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ScienceDirect
Aquatic Botany 85 (2006) 324–330
Aquatic botany
www.elsevier.com/locate/aquabot

Vegetation patterns and spontaneous regression of *Caulerpa taxifolia* (Vahl) C. Agardh in Malinska (Northern Adriatic, Croatia)

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Received 18 October 2005; received in revised form 12 June 2006; accepted 26 June 2006

Abstract

The green alga *Caulerpa taxifolia* was recorded at Malinska in 1994 and this actually represents the highest northern latitude (45°7′30″N) at which this invasive alga has been found in the world. The alga was widespread at four sites from which it was eradicated by suction pumps during 1996 and 1997. However, it immediately and intensively recolonized all but one site. Throughout 1998 and 1999 the renewed vegetation showed consistent seasonal patterns. The alga nearly disappeared in April and May while regenerating from over-wintering parts of the thalli in summer. The maximum development occurred in autumn and winter with values of biomass (around 200 g dry weight m^{-2}) and frond number (around 2000 m^{-2}) generally lower than those reported for the north-western Mediterranean. Values for the frond length (10–18 cm) were in the same range as those in the north-western basin. Throughout 1998 and 1999 the biomass was closely correlated to frond number and length (adjusted $R^2 = 0.90$). During the following years *C. taxifolia* entered a phase of regression. The total colonized area, which amounted to several thousands of square metres in 1998, spontaneously declined in 2000 and 2001 so that only several thalli were found in 2004 during a detailed survey of the settlement. No major changes in winter seawater temperatures, ranging from 9.5 to 10.5 °C, were observed in the area from 1994 to 2004. Thus, other unknown processes could likely play a role on specific vegetation patterns of *C. taxifolia* in Malinska. Accordingly, it is difficult to explain why the still surviving thalli did not proliferate during the favourable summer–autumn period.

Keywords: *Caulerpa*; Covered area; Eradication; Vegetative cycle; Temperature

1. Introduction

The invasive green alga *Caulerpa taxifolia* (Vahl) C. Agardh was found for the first time in 1984 along the Monegasque coast (Meinesz and Hesse, 1991) and, since then, it has been invading wide areas of the Mediterranean coastal waters, behaving as a highly successful, fast-spreading species (Meinesz and Hesse, 1991; Boudouresque et al., 1992; Meinesz et al., 1993; Belsher and Meinesz, 1995; Meinesz et al., 2001). In the Mediterranean, winter temperatures (9–17 °C) fall largely below the lower limit of tropical temperatures (20 °C). However, *C. taxifolia* has also been found to spread in the coldest parts i.e. the north-western basin and the northern Adriatic (Meinesz and Hesse, 1991; Meinesz and Boudouresque, 1996; Iveša et al., 2004).

Added to macrophytobenthos diversity constraints (de Villèle and Verlaque, 1995; Ceccherelli and Cinelli, 1997; Balata et al., 2004), the colonization by *C. taxifolia* induces significant changes in ecosystems with serious threats at the habitat diversity level as well as for echinoderms and benthivorous fish assemblages (Boudouresque et al., 1995; Francour et al., 1995; Harmelin-Vivien et al., 1999; Longepierre et al., 2005). However, it was suggested recently that the alga is in a regression phase in some sites along the French Mediterranean coast (Jaubert et al., 2003).

This study reports on the spreading and subsequent regression of the settlement of *C. taxifolia* at Malinska (Island of Krk, northern Adriatic, Croatia). Surveys were carried out from 1997 to 2004, and patterns of the vegetative cycle as well as temporal variation of the surface covered by the alga were assessed. This settlement is of particular interest because it has been considered to represent the highest northern latitude (45°7′30″N) at which a population of the genus *Caulerpa* has been found in the world (Komatsu et al., 1997). However, in August 2004, a population of *Caulerpa racemosa* (Forsskål) J. Agardh was found in the harbour of Vrsar (Istrian peninsula,

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doi:10.1016/j.aquabot.2006.06.009

Croatia, 45°8′52″N) which is slightly more north than Malinska (Ljiljana Iveša, personal observation).

2. Materials and methods

2.1. The settlement in Malinska

C. taxifolia was observed in the harbour of Malinska (45°7′30″N, 14°31′56″E) in November 1994 (Site I). During 1995 the alga was found at two other sites (Sites II and III) and in 1996 at more one site (Sites IV). All sites were characterized by a sandy–muddy bottom gently sloping to depths of 12–18 m. Dense *C. taxifolia* colonies were scattered over the sea bottom between 1 and 10 m. Sparse thalli were found down to the depth of 15 m. In same places the alga grew inside meadows of *Cymodocea nodosa* (Ucria) Ascherson and *Zostera noltii* Hornemann. In 1996 and 1997, during spring, the alga was extensively eradicated using suction pumps (Žuljević, 2001). After eradication the alga reappeared, so the sites were surveyed yearly and the covered surface, as the sum of the surface areas of the various colonies present, was estimated according to de Vaugelas et al. (1999).

2.2. Sampling and biometry

At Site III the alga was collected monthly by SCUBA diving from October 1997 until November 1999. Sampling was performed over an area of 200 m^2 characterized by a stable sandy–muddy plateau at 8 m depth where the alga was evenly distributed. At each date of sampling, three quadrates of 25 cm × 25 cm were scattered at random over the sampling area. The quadrates were first photographed after which the alga was sampled by hand, including the sediment to a depth of 5 cm. The area was considered sufficiently large to warrant independence of sampling. After transport to the laboratory the samples were cleaned of epiphytes and sediment. Then, the number and the length of primary fronds, taken here as the erect parts of the thallus originating from stolons (Meinesz et al., 1995), was determined. The total dry weight was measured

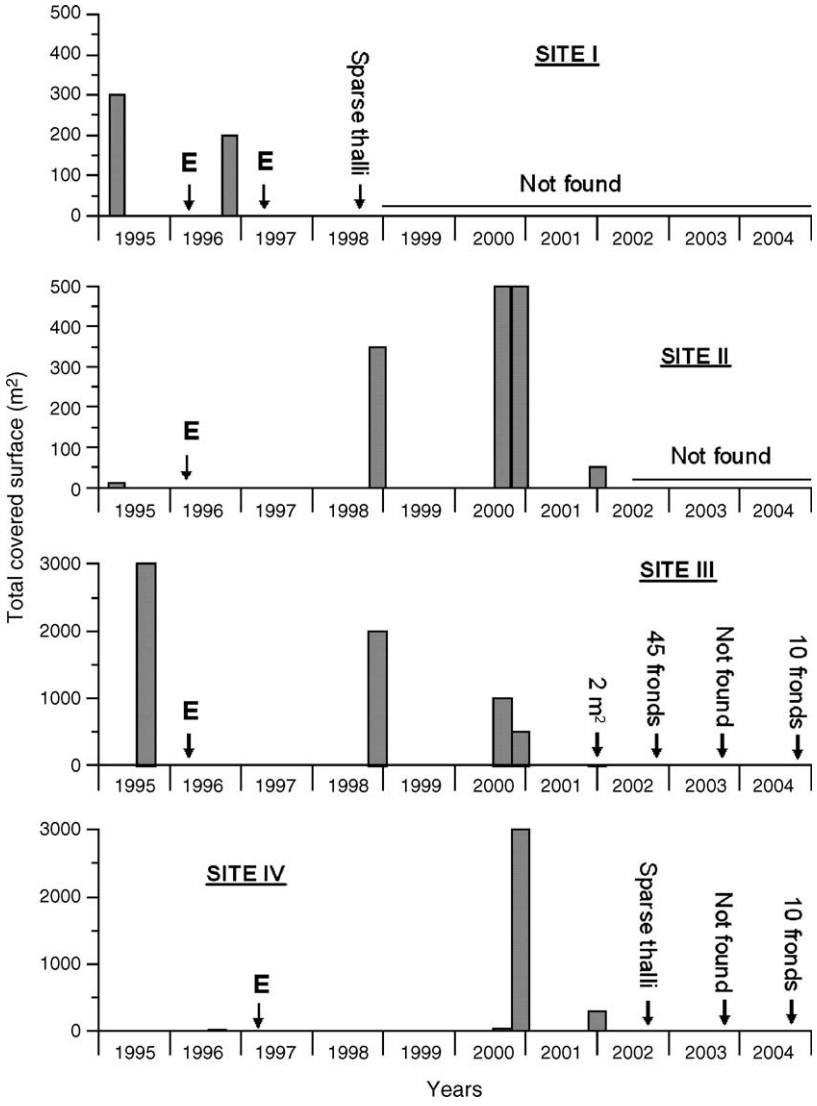

Fig. 1. Changes in the area covered by *Caulerpa taxifolia* at four sites at Malinska from 1995 to 2004. E indicates times of eradication.

after drying the samples for 24 h at 80 °C. Cover, representing the portion of the sea bottom covered by *C. taxifolia* was estimated from photographs by subtracting the bare area from the total area of the quadrat (Bianchi et al., 2004).

At each date of sampling, the temperature was measured at 8 m depth. Additionally, daily temperatures were measured from November 2002 to August 2003 using Temperature Data Loggers (Onset) placed in the sampling area. For the period from 1994 to 2004, surface seawater temperature was measured daily at Opatija, a coastal locality near the Island of Krk at 25 km from Malinska harbour.

2.3. Data analysis

The interrelationship among *C. taxifolia* traits was analysed by multiple regression in which the biomass was the dependent variable and the number of fronds, the length of fronds and cover were independent variables. As it may be supposed that the relation varies between years, a dummy variable was included in the analysis after binary coding of 1998 and 1999 by 0 and 1, respectively (Zar, 1999).

The computer software package SYSTAT (Version 10, Systat) was used for multiple regression analysis. Independent variables were selected by the backward elimination procedure (Zar, 1999) at the level of significance $p < 0.05$.

3. Results

3.1. Survey of the sites

Until 1997 the extension of *C. taxifolia* meadows at Malinska was reported in Meinesz et al. (1998). In Fig. 1 such data are shown in combination with our subsequent estimations of the areas covered by *C. taxifolia*. After its recognition, the

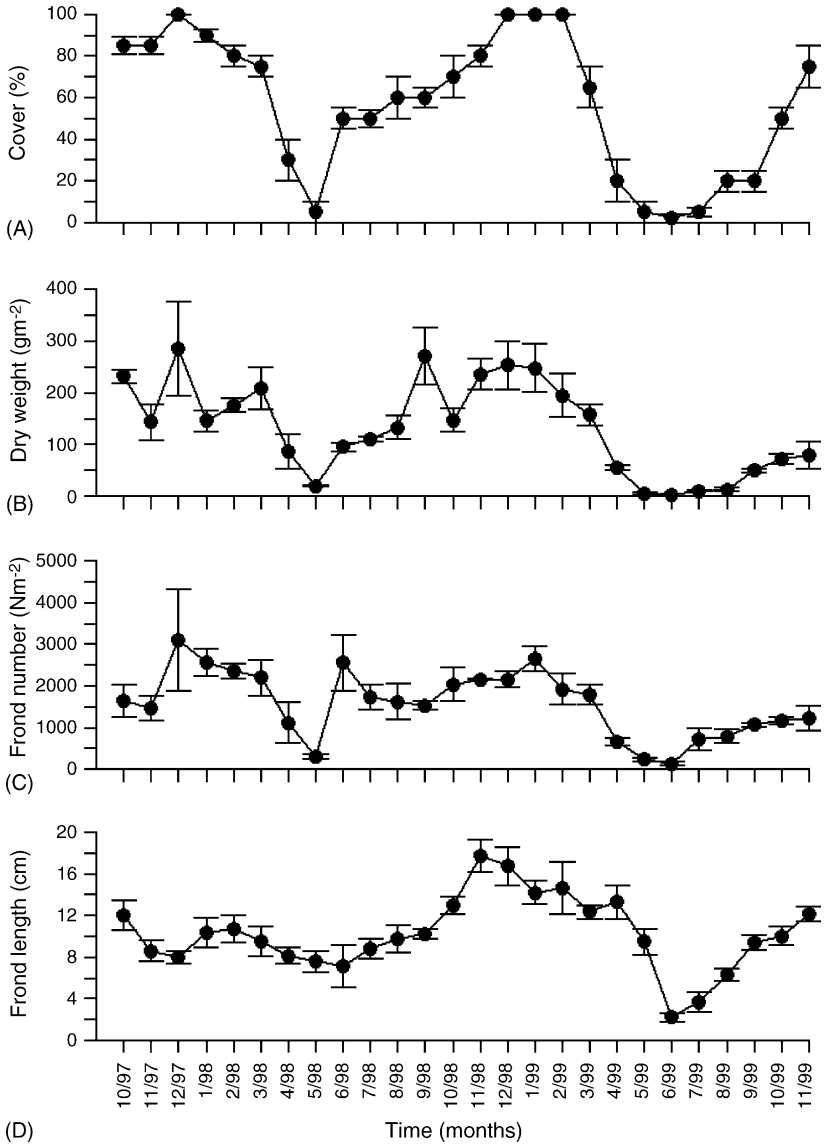

Fig. 2. Temporal variation of *C. taxifolia* in cover (A), biomass (B), frond number (C) and frond length (D) at Malinska. Data are given as the mean ± standard deviation of three samples (25 × 25 cm quadrates).

alga was eradicated by suction pumps in 1996 and 1997 yet it reappeared although with differing patterns of colonization among sites. At Site I only sparse thalli were found during 1998 while during the following yearly surveys (1999–2004) the alga was not found. At Site II the alga intensively reappeared, forming a large meadow in November 1998. The covered surface increased to August 2000 and remained at similar levels in November of the same year. On the contrary, at Site III the extent of the meadow which had been forming until November 1998 decreased to December 2000, whereas at Site IV the covered area abruptly increased from August to November 2000. After 2000 the covered surface spontaneously and suddenly decreased at all these sites. Only sporadic fronds were found during the following surveys, i.e. until 2004 (Fig. 1).

3.2. Vegetation temporal variations

During the autumn–winter maximum development the coverage of the sandy–muddy substratum was from 70 to 100%. In winter the fronds showed signs of necrosis. In spring the cover abruptly decreased to minimum values of less than 10% in May. The cover increased to 50% in June 1998 while in 1999 a cover of less than 10% persisted until July (Fig. 2A).

Temporal variations of the biomass dry weight showed marked seasonal patterns (Fig. 2B). From October 1997 to March 1998, as from September 1998 to March 1999, the biomass was around 200 g m^{-2}. An abrupt decrease in biomass occurred from April to May of both years. During summer 1998 the biomass recovered more rapidly than in summer 1999.

The frond number showed patterns similar to those of the biomass with values fluctuating around 2000 m^{-2} during the autumn–winter period and an abrupt decrease to around 300 m^{-2} in May. In June 1998 the frond number suddenly increased (2500 m^{-2}). In 1999 the recovery was very slow leading to a mean frond number of 1232 m^{-2} in November which was, however, close to values for the same month in 1997 (Fig. 2C).

Changes of the frond length showed different patterns from biomass and frond number. From October 1997 to October 1998 it fluctuated around 10 cm and increasing to a mean value of 18 cm in November 1998. Then the length steadily decreased to March and abruptly to June 1999 (around 2 cm). The frond length increased rapidly throughout summer 1999 (Fig. 2D).

Multiple regression analysis established a linear equation enabling the prediction of biomass from frond number and length. Firstly, data for 1998 and 1999 were analysed coding years as a dummy variable. However, backward selection eliminated the dummy variable and cover from the model (analysis not shown). A subsequent analysis was performed without the use of the annual dummy variable and including data for the last 3 months of 1997. Also in this backward selection of independent variables cover was eliminated from the model (Table 1). The resulting equation (adjusted $R^2 = 0.90$) was:

$$\text{Weight} = -8.348 + 1.214 \times \text{Number} + 0.896 \times \text{Length}$$

where all variables were logarithmically transformed.

Table 1
Multiple regression analysis testing of the dependence of *C. taxifolia* biomass dry weight on number of fronds, length of fronds and cover

Effect	Coefficient	Standard coefficient	*t*	*p*
Constant	−8.348		−8.459	<0.001
Number	1.214	0.735	7.539	<0.001
Length	0.896	0.307	4.594	<0.001
Cover	Deleted by backward selection, $p > 0.05$			

The alga was sampled monthly from October 1997 to November 1999. $N = 26$; transformation, ln; adjusted $R^2 = 0.900$; S.E. of estimate = 0.410; ANOVA, $F = 113.036$; $p < 0.001$; d.f. (regression) = 2; d.f. (residual) = 23.

3.3. Seawater temperature

Winter seawater temperatures, measured monthly at the time of *C. taxifolia* sampling, were not lower than 11 °C in 1998 and between 9 and 10 °C in 1999 (Fig. 3A). A more complete depiction of temperature fluctuations at Malinska was obtained by daily measurements (Fig. 3B). The temperature descended below 15 °C from 7 December 2002 increasing over this threshold from 7 May 2003. Temperatures less than 11 °C, fluctuating approximately between 10.5 and 9.5 °C, occurred from 11 February 2003 until 15 April 2003. These results are in agreement with daily surface temperature measurements at Opatija for the whole period encompassed by this study i.e. from 1994 to 2004. Minimum winter temperatures were between 9 and 10 °C in 1996, 2002, 2003 and 2004 and between 10 and 11 °C during the other years (Fig. 3C).

4. Discussion

The colonization of the sheltered settlement of Malinska by the alga *C. taxifolia* showed two distinct long-term patterns. Firstly, from its recognition until 2000 the alga was in a phase of active spreading in spite of intensive eradication efforts during 1996 and 1997. Secondly, after 2000 the alga entered a phase of apparently spontaneous regression.

During the period of active spreading, the alga had been showing clear seasonal vegetation changes. Over-wintering fronds decayed intensively during spring. The coverage decreased to approximately 30% in April and to less than 10% in May while increasing during the summer. However, the vegetation did not recover fully during the summer so that the development maximum shifted to autumn and winter when fronds showed evident signs of necrosis. On the contrary, in the north-western Mediterranean populations, the maximum development occurs during the summer and autumn period with a usually constant 100% coverage of the colonized substratum over the year (Verlaque and Fritayre, 1994; de Villèle and Verlaque, 1995; Meinesz et al., 1995; Thibaut et al., 2004). An exception was reported for a very exposed settlement along the Tuscan coast (Italy) where the coverage in May was extremely low because of the exposition of the study location to storms that may remove *C. taxifolia* after the end of the growth period (Balata et al., 2004).

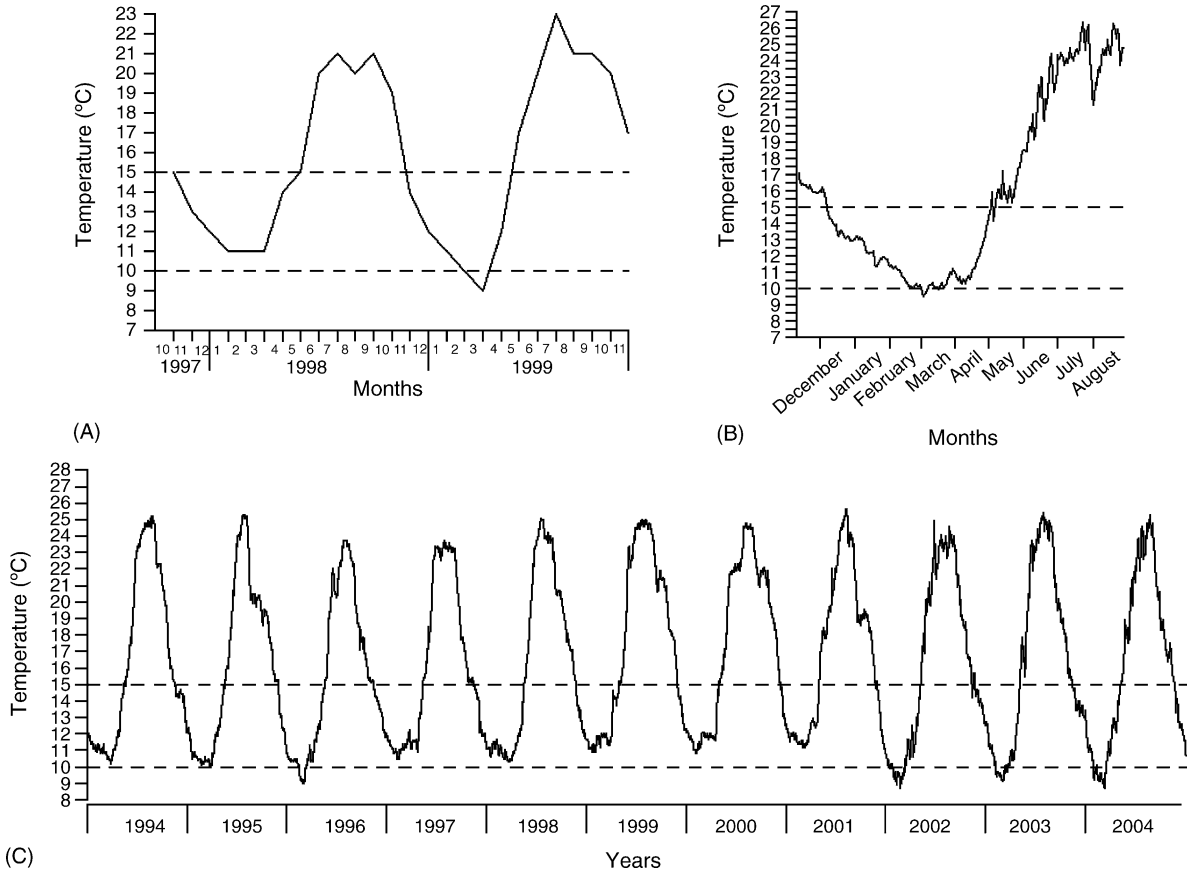

Fig. 3. Seawater temperature at Malinska measured monthly from October 1997 to November 1999 at a depth of 8 m (A). Daily seawater temperature at 8 m depth at Malinska from 12 November 2002 to 28 August 2003 (B). Daily surface seawater temperatures at Opatija (region of the Island of Krk) from 1994 to 2004 (C). The broken lines indicate the 10 °C lethal threshold and the 15 °C threshold below which there is no growth of *C. taxifolia* (according to Komatsu et al., 1997).

At maximum development biomass dry weight of *C. taxifolia* at Malinska was lower than in similar habitats of the north-western Mediterranean, with values fluctuating around 200 g m^{-2} in the former and around 500 g m^{-2} in the latter settlements (Meinesz et al., 1995; Thibaut et al., 2004). Accordingly, the number of fronds was around 2000 and 14000 m^{-2} at Malinska and in the north-western Mediterranean (Meinesz et al., 1995), respectively. However, values for the frond length, ranging from 10 to 18 cm during the maximum development, were close to those reported for similar habitats in the north-western Mediterranean. For example, at Cap Martin (France) in a settlement on the sandy–muddy substratum at 9 m depth during autumn the length of primary fronds was between 8 and 20 cm (Meinesz et al., 1995).

Major factors affecting *C. taxifolia* vegetation patterns include seawater temperature, depth, exposition and the type of substratum (Thibaut et al., 2004). The presence of seagrasses such as *Posidonia oceanica* (Linnaeus) Delile and *C. nodosa* also strongly influence seasonal changes in frond number and length (Ceccherelli and Cinelli, 1998). Among these factors, probably cold winter seawater temperatures formed the basis of the specific vegetation patterns at Malinska during the period of active spreading of the alga. The lower lethal temperature of the Mediterranean strain of *C. taxifolia* is between 9 and 10 °C, where frond segments resist for 3 months at 10 °C while at 9 °C all fronds die in less than 2 months, and new stolons and new fronds develop at 15 and 17.5 °C, respectively (Komatsu et al., 1997). Similar results were obtained for Moreton Bay (Australia) samples of *C. taxifolia*: a lethal temperature threshold of between 9 and 11 °C over periods of 4–6 weeks was ascertained (Chisholm et al., 2000).

Thus, the *C. taxifolia* population at Malinska had been subject to very adverse seawater temperatures, which could be in the range where growth does not occur for 5 months, fluctuating around the lethal threshold for 2 months. In contrast, in the north-western Mediterranean the seawater temperature is more favourable. For example, just below the Oceanographic Museum of Monaco, where the alga was firstly recorded in 1984, winter daily seawater temperatures, from 1978 to 1991, were never below 11 °C but for 3 days during 1978 (Meinesz and Hesse, 1991).

Low winter seawater temperatures could also be the basis for the very slow recovery of the alga during summer 1999 in comparison to summer 1998. From January to March 1999 the temperature had been fluctuating between 9 and 10 °C while in 1998 the temperature did not decrease below 11 °C during winter. However, this should be considered with reservation as the temperature was measured once per month. Perhaps the difference in recovery between 1998 and 1999 could be also

considered as a first signal of the regression of the alga in the settlement.

The reasons of a regression, after rapid proliferation, of some species of the genus *Caulerpa* as well as of *C. taxifolia* in the settlement below the Oceanographic Museum of Monaco are not well understood (Jaubert et al., 2003). Regarding the settlement at Malinska, the regression of *C. taxifolia* cannot be related directly to cold winter seawater temperatures. Temperature patterns in the area did not vary substantially from 1994 to 2004 and during the period of the abrupt decrease of the covered surface (2000 and 2001) winter temperatures were above the 10 °C threshold. Accordingly, the meadow at Site III declined during 2000, whereas the meadows at Sites II and IV, experiencing the same temperature conditions, were expanding. However, in combination with persistant winter temperatures near the lethal threshold, other environmental factors as, for example, changes in sediment nutrient concentrations, interactions with other species (Ceccherelli et al., 2002) including herbivores (Longepierre et al., 2005) or changes in hydrodynamic conditions, could form the basis of the regression. Studies on nutrient addition to sediment have showed that the response of the alga varies over time (Delgado et al., 1996; Ceccherelli and Cinelli, 1997; Ceccherelli and Sechi, 2002). It could be that a lack of nutrients in spring, after a particularly cold winter, may compromise the summer recovery limiting the growth of new parts of the thallus. Thus, manipulative studies are needed in the future to identify and test the ecological factors responsible for the regression of *C. taxifolia*.

Acknowledgements

Financial support was provided by the Ministry of Science and Technology of the Republic of Croatia (projects 0098111 and "Jadran"). We are thankful to Dr. Milan Hodžić, Meteorological and Hydrological Service, Marine Meteorological Center, Split for providing us with data on seawater temperatures at Opatija from 1994 to 2004. The authors thank Dr. Daniel Mark Lyons for critical proof reading.

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