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Invasion of *Caulerpa racemosa* var. *cylindracea* (Caulerpales, Chlorophyta) in the Mediterranean Sea: an assessment of the spread

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Abstract – The aim of this paper is to evaluate the colonization of the green alga *Caulerpa racemosa* var. *cylindracea* thirteen years after it was signalled in the Mediterranean Sea. The alga has been recorded along the coasts of 11 nations, developing on all kind of substrata, both in polluted and in unpolluted areas, between 0 and 70 m depth. The length of coastline affected by the invasion of *C. racemosa* var. *cylindracea* in Spain, France, Italy and Croatia ranged from 700 to 750 km at the end of 2003. The main aspects of the ecology of the species in the Mediterranean Sea and the effects of the invasion on human activities in coastal areas are also discussed.

Biological invasion / *Caulerpa racemosa* / distribution / ecology / Mediterranean Sea

Résumé – Invasion de l'algue *Caulerpa racemosa* (Caulerpales, Chlorophyta) en Mer Méditerranée : le bilan de treize années de colonisation. L'article a comme objet de présenter un bilan de la colonisation de la Méditerranée par l'algue verte introduite *Caulerpa racemosa* var. *cylindracea*, treize années après le début de son expansion. L'algue a été signalée le long des côtes de 11 états. Elle pousse entre 0 et 70 mètres de profondeur sur tous les types de substrats, aussi bien en zones polluées qu'en zones non polluées. Le linéaire de côte concernée par l'invasion de *C. racemosa* var. *cylindracea* entre l'Espagne, la France, l'Italie et la Croatie a été estimé entre 700 et 750 km fin 2003. Les aspects majeurs de l'écologie de l'espèce en Méditerranée les conséquences de son expansion sur les activités humaines en zone côtière sont également discutés.

***Caulerpa racemosa* / distribution / écologie / invasion / Mer Méditerranée**

INTRODUCTION

Biological invasions represent an important aspect of human-induced global change and a serious ecological problem (Carlton, 1989; Abrams, 1996; Vitouseck *et al*., 1997; Harris & Tyrrell, 2001). Alien species are widely studied by ecologists and environmental managers. In fact, knowledge of ecological traits of invaders and assessment of damage are fundamental for predicting the consequences of invasions and finding effective methods to control and mitigate this form of pollution (Bax *et al*., 2001; Allendorf & Lundquist, 2003).

Species of macroalgae have been responsible for some of the most dramatic invasions in marine habitats (Carlton & Scanlon, 1985; Rueness, 1989; Verlaque, 1994; Meinesz *et al*., 2001; Silva *et al*., 2002). In the Mediterranean Sea, more than 90 taxa of red, brown and green algae have been introduced and at least 8 of them are considered invasive (Boudouresque & Verlaque, 2002). Among these latter, two species of *Caulerpa* J.V. Lamouroux, *Caulerpa taxifolia* (Vahl) C. Agardh and *C. racemosa* (Forsskål) J. Agardh, have caused serious biological pollution. Invasions of *Caulerpa* species are particularly threatening because of (1) their ability to spread rapidly over all kind of substrata, (2) their high rates of vegetative dispersal and (3) their high competitiveness related to overgrowth capabilities, production of allelopathic substances and pseudo-perennial habit (Meinesz & Hesse, 1991; Lemée *et al*., 1993; Verlaque & Fritayre, 1994; Smith & Walters, 1999, Ceccherelli & Piazzi, 2001).

Caulerpa racemosa is considered a Lessepsian migrant (migrated from the Red Sea to the Mediterranean through the Suez Canal) (Lipkin, 1972) that colonized the eastern part of the Mediterranean Sea since the 1920s (Hamel, 1926; Rayss, 1941). Two varieties are recognized in the Mediterranean: an intermediate between var. *turbinata* (J. Agardh) Eubank and var. *uvifera* (C. Agardh) J. Agardh termed "*turbinata-uvifera*" and var. *lamourouxii* (Turner) Weber-van Bosse f. *requienii* (Montagne) Weber-van Bosse (Verlaque *et al*., 2000). Since the early 1990s, a new invasive variety of *C. racemosa* has been spreading rapidly in the Mediterranean Sea. On the basis of a morphological study, Verlaque *et al*. (2000) considered this latter as a new introduced taxon close to *C. racemosa* var. *occidentalis* (J. Agardh) Børgesen. Molecular studies confirmed the presence of three different varieties of *C. racemosa* in the Mediterranean Sea and the introduction hypothesis for the invasive variety. Famà *et al*. (2000) found that invasive Mediterranean plants and Western Australian specimens were closely related. Durand *et al*. (2002) suggested that the invasive variety could be a hybrid between var. *turbinata-uvifera* and an unknown tropical strain. Nevertheless, Verlaque *et al*. (2003) disproved this hypothesis and demonstrated that the invasive event that has affected the Mediterranean since the early 1990s resulted from a recent introduction from south-western Australia. The invasive variety was identified as a poorly known taxon described from the Perth region as *Caulerpa cylindracea* Sonder (= *C. racemosa* var. *laetevirens* f. *cylindracea* (Sonder) Weber-van Bosse). Verlaque *et al*. (2003) proposed the new combination *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque.

Recorded for the first time in the Mediterranean in the early 1990s in Libya (Nizamuddin, 1991), *C. racemosa* var. *cylindracea* was almost immediately found in other parts of the basin (Alongi *et al*., 1993; Panayotidis & Montesanto, 1994; Piazzi *et al*., 1994) and showed traits of invasiveness right from its first phases of spread (Piazzi *et al*., 1997a). Thirteen years later, nearly the whole Mediterranean basin is colonized and the Canary Islands have just been reached (Verlaque *et al*., 2004). Although highly invasive, *C. racemosa* var. *cylindracea* has not been the subject of large-scale research projects to describe its expansion. Several studies have been carried out on the ecology of this alga, but its spread was not quantified at a Mediterranean level. The aim of this paper is to assess the colonization of *C. racemosa* var. *cylindracea* thirteen years after the first record in the Mediterranean Sea. Furthermore, by means of available references, data of the web site *Caulerpa on line* (LEML-ENSA, 2003) and unpublished data, we try both to assess the scale of its invasion and to review the main aspects of the ecology of the alga.

RESULTS

Mediterranean distribution at the end of 2003

The colonization of *Caulerpa racemosa* var. *cylindracea* (hereafter: "*C. racemosa*") has been documented along the coasts of 11 nations throughout the Mediterranean basin (Verlaque *et al*., 2004) (Tab. 1; Figs 1, 2, 3). The alga develops on all kind of substrata, both in polluted and unpolluted areas, between 0 and more than 50 m depth, down to 70 m depth in Cyprus (Argyrou, unpublished data) and in Southern Italy (Piazzi, unpublished data).

In France there are large populations in the Gulf of Marseille and in the Bays of Toulon, Hyères and Villefranche-sur-Mer (Verlaque *et al*., 2000; Belsher *et*

Table 1. Mediterranean localities of *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque (Situation December 2003). See reference localities in Figs 1-3.

Nations and regions	*Localities concerned*
FRANCE	
Provence-Alpes-Côte d'Azur	Bay of Marseille (01), Bay of Toulon (02), Gulf of Giens (03), Bay of Hyères (03), Porquerolles Island (03) Port-Cros Island (03), Saint-Tropez (04), Bay of Villefranche-sur-Mer (05), Nice (05)
Corsica	Coast of Bastia (06), East of Bonifacio (07)
ITALY	
Liguria	Bergeggi Island (08), Varazze (08), Genova (08), Bay of Monterosso (09), Palmaria Island (09), Gulf of La Spezia (09)
Tuscany	Meloria Shoals (10), Livorno (10), Vada Shoals (10), Capraia Island (11), Elba Island (12), Giglio Island (13)
Sardinia	Gulf of Asinara (14), Asinara Island (15), Bay of Malfatano (16), Gulf of Cagliari (16), Serpentera Island (17)
Latium	S. Agostino (18), S. Marinella (18), Sperlonga (19), Ponza Island (20), Zannone Island (20), Ventotene Island (21)
Campania	Ischia Island (22), Procida Island (22), Cape Miseno (22), Capri Island (23), Point Campanella (23), Gulf of Salerno (24)
Calabria	Vibo Marina (25), Cape Vaticano (25), Palmi (25), Scilla (25), C. Rizzuto (26)
Sicily	Catania (27), Siracusa (28), Cape Passero (29), Pozzallo (30), Cape Feto (31), Marsala (32), Trapani (32), Gulf of Castellammare (33), Termini Imerese (34), Pantelleria Island (35), Lampedusa Island (36), Linosa Island (37), Favignana Island (38)
Apulia	Taranto (Mar Grande, Mar Piccolo) (39), S. Vito (39), Pulsano (40), Lizzano (40), Maruggio (40), Nardò (40), Ugento (40), Otranto (41), Brindisi (42), Monopoli (43)
CROATIA	Cavtat (44), Dubrovnik (44), Mljet Island (Sobra) (45), Glavat Islet (45), Pelješak Peninsula (Prije ba Cove, Mirce, Cape Lovište) (46), Hvar Island (V. Garška Cove) (47), Marinkovac Islet (47), Biševo Island (Mezuporat Cove) (48)
SPAIN	
Valencia	Castelló de la Plana (49), Sagunt (50), Alacant (50)
Balearic Islands	Mallorca (Dragonera, Bay of Palma, Cap de Regana, Cap Blanc, Ses Fontanelles) (51), Cabrera (52), Eivissa (53)
MALTESE ISLANDS	Gozo Island (Dwejra, Xatt l-Ahmar) (54), Malta Island (eastern and southern coasts: from St. Georges's Bay to Ghar Lapsi, Hard Bank) (55)
TUNISIA	Sidi Daoud (56), Metline (56), Cap Bon (Korbus, Sidi Daoud) (57), Beni Khiar (58), Hammamet (59), Monastir (60), Madhia (61), Kerkenna Islands (62), Zarzis (63)
GREECE	
North Aegean	Chalkidiki (64), Lesbos Island (65), Chios Island (66)
South Aegean	Gulf of Saronikos (67), Cape Sounion (68), Cyclades Archipelago (69), Rodos Island (70), Crete (71)
Ionian	Pilos (72), Korinthiacos Gulf (Antikira, Loutraki) (73), Zakintos Island (74), Kerkyra Island (75)
TURKEY	Bozcaada (76), Izmir (Eskifoça, Karaburun) (77), Cesme (78), Kusadasi (79), Didim (80), Bodrum Peninsula (81), Bay of Gokova (82), Marmaris (83)
CYPRUS	Paphos (84), Limassol Bay (including Moni area) (85), Cape Greco (86), Famagusta (87)
ALBANIA	Dherm (88), Porto Palermo (89)
LIBYA	Tripoli

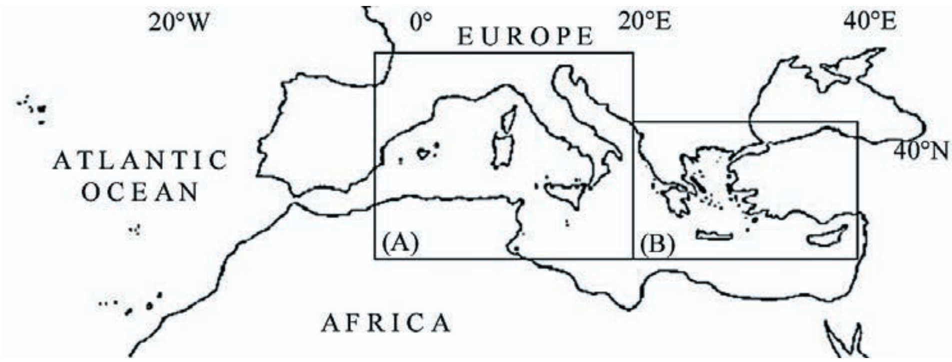

Fig. 1. Map of The Mediterranean Sea with the sectors represented in Fig. 2 (A) and in Fig. 3 (B).

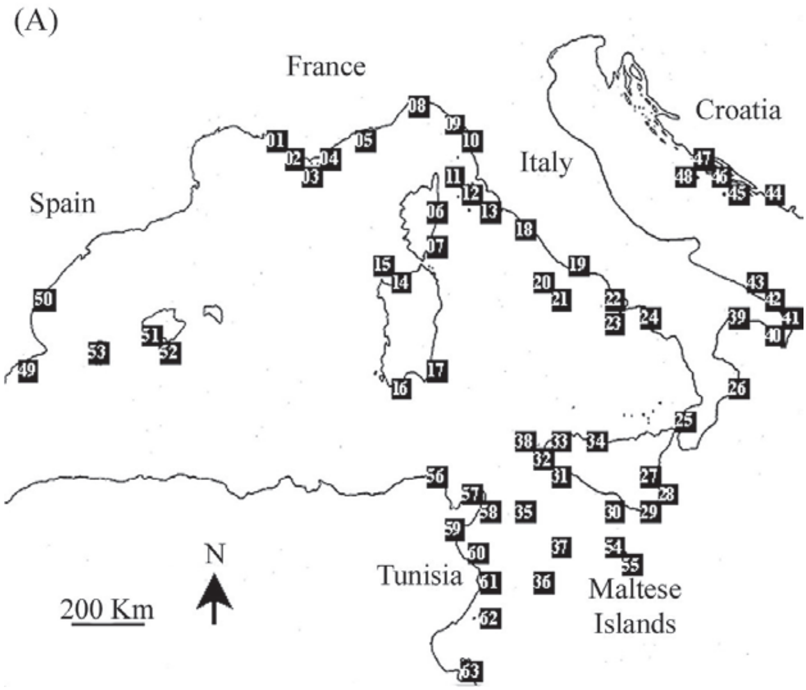

Fig. 2. Distribution of *Caulerpa racemosa* var. *cylindracea* in the western Mediterranean Sea. See Table 1 for key to locations.

al., 2003; LEML-ENSA, 2003; Meinesz *et al*., 2003). Wide areas have been colonized in Libya (Nizamuddin, 1991), Greece (Panayotidis & Montesanto, 1994; 1998; 2001), Albania (Di Martino & Giaccone, 1995; Cinelli, unpublished data), Cyprus (Argyrou *et al*., 1999), Spain (Ballesteros *et al*., 1999; Aranda *et al*., 2003),

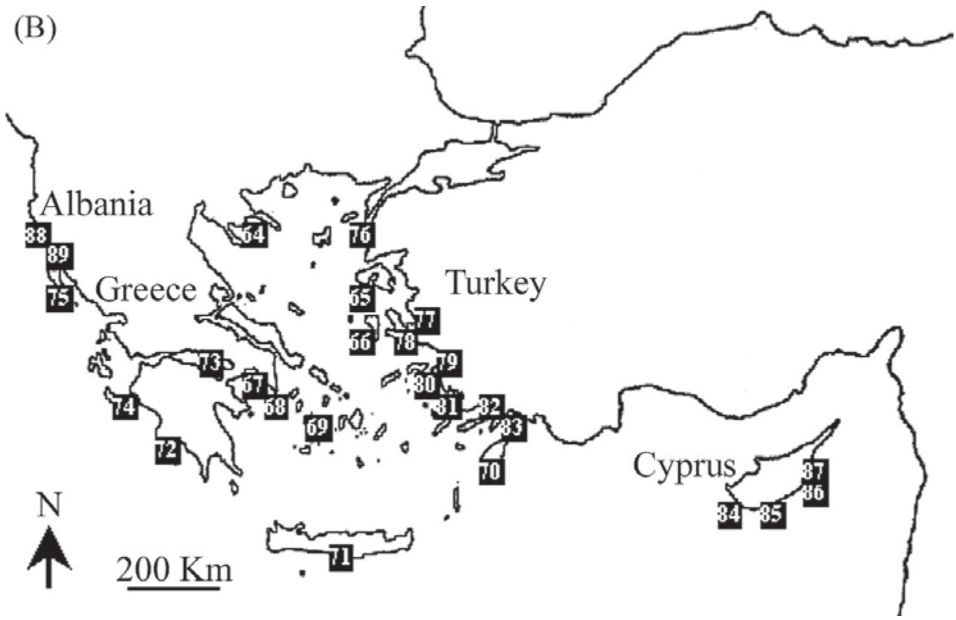

Fig. 3. Distribution of *Caulerpa racemosa* var. *cylindracea* in the eastern Mediterranean Sea. See Table 1 for key to locations.

Maltese Islands (Stevens, 1999; Mifsud *et al*., 2003), Tunisia (Djellouli, 2000; Langar *et al*., 2003), Turkey (Tolay *et al*., 2001; Cirik & Akçali, 2003) and Croatia (Žuljević *et al*., 2003). In Italy, the spread of *C. racemosa* appears particularly threatening: the alga is now present along the coasts of Sicily (Giaccone & Di Martino, 1995; Serio & Pizzuto, 1999; Calvo, unpublished data), Liguria (Bussotti *et al*., 1996; Modena *et al*., 2000; Peirano, unpublished data), Tuscany (Piazzi *et al*., 1997a; 1997b; 2001b; De Biasi *et al*., 1999), Sardinia (Cossu & Gazale, 1997; Cossu *et al*., 2003), Campania (Gambi & Terlizzi, 1998; Buia *et al*., 2001; Buia *et al*., 2003), Apulia (Buia *et al*., 1998; Bottalico *et al*., 2002; Costantino *et al*., 2002; Cecere & Petrocelli, 2004), Calabria (Cantasano, 2001; Di Martino, 2001) and Latium (D'Archino, unpublished data).

In spite of these records, it is difficult to determine the extent of the colonization in terms of area affected by *C. racemosa* in the Mediterranean Sea, because of the lack of mapping and accurate evaluations of colonized surfaces. The linear extent of coastline adjacent to each affected area (Vaugelas *et al*., 1999) is the only measure evaluated to date and it is available only for a few zones. The length of the coastline affected by the colonization of *C. racemosa* can be estimated as 80 km along French coasts, about 500 km of western Italian coasts (from Liguria to Sicily), about 120 km in the Balearic Islands (Spain) and about 15 km along Croatian coasts (data evaluated on 1:25000 maps). No quantitative data are available for other Mediterranean coasts, but it is fair to suppose that colonized surfaces relative to the north western area could double if the whole Mediterranean basin is considered.

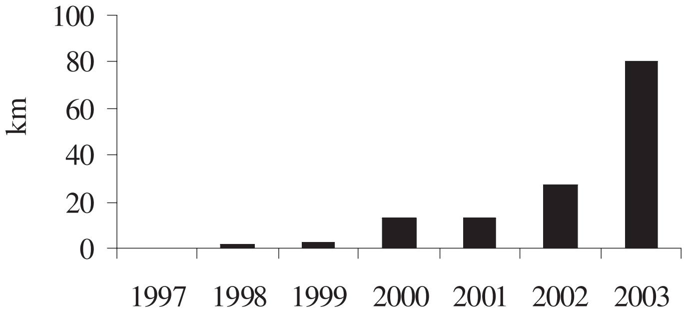

Fig. 4. Increase in length of coastline affected by *Caulerpa racemosa* var. *cylindracea* along French Mediterranean coasts from 1997 to 2003 (from Meinesz *et al.*, 2003, amended).

Spread strategies

Like other invasive species of the same genus, *Caulerpa racemosa* shows high rates of elongation of stolons allowing a rapid colonization of the substratum: during the period of maximal growth, from June to November (Piazzi & Cinelli, 1999), stolons may grow up to 2 cm per day (Piazzi & Cinelli, 1999; Piazzi *et al.*, 2001a). *C. racemosa* vegetatively propagates by fragments. Fragments easily re-establish with variable performance according to season and several days of detachment do not alter the capability of establishing (Ceccherelli & Piazzi, 2001). Moreover, this species reproduces by specialized propagules (Renoncourt & Meinesz, 2002) and probably sexually (Panayotidis & Žuljević, 2001). The availability of several modes of reproduction, multiplication and dispersion allows *C. racemosa* to rapidly extend the colonized areas (Fig. 4) and confers a level of invasiveness to this species that may be higher than that of *C. taxifolia*. For example, in an area in front of Livorno (Italy, north-western Mediterranean Sea) where the two species co-occur, the surface colonized by *C. racemosa* and *C. taxifolia* increased by 248 % and 64.5 % in one year, respectively (Piazzi *et al.*, 2001a).

Impact on recipient communities

Caulerpa racemosa shows invasive characteristics, strongly interfering with recipient communities (Boudouresque & Verlaque, 2002). The mechanism of stolonization allows it to overgrow most of the coastal benthic organisms of the Mediterranean Sea. Native benthic communities are not able to avoid overgrowth by *C. racemosa*, especially when natural complexity has been lost due to other factors (Ceccherelli *et al.*, 2002). When stolons completely cover all available substrata, they constitute multi-layered structures up to 10-15 cm wide (Piazzi *et al.*, 1997a). These structures represent a trap for sediments, contributing to suffocate sessile benthic organisms (De Biasi *et al.*, 1999; Piazzi & Cinelli, 1999; Buia *et al.*, 2001). Most of the native species are outcompeted and species diversity of littoral ecosystems strongly decreases (Žuljević, unpublished data). The cover and species number of macroalgal communities invaded by *C. racemosa* decline and the structure of the assemblages greatly change (Piazzi *et al.*, 2001c). Susceptibility of particular species is different in comparison with that described for algal assemblages colonized by *C. taxifolia* in the Mediterranean Sea (Balata *et al.*, 2004). Encrusting species are more affected than erect species by the invasion of *C. racemosa* (Piazzi *et al*., 2001c), while they show the highest resistance when colonized by *C. taxifolia* (Verlaque & Fritayre, 1994). These differences may be due to different competitive mechanisms of the two introduced species: *C. racemosa*, which has short fronds, can compete with erect species less easily than *C. taxifolia*, while it is able to cover completely the substratum in a very short time, damaging the lowest vegetation layers. However, when colonization by *C. racemosa* persists, erect species can be also affected. For example, in both the Mar Piccolo and the Mar Grande of Taranto (southern Italy), *C. racemosa* is completely replacing *C. prolifera* (Forsskål) J.V. Lamouroux meadows (Mastrototaro *et al*., 2004).

Seagrass beds are also affected by *C. racemosa*. Beds of *Cymodocea nodosa* (Ucria) Ascherson and *Nanozostera noltii* (Hornemann) Tromlinson & Posluzny are easily invaded and both shoot and flower density of plants are influenced by the invader (Ceccherelli & Campo, 2002). On the contrary, the high-canopy species *Posidonia oceanica* (Linnaeus) Delile is able to avoid invasion, especially where dense beds are present (Piazzi *et al*., 1997a, b; Piazzi & Cinelli, 1999), interfering with growth (Ceccherelli *et al*., 2000) and the production of caulerpenyne (Dumay *et al*., 2002b) by the alga. However, recent studies demonstrated that *P. oceanica* shows modifications in its vegetative cycle and primary production when in contact with *C. racemosa* (Dumay *et al*., 2002a), suggesting the occurrence of an adaptive strategy for the plant.

On soft bottoms highly colonized by *C. racemosa*, macrofaunal assemblages are profoundly modified, as reported for a bay in Cyprus (Argyrou *et al.,* 1999). In this case, some taxa, (e.g. gastropods and crustaceans) decreased whereas other taxa (e.g. polychaetes) increased, causing deep modifications in the structure of the invaded communities. The colonization of barren sandy bottoms may increase space, food and microhabitat availability for benthic organisms. In the Gulf of Salerno (South Italy), Buia *et al*., (2001) observed a high species richness of molluscs in an area invaded by *C. racemosa*; however, most of the identified molluscs were characteristic of other plant systems and were represented only by juvenile stages (Buia *et al*., 2001).

Interaction with other invasive introduced species

The co-occurrence of two or more invasive introduced species may cause the establishment of competitive or synergistic mechanisms. In some localities along the Tuscan and French coasts, *Caulerpa racemosa* co-occurs with at least three of these species: *C. taxifolia* and the two turf-forming Rhodophyceae *Acrothamnion preissii* (Sonder) Wollaston and *Womersleyella setacea* (Hollenberg) R.E. Norris (Piazzi & Cinelli, 2003; Verlaque, unpublished data).

The interaction between *C. racemosa* and *C. taxifolia* has been investigated near Livorno (Italy) in natural mixed beds (Piazzi *et al*., 2003a) and through manipulative experiments (Piazzi & Ceccherelli, 2002). In both cases *C. racemosa* showed higher competitive ability than *C. taxifolia*. In fact, while the former was unaffected by the presence of the other species, *C. taxifolia* stopped growing and decreased its cover when it co-occurred with *C. racemosa* (Piazzi & Ceccherelli, 2002). Conversely, at Villefranche-sur-Mer (France), *C. taxifolia* almost completely eliminated *C. racemosa* in a large area (>1 ha) sited between 16 and 20 m depth (Meinesz, unpublished data). Also, the effect of *C. racemosa* on recipient communities is not affected by co-occurrence with *C. taxifolia*, showing similar trends in isolated and mixed beds (Piazzi *et al*., 2003a).

Synergistic mechanisms have been observed between *C. racemosa* and the turf-forming introduced *A. preissii* and *W. setacea*. Hence, the growth and the spread of *C. racemosa* are enhanced where the turf-forming algae already dominated, probably interacting with sediment deposition and causing more profound effects on invaded communities (Ceccherelli *et al*., 2002; Piazzi *et al*., 2003b; Ballesteros, unpublished data).

DISCUSSION AND CONCLUSIONS

This assessment of thirteen years of spread of *Caulerpa racemosa* var. *cylindracea* shows that this is the most serious invasive event ever documented in the Mediterranean Sea. *C. racemosa* has colonized large areas in both the western and eastern Mediterranean Sea and its spread is still continuing. A lot of ecological studies point out the invasiveness of this variety and the negative effects of its colonization on native Mediterranean biota.

Concerning the effects of *C. racemosa* invasion on human activities in coastal areas, no quantitative studies have been performed. Along the Tuscan coasts, a negative impact on fisheries has been suggested in relation to the spread of *C. racemosa* (Magri *et al*., 2001). In this case, the decrease in catches was linked to the obstruction of fishing nets by uprooted fragments of *C. racemosa*, while no data were available on the effects of the invasion on the stocks. It is likely that a decrease in biodiversity of benthic communities could have effects through a trophic drop, thus causing a decrease of predators, but quantitative data are not available. The impact of the invasion of *C. racemosa* on diving tourism has to be also taken into account. In highly invaded areas, e.g. Italy, Croatia and Turkey, *C. racemosa* weaves an ungainly "cobweb" above the bottom (Tolay *et al*., 2001; Piazzi, unpublished data; Žuljević, unpublished data). Its colonization of several habitats highly appreciated by divers and the large-scale homogenisation of underwater landscapes could decrease the economic values of invaded sites. Moreover, the spread of *C. racemosa*, like most of biological invasions and contrarily to other environmental alterations, can also concern areas characterized by high ecological and heritage value, such as National Parks and Marine Protected Areas (e.g. National Park of Port-Cros, France; National Park of the Tuscan Archipelago; National Park of Mljet, Croatia) and call into question ecosystem conservation.

Considering the spread kinetics, it can be expected that all coasts of the Mediterranean Sea may be impacted by *C. racemosa*. Moreover, due to its spread mechanisms and its large distribution, the eradication of *C. racemosa* throughout the Mediterranean cannot be considered feasible. These data suggest the need of large-scale monitoring programs to assess the distribution of the alga all around the Mediterranean Sea. The impact of the invasion on human activities, such as tourism and fishing, should be also evaluated in order to estimate the cost of this large-scale biological pollution. *C. racemosa* ought to be considered as a potential threat and an international experimental programme should be quickly set up to investigate on the large scale variations of its impact on native communities and potential control.

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