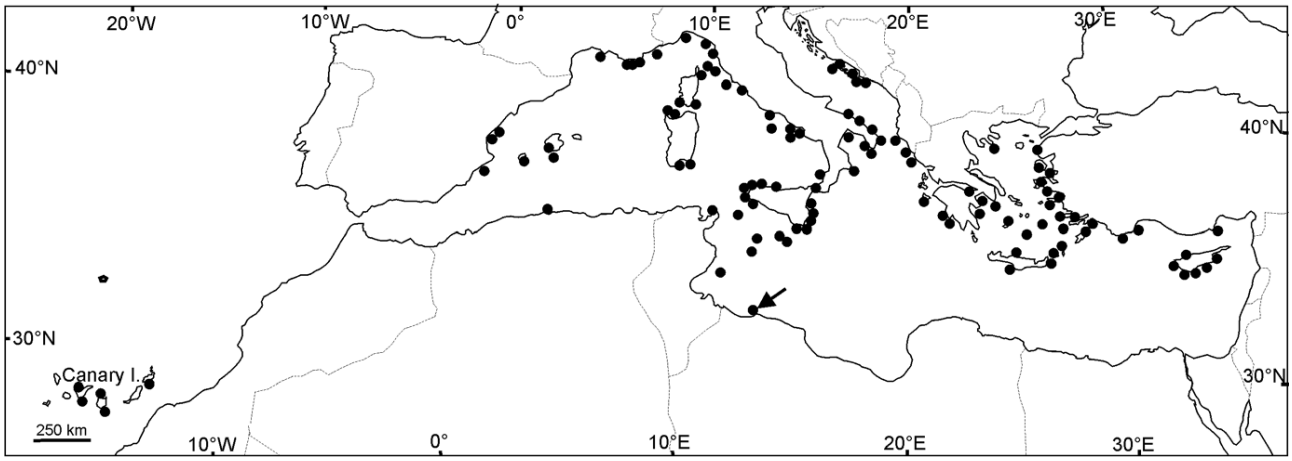
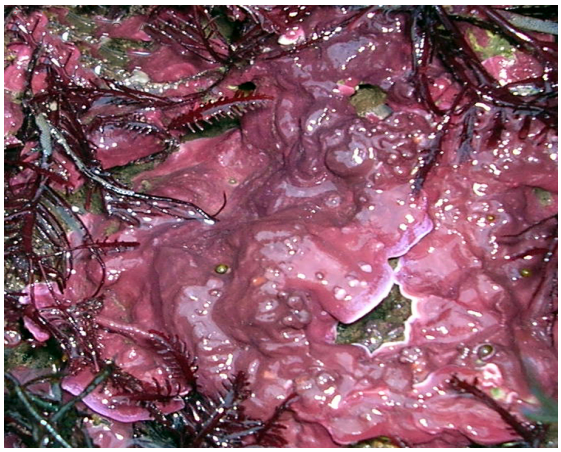


Figure 5. Coralligenous algal builders: **a)** *Mesophyllum alternans*, **b)** *Peyssonnelia rubra*, **c)** *Lithophyllum stictaeforme*, **d)** *Neogoniolithon mamillosum*



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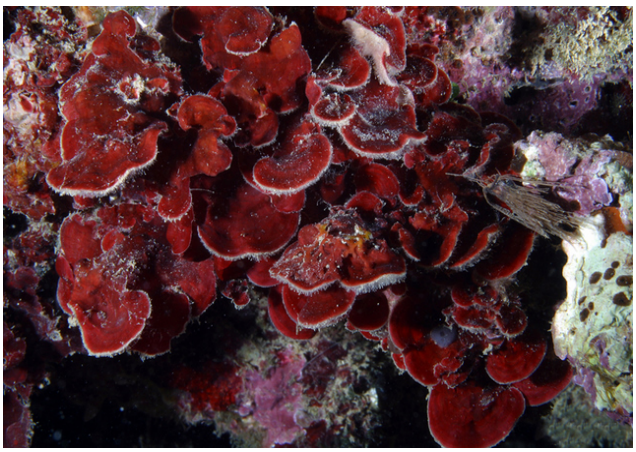


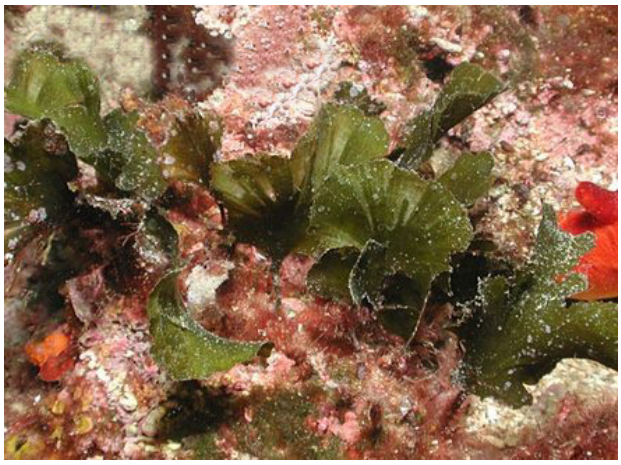
b)

c)

d)

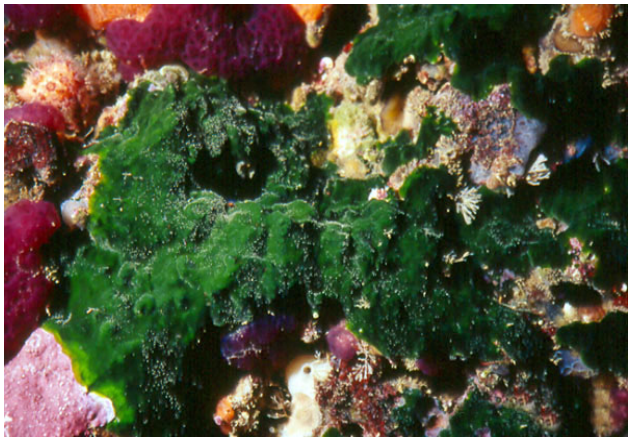
Figure 6. Coralligenous erect algae: **a)** *Halimeda tuna*, **b)** *Flabellia petiolata*

a)



b)

Figure 7. Coralligenous algae: **a)** *Palmophyllum crassum*, **b)** *Kallimenia* sp., **c)** *Gloiocladia repens* sp.**, d)** *Predaea* sp.



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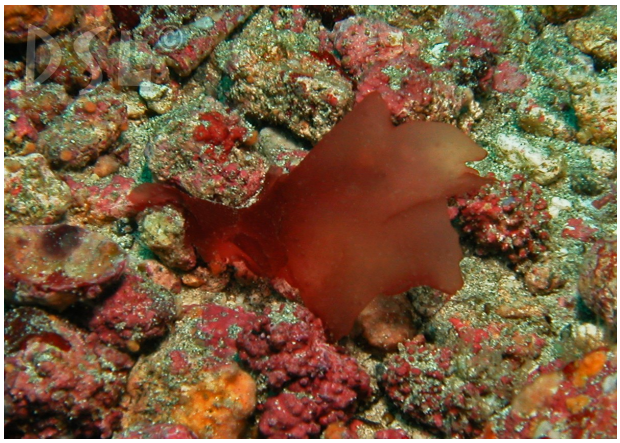

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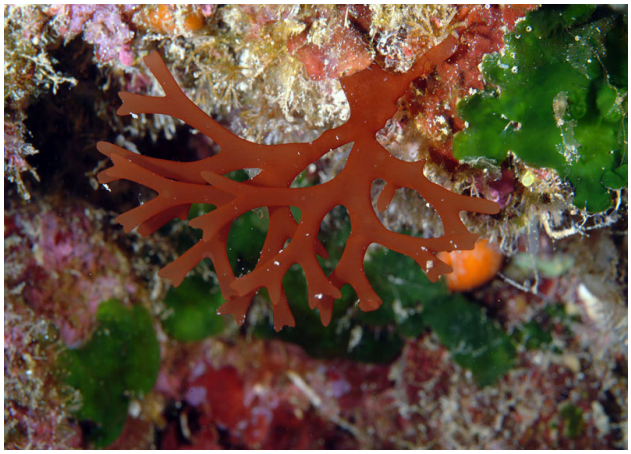

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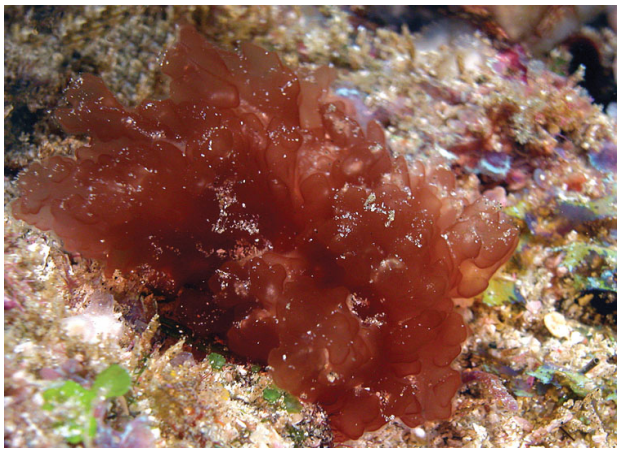

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Figure 8. Images of well structured coralligenous habitats in pristine sites (Giglio Island, Italy) (photos by Andrea Lampis)

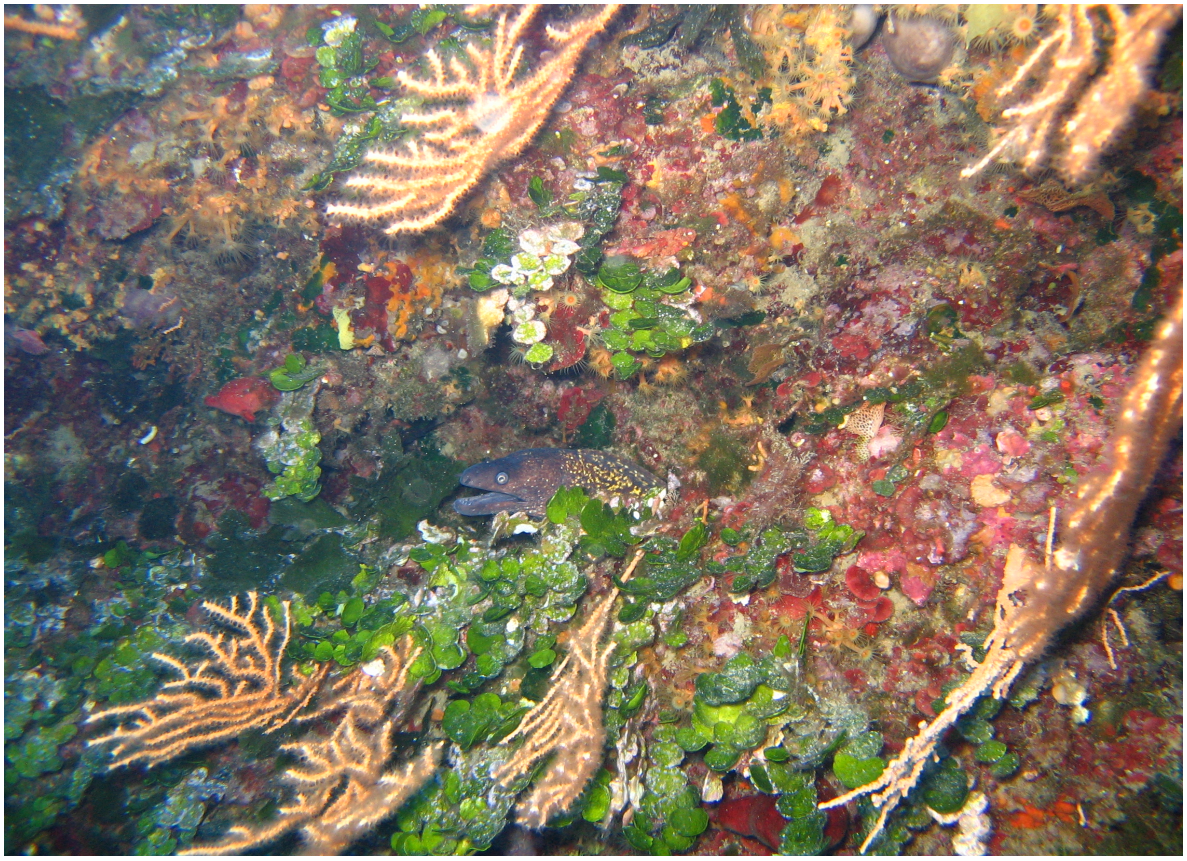
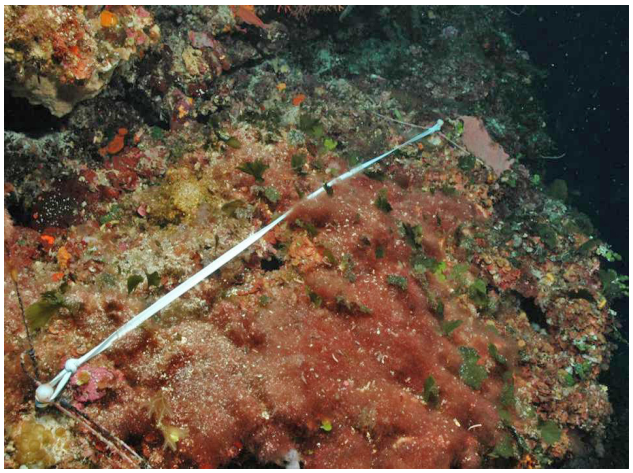


Figure 9. Coralligenous turf species **a)** *Womersleyella setacea*, **b)** *Pseudochlorodesmis furcellata*, **c)** *Heterosiphonia* spp.



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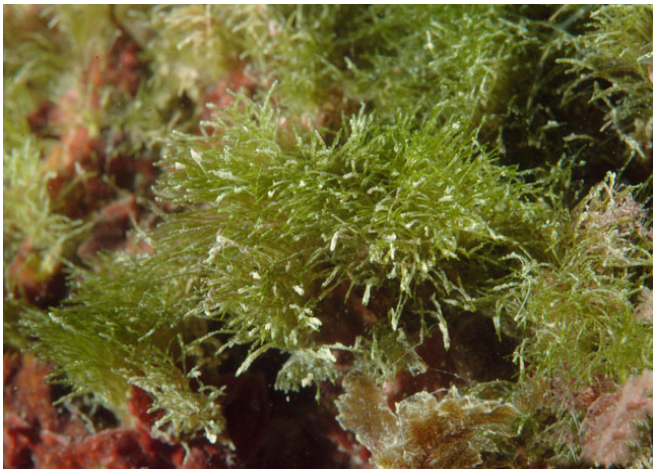

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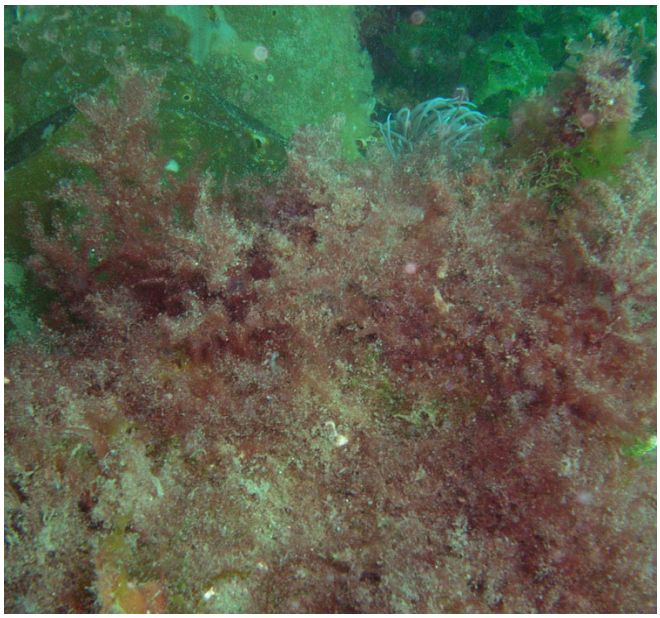
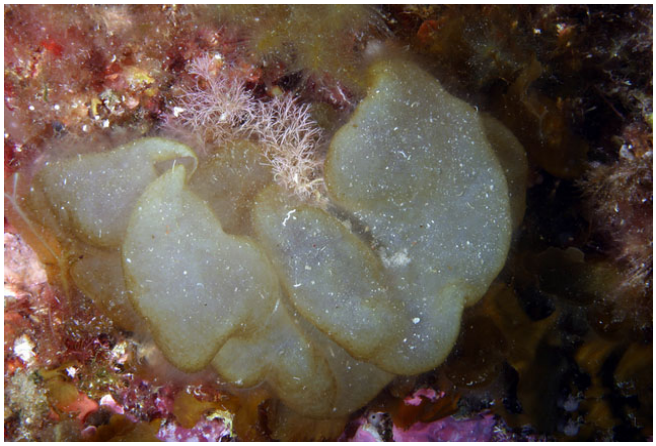


c)

Figure 10. Coralligenous flattened Rhodophyta **a)** *Halimenia floresia* and Heterokontophyta **b)** *Colpomenia sinuosa*

a)



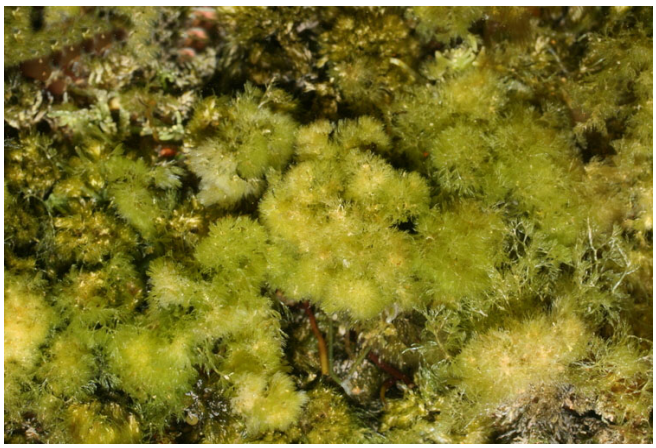
b)

Figure 11. Coralligenous erect species **a)** *Meredithia microphylla*, **b)** *Laurencia chondroides,* **c)** *Halopithys incurva*, **d)** *Cladophora prolifera* and encrusting species **e)** *Zanardinia typus*

a)

b)

c)



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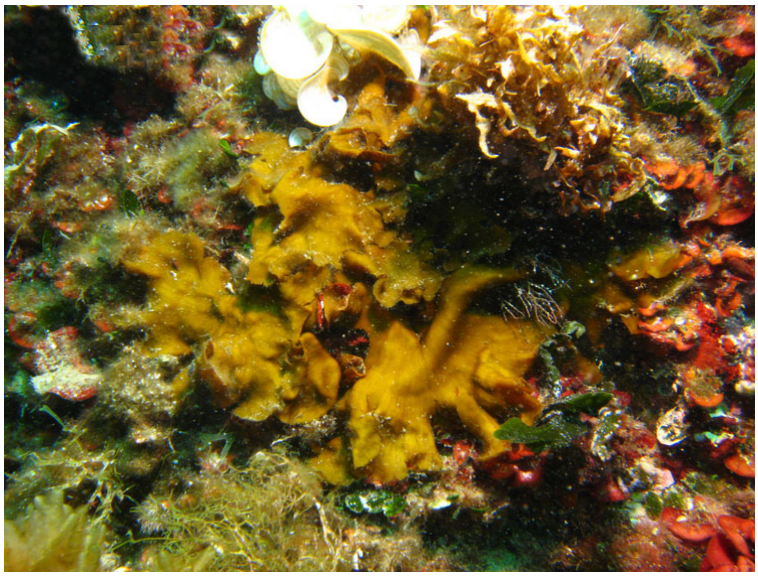

e)

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