

Vulnerability of marine habitats to the invasive green alga Caulerpa racemosa var. cylindracea within a marine protected area

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1	Vulnerability of marine habitats to the invasive green alga Caulerpa racemosa
2	var. cylindracea within a marine protected area
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23 Abstract

24

25	The relative vulnerability of various habitat types to Caulerpa racemosa var.
26	cylindracea invasion was investigated in the National Marine Park of Zakynthos
27	(Ionian Sea, Greece). The density of <i>C. racemosa</i> fronds was modelled with
28	generalized additive models for location, scale and shape (GAMLSS), based on an
29	information theory approach. The species was present in as much as 33% of 748
30	randomly placed quadrats, which documents its aggressive establishment in the area.
31	The probability of presence of the alga within randomly placed 20 x 20 cm quadrats
32	was 83% on 'matte morte' (zones of fibrous remnants of a former P. oceanica bed),
33	69% on rocky bottoms, 86% along the margins of <i>Posidonia oceanica</i> meadows, 10%
34	on sandy/muddy substrates, and 6% within P. oceanica meadows. The high frond
35	density on 'matte morte' and rocky bottoms indicates their high vulnerability. The
36	lowest frond density was observed within P. oceanica meadows. However, on the
37	margins of P. oceanica meadows and within gaps in fragmented meadows relative
38	high C. racemosa densities were observed. Such gaps within meadows represent spots
39	of high vulnerability to C. racemosa invasion.

40

41 Key words: benthic ecology; biological pollutants; *Caulerpa racemosa*; invasive
42 macrophytes; phytobenthos; seagrass; vulnerability; Mediterranean; MPA; Greece
43

45 **1. Introduction**

46

47 More than 900 introduced species have been reported so far from the Mediterranean 48 Sea, of which ~500 are considered as established. Among them, there are more than 49 100 established alien macrophytes (Zenetos et al., 2008). Approximately one tenth of 50 these species can be considered as invasive, i.e. they have overcome biotic and abiotic 51 barriers, are able to disseminate away from their area of initial introduction, and have 52 a noticeable ecological and economic impact. Decline of biodiversity, effects on 53 phytobenthic, fish and invertebrate biota, threat to the ecological stability of invaded 54 ecosystems, and pressures on economic activities are among the impacts of invasive 55 macrophytes (Boudouresque and Verlaque, 2002; Zenetos et al., 2006; Schaffelke and 56 Hewitt, 2007; Piazzi and Balata, 2009). 57 58 The green alga Caulerpa racemosa (Forsskål) J. Agardh sensu lato (Chlorophyta: 59 Bryopsidales) is widely distributed in tropical and warm temperate seas (Verlaque et

al. 2003). Three intraspecific taxa of *C. racemosa* have been identified in the

61 Mediterranean Sea, among which C. racemosa var. cylindracea (Sonder) Verlaque,

62 Huisman, and Boudouresque (Verlaque et al., 2003; Klein and Verlaque, 2008)

63 (hereafter *C. racemosa*) is one of the most aggressive invaders in the basin (Streftaris

and Zenetos, 2006; Verlaque et al., 2004; Klein and Verlaque, 2008). This variety was

65 first found in the Mediterranean Sea along the Libyan coast in 1990 (Nizamuddin,

66 1991), being introduced from south-western Australia (Famà et al., 2000; Verlaque et

al., 2003). It has rapidly spread throughout the entire basin, reaching as far as the

68 Canary Islands in the Eastern Atlantic Ocean (Verlaque et al., 2004). The species has

69 been reported from all kind of substrata with a variety of benthic assemblages,

70	between 0 and 70 m depth, in both polluted and unpolluted areas, and has
71	demonstrated an excessive rate of proliferation and high adaptability to physical
72	stressors (Piazzi et al., 2005; Streftaris and Zenetos, 2006; Klein and Verlaque, 2008;
73	Tsiamis et al., 2008). Its stolons can quickly elongate and easily overgrow other
74	macroalgal (Piazzi et al., 2001; Piazzi and Ceccherelli, 2006) or invertebrate species
75	(Kružić et al., 2008; Baldacconi and Corriero, 2009). Quite often C. racemosa forms
76	compact meadows in the Mediterranean Sea (Argyrou et al., 1999; Ruitton et al.,
77	2005; Klein and Verlaque, 2008; Katsanevakis and Thessalou-Legaki, 2009), contrary
78	to its native range in south-western Australia, where it does not form monospecific
79	stands but grows intermixed with other algae (Verlaque et al., 2003). It has a high
80	potential for dispersal by fragmentation and re-establishment of stolons (Ceccherelli
81	and Piazzi, 2001), formation of propagules (Renoncourt and Meinesz, 2002), and
82	sexual reproduction (Panayotidis and Žuljević, 2001).
83	
84	C. racemosa was initially reported in Greece from Zakynthos Island and Pylos Bay
85	(Ionian Sea) in 1993 (Panayotidis and Montesanto, 1994). Since then, the species has
86	been spreading extremely rapidly along Greek coasts and it is now found on the
87	majority of the Greek coastal areas (Tsiamis et al., 2010; Salomidi et al., 2009).
88	
89	There are a few studies in the literature comparing invasion success of C. racemosa

90 on different substrates such as varying shoot densities of *Posidonia oceanica* (L.)

91 Delile meadows (Ceccherelli et al., 2000) or different types (encrusting, filamentous,

92 and erect) of vegetation layers (Ceccherelli et al., 2002). However, the extent to which

93 biotic and abiotic interactions influence the spread of the alga is not fully understood,

94 although there are some relevant efforts (e.g., Bulleri and Benedetti-Cecchi, 2008). So

95	far, there is no comparative study investigating the relative vulnerability of the main
96	Mediterranean habitat types to C. racemosa invasion. To provide such insight, in the
97	present study we investigated the relative vulnerability of a variety of habitat types to
98	C. racemosa, in one of the sites of its first appearance in the early 90's (Laganas Bay,
99	Zakynthos Island, Ionian Sea). Special focus was given on various substrate types
100	within fragmented Posidonia oceanica meadows. Hereafter, vulnerability is defined
101	as the susceptibility to the introduction, establishment and spatial spread of the
102	invader, i.e. how easily it may attain high densities.
103	
104	Until lately Marine Protected Areas (MPAs) were established to protect biodiversity
105	via the complete removal of human exploitation and other activities, and thus were
106	intended to be "islands" of nature and tranquility in a sea of hostile environment
107	(Simberloff 2000; Boudouresque et al. 2005). However, in many cases MPAs have
108	not been able to stop or limit the expansion of invasive alien species. For example, the
109	boundaries of many northwestern Mediterranean marine parks offered no protection
110	to the invasion of the green alga Caulerpa taxifolia, once it was present along
111	neighboring coasts (Meinesz 1999). International shipping is usually prohibited in
112	MPAs but recreational or small fishing boats could equally well be the vectors of
113	alien species introductions. Indeed an assessment of the importance of recreational
114	boating carried out in 100 yachts in Scotland has confirmed that boating must be
115	considered as a high risk vector for non-native species (Ashton et al. 2006). The
116	spreading of both Caulerpa racemosa and C. taxifolia in the western Mediterranean
117	was facilitated by fishing activity, in particular by bottom trawlers and trammel nets
118	(Relini et al. 2000; Magri et al 2001). Restrictive measures on the activities of
119	recreational and fishing boats within MPAs might have a positive effect by

120	decelerating the invasion rates of some alien macrophytes. Another aim of this study
121	was to investigate whether protection measures within an MPA (the National Marine
122	Park of Zakynthos) had any effect on C. racemosa spread.
123	
124	Specifically, we tested the following hypotheses:
125	1. Various habitat types have different vulnerability to the invasive alga <i>C</i> .
126	racemosa.
127	2. Within fragmented <i>Posidonia oceanica</i> meadows vulnerability differs among
128	structural substrate types such as the meadow margin and gaps of various sizes
129	without alive <i>P. oceanica</i> .
130	3. Protection measures in MPAs, especially restrictions on recreational boating
131	and fishing activities, effectively restrain the expansion of C. racemosa.
132	For all the points above we aimed to quantify the potential differences among
133	habitats/substrate types and management zones by appropriately modelling the
134	frond density of C. racemosa.
135	
136	
137	2. Materials and Methods
138	
139	2.1 Study area
140	
141	The survey was conducted in the National Marine Park of Zakynthos (NMPZ) (Fig.
142	1). The bay of Laganas in Zakynthos Isl. hosts the most important known nesting
143	aggregation of the endangered loggerhead sea turtle, Caretta caretta (Linnaeus,

144 1758), in the Mediterranean. NMPZ was founded in 1999, with the protection of the
145 critical nesting habitat of the loggerhead sea turtle being its main objective.
146

147 Within the marine area of the NMPZ there are three main management zones (A, B, 148 C) in Laganas Bay and a buffer zone (Ia) (Fig. 1). In Zone A no recreational boat 149 activity is allowed, in Zone B boats are allowed to enter with a speed limit of 6 knots 150 but anchoring is forbidden, and in Zone C boats are allowed to travel with a speed 151 limit of 6 knots and also to anchor. Commercial fishing using mobile gear and 152 recreational fishing is prohibited in all zones (including the buffer zone) and 153 commercial fishing using static gears is prohibited in Zone A from the beginning of 154 May until the end of October. The management zones do not conform to some 155 specific features of the marine environment, but they were established almost 156 exclusively on criteria regarding undisturbed approach of turtles to the nesting 157 beaches. The three management zones and the buffer zone provide a quasi-158 experimental setting of varying level of protection (from very low in Ia to high in zone A), which was exploited in this study to test our third hypothesis. 159

160

161 *2.2 Field work*

162

Field work was conducted during the first fortnight of October 2009. Two
independent surveys were conducted. The aim of the first survey was to assess
vulnerability of all main habitat types of the survey area, while the second survey
focused on *Posidonia oceanica* beds, specifically on the relative vulnerability of
different substrate types within fragmented meadows. Fragmented meadows are
defined as those where the continuity of the meadow is interrupted by gaps of various

sizes without alive *P. oceanica* (mentioned as 'patches' hereafter), which could be
either sandy or 'matte morte' areas, i.e. zones of fibrous remnants (dead rhizomes) of
a former *P. oceanica* bed.

172

In the first survey, three 50-m line transects were surveyed with SCUBA diving in 173 each of 23 sites. The selection of the 23 sites was based on the following 174 requirements: (1) good spatial coverage of the study area; (2) representative samples 175 176 on all major habitat types of the study area; (3) narrow range of surveyed depths. The 177 latter requirement was to avoid adding depth as an extra covariate, as there is an 178 important bathymetry-related variation of C. racemosa density (Salomidi et al., 2009), 179 and also for logistical reasons for diving. Thus, all measurements were conducted at depths between 5 and 13 m. The above restrictions caused a non-uniform spatial 180 181 distribution of the sampling sites in the study area. Specifically, the central regions of zones B and Ia were not sampled as they were generally deep (reaching 70 m in zone 182 183 Ia), while the shallow regions (north part of zone B) had exclusively sandy bottoms 184 (all other habitat/substrate types were absent).

185

The line transects were defined with a nylon line, marked with water-resistant numbered signs every five meters, that was deployed using a diving reel. After deploying each line transect, the number of *C. racemosa* fronds within a 20x20 cm quadrat was counted at each sign, i.e. eleven measurements were conducted along each line. For each quadrat, the habitat type was also logged. Five different habitat types were identified: unvegetated sandy bottoms (S); *Posidonia oceanica* meadows (PO); 'matte morte' (MM); margins of *P. oceanica* meadows, usually with sandy

193	bottoms or 'matte morte' (PM); and rocky bottoms (R). Although, PM is strictly not a
194	separate 'habitat type' than PO, we catachrestically use this terminology hereafter.
195	
196	In the second survey, the number of C. racemosa fronds within 20x20 cm quadrats
197	was measured in a total of 44 patches distributed in 11 sites (Fig. 1), where
198	fragmented P. oceanica meadows was the dominant ecotope. In each site, a 200-m
199	line was deployed defining a straight line transect. When the line crossed a patch,
200	frond measurements were conducted in six locations along the line, representing three
201	different substrate types: at the two intersections of the patch margin and the line
202	(PM), within the <i>P. oceanica</i> meadow at a 2 m distance from the margin of the patch
203	(PO), and in two randomly chosen spots within the patch (Pa) (Fig. 2). The size of the
204	patch, defined as its maximum dimension (in m), was also recorded.
205	
206	2.3 Modelling frond counts
207	
208	Some distinctive features of data collected on the abundance of organisms (count
209	data) are: (i) the tendency to contain many zero values (zero-inflated dataset); (ii)
210	overdispersion, defined as the extra variation, which is not explained by the Poisson
211	distribution alone; (iii) heterogeneity of variances (where the variance of the

212 distribution of the response variable changes with explanatory variables). Failure to

213 account for these issues will cause bias in parameter estimations and the associated

214 measures of uncertainty, can reduce the capability to detect relationships, or even lead

to incorrect inference (Martin et al., 2005; Stasinopoulos and Rigby, 2007).

217	Herein, generalized additive models for location, scale and shape (GAMLSS; Rigby
218	and Stasinopoulos, 2005) were applied to effectively confront the abovementioned
219	issues. GAMLSS are regression type models that overcome many of the limitations
220	associated with the popular generalized linear models (GLM; McCullagh and Nedler,
221	1989) and generalized additive models (GAM; Hastie and Tibshirani, 1990). In
222	GAMLSS the exponential family distribution assumption for the response variable is
223	relaxed and replaced by a general distribution family, and the systematic part of the
224	model is expanded to allow modelling not only of the mean (or location) but also
225	other parameters of the distribution (Stasinopoulos and Rigby, 2007). For fitting the
226	models, the gamlss package (Stasinopoulos and Rigby, 2007) was used in R v.2.8.0
227	(R Development Core Team 2008).
228	
229	Inference was based on the information theory approach (Burnham and Anderson,
230	2002), i.e. an integrated process of <i>a priori</i> specification of a set of candidate models,

231 model selection based on the principle of parsimony according to Akaike's

information criterion (AIC; Akaike, 1973), and the estimation of parameters and theirprecision.

234

For data collected in the first survey, two categorical variables, habitat type (*habitat*) and the corresponding management zone of the NMPZ (*zone*) were used as potential predictor variables of the *C. racemosa* frond counts. Seven different GAMLSS, g_i , i =0 to 6, were fitted (Table 1). Either only the mean response (models g_1-g_3) or both the mean response and the standard deviation (models g_4-g_6) were modelled, with one or both predictor variables, i.e. in models g_1-g_3 the standard deviation was assumed

241	constant, while in g_4 - g_6 dependent on the predictor variables. Model g_0 was the null
242	model, with no predictor variable, while g_6 was the full model.
243	
244	To identify the best underlying distribution of the response variable, six potential
245	distributions were compared: Poisson, negative binomial (Anscombe, 1950), zero-
246	inflated Poisson (Lambert, 1992), Poisson-inverse Gaussian (Dean et al., 1989),
247	Sichel (Rigby et al., 2008), and Delaporte (Rigby et al., 2008). Comparisons among
248	different error distributions were based on the full model (g_6) , and selection was based
249	on AIC.
250	
251	The AIC differences, $\Delta_i = AIC_i - AIC_{min}$, were computed over all candidate models.
252	Models with $\Delta_i > 10$ had essentially no support and could be omitted from further
253	consideration, while all models with $\Delta_i < 2$ had substantial support (Burnham and
254	Anderson 2002). To quantify the plausibility of each model, given the data and set of
255	six models, the 'Akaike weight' w_i of each model was calculated, where
256	$w_i = \exp(-0.5\Delta_i) / \sum_j \exp(-0.5\Delta_j)$. The 'Akaike weight' is considered as the weight of
257	evidence in favour of model <i>i</i> being the actual best model of the available set of
258	models (Akaike, 1983; Buckland et al., 1997; Burnham and Anderson, 2002).
259	Estimates of the relative importance of predictor variables <i>j</i> was made by summing
260	the Akaike weights across all the models in the set where each variable occurs $[w_+(j)]$;
261	the larger the sum of Akaike weights the more important that variable is, relative to
262	the other variables (Burnham and Anderson, 2002).
263	

For data collected in patches within *P. oceanica* meadows (second survey), two
potential predictor variables were included in the candidate models, patch size (*size*),

266	which was a continuous variable, and the location of the sampled quadrat in the region
267	of the patch (location). Location was a categorical variable with three levels (Pa, PM,
268	and PO) (Fig. 2). Seven different GAMLSS, h_i , $i = 0$ to 6, were fitted (Table 2). Either
269	only the mean response (models h_1 – h_3) or both the mean response and the standard
270	deviation (models h_4 - h_6) were modelled, with one or both predictor variables. Model
271	h_0 was the null model, with no predictor variable, while h_6 was the full model. The
272	same approach as with the data of the first survey was followed for the identification
273	of the best underlying statistical distribution and for model selection.
274	
275	
276	3. Results
277	
278	3.1 Vulnerability of habitat types (Survey 1)
279	
280	Among the six tested distributions, negative binomial gave the lowest AIC and was
281	selected as the underlying distribution for modeling the counts of C. racemosa fronds
282	(Table 3). The Delaporte distribution also had substantial support by the data with
283	only 1.9 units higher AIC score, while all other distributional assumptions were not
284	supported ($\Delta_i >> 10$).
285	
286	The best models of the expected number of <i>C</i> . <i>racemosa</i> fronds were g_4 ($w_4 = 49.7\%$)
287	and $g_6 (w_6 = 50.3\%)$ with almost equal support, while all other models had essentially
288	no support ($\Delta_i >> 10$). The habitat type was more important as predictor variable of <i>C</i> .
289	<i>racemosa</i> frond counts $[w_+(habitat) = 1.00]$ than zone $[w_+(zone) = 0.50]$. Model g_4
290	was nested within g_6 (full model), and their only difference was in the inclusion of

291	<i>zone</i> in g_6 . In relation to habitat type (<i>habitat</i>) the output of the two models did not
292	differ, and thus only g_6 is presented herein (Fig. 3). Models that considered constant
293	variance (g_0-g_3) had essentially no support $(\Delta_i >> 10)$ indicating that heterogeneity of
294	variances could not be ignored in our case. As assessed by normal QQ-plots (plots of
295	the quantiles of the normal distribution against the distribution of the residuals), the
296	normalized residuals of model g_6 behaved well, while in model g_3 , which is the same
297	as g_6 for the mean response but did not include standard deviation modelling, the
298	residuals deviated from the normal distribution (Figure 4).
299	
300	C. racemosa was found in 245 of the 748 quadrats that were sampled (33%). The
301	probability of presence within a randomly placed 20 x 20 cm quadrat was 83% in
302	MM, 69% in R, 86% in PM, 10% in S, and 6% in PO. The frond density was the
303	highest on matte morte and rocky bottoms (mostly rocky reefs with photophilic
304	macroalgal assemblages, dominated by Cystoseira spp.) and the lowest within P.
305	oceanica meadows (Fig. 3; Table 4). C. racemosa was completely absent in
306	unfragmented robust <i>P. oceanica</i> beds, and was only recorded in a few spots of low <i>P</i> .
307	oceanica density in fragmented meadows. On the margins of P. oceanica meadows,
308	intermediate C. racemosa densities were observed. On sandy bottoms C. racemosa
309	density was generally low and highly variable (Fig. 3). Similar values of frond density
310	were observed in the three management zones of the NMPZ (A, B, and C), while a
311	slightly lower mean value was observed in the buffer zone Ia (Fig. 3; Table 4).
312	
313	3.2 Vulnerability of fragmented P. oceanica meadows (Survey 2)

315	Among the six tested distributions, negative binomial gave the lowest AIC and was
316	selected as the underlying distribution for modeling the counts of C. racemosa fronds
317	(Table 3). The Delaporte distribution also had substantial support, the Sichel
318	distribution had substantially less support, while all other distributional assumptions
319	were not supported ($\Delta_i >> 10$).
320	
321	The best model of the expected number of C. racemosa fronds in the region of
322	patches within <i>P.oceanica</i> meadows was h_4 ($w_4 = 59.6\%$) (Table 2). Model h_6 also

had substantial support ($w_6 = 23.0\%$), and models h_1 and h_3 had essentially less

324 support. The other models were not supported by the data ($\Delta_i >>10$). Location was

325 more important as a predictor variable of *C. racemosa* frond counts $[w_+(location) =$

326 1.00] than patch size $[w_+(size) = 0.33]$. Only model h_4 is presented herein; in h_6 size

327 was included as an additional variable but it was not significant either for the mean (p

328 = 0.22) or for the standard deviation (p = 0.72), thus h_6 did not provide any additional 329 information and was not investigated further. Models that assumed constant variance

330 (g_0-g_3) had less support $[w_+(g_0-g_3) = 17.4\%]$ than models assuming heterogeneous 331 variances $[w_+(g_4-g_6) = 82.6\%]$. Model h_4 provided a good absolute fit, as assessed by 332 the Q-Q plot and the distribution of normalized residuals.

333

C. racemosa was present in 50% of the quadrats in PM, 19.3% of those in Pa, and
only 4.5% of those in PO. The frequency of presence of the alga in PM was
significantly higher than the frequency of presence in Pa (chi-square test, p < 0.001).
The frond density in Pa (2.0–8.5 fronds in 20 x 20 cm quadrats; 95% CI) was not
significantly different (p = 0.19) than the frond density in PM (4.7–11.3 fronds) but
was significantly higher (p < 0.001) than the frond density in PO (0.03–0.32 fronds)

340	(Fig. 5). Conditional on presence, the counts of C. racemosa fronds did not differ
341	between Pa (7.8–12.9 fronds) and PM (9.4–13.3 fronds) but were significantly lower
342	in PO (1.1-3.3 fronds) (95% Tukey test, based on log-transformed counts to
343	homogenize variances).
344	
345	
346	4. Discussion
347	
348	The habitat types investigated were found to have markedly different vulnerabilities to
349	the Caulerpa racemosa invasion. The highest frond densities were observed in matte
350	morte and rocky habitat types, indicating their high vulnerability. On sandy/muddy
351	bottoms the frond density was substantially lower indicating lower vulnerability of
352	this habitat type, especially in unstable soft substrata. Similar qualitative observations
353	have been reported elsewhere, e.g. at Marseilles, dense C. racemosa meadows have
354	colonized matte morte areas and coarse sediment but the sandy bottoms were only
355	poorly colonized by few stolons (Ruitton et al., 2005). Under certain conditions, C.
356	racemosa may form compact dense mats on soft bottoms but such mats seem to
357	mostly occur in matte morte zones (Argyrou et al., 1999; Ruitton et al., 2005) or areas
358	where native meadows pre-existed, e.g. in Caulerpa prolifera beds (S.K., pers. obs.),
359	and not in previously unvegetated sandy/muddy bottoms.
360	
361	Probability of <i>C. racemosa</i> presence in <i>P. oceanica</i> meadows was low and the alga
362	was mostly restricted in the narrow margins of the seagrass meadows and in gaps

364 density was high in the meadow margins and in patches, while it abruptly declined to

363

within fragmented meadows. As demonstrated by this study, C. racemosa average

365	practically zero within the meadow at a short distance from the margin. Thus, in
366	fragmented seagrass meadows, the sandy or matte morte patches represent the spots of
367	high vulnerability to C. racemosa invasion. As indicated by the significantly higher
368	probability of C. racemosa presence in PM than in Pa locations, the margins of
369	patches represent the preferable location within a fragmented meadow for the
370	successful establishment of the alga. Other studies have indicated that both the
371	vertical and horizontal algal growth is negatively influenced by seagrass density, and
372	dense and healthy P. oceanica meadows represent a barrier to the colonization of C.
373	racemosa (Ceccherelli et al., 2000; Klein and Verlaque, 2008).
374	
375	The above results seem to be partly due to the dispersal mechanism of the species by
376	fragmentation, which is one of the main reasons for the fast spread of C. racemosa in
377	the Mediterranean. Fragments of the species, produced by either natural or
378	anthropogenic (fishing gear, anchoring) processes, have to stabilize for some time on
379	the substrate in order to get firmly anchored with their rhizoids and become resistant
380	to hydrodynamic forces. Once anchored, the stolons will elongate and the clone will
381	quickly expand locally. Matte morte, rocky habitats, and the margins of P. oceanica
382	meadows provide appropriate substrates with many overhangs and other spots of easy
383	attachment of algal fragments, contrary to sandy/muddy substrates. For example,
384	fragments drifting by waves or currents will easily be brought to a halt when they
385	reach the margin of a sea grass meadow as they will get entangled to sea grass
386	rhizomes or leaves. Similarly, on sandy/muddy bottoms it is not uncommon to
387	observe C. racemosa fragments attached to small 'hard' objects such as marine litter
388	or sponge colonies, while the alga is completely absent from everywhere else in the
389	surrounding soft bottom (SK, pers. obs.). Such hard objects probably act as anchoring

390 points of drifting *C. racemosa* fragments. We assume that this mechanism of

391 attachment of algal fragments is the cause of a substantial part of the variation of *C*.

392 *racemosa* frond density among habitat/substrate types.

393

394 In seagrass beds that are not in a good state (high fragmentation, large areas of matte morte, low shoot density) vulnerability to C. racemosa invasion would be higher. 395 Scars created by anchoring in seagrass beds will also favour the distributional 396 397 expansion of the alga. It has been demonstrated that boat anchoring has a destructive 398 impact on seagrass meadows destroying many shoots and creating scars that can take 399 a long-time to be re-colonized, especially in meadows of slow growth seagrass species 400 such as P. oceanica (Francour et al., 1999; Milazzo et al., 2004; Ceccherelli et al., 401 2007; Montefalcone et al., 2008). Thus, anchoring in *P. oceanica* beds creates 402 favourable microhabitats for the settlement and expansion of C. racemosa. In this respect, a ban of anchoring in seagrass beds, apart from being a management measure 403 for the protection of the meadow, is a measure against the further distributional 404 405 expansion of C. racemosa.

406

407 Fishing, especially with mobile gears, such as otter trawls and boat seines, but also 408 with trammel nets, substantially contributes to the spread of *Caulerpa* spp (Relini et 409 al. 2000; Magri et al 2001). Fragments of the species are collected by fishing gear and 410 then discarded by fishermen together with all by-catch and debris, sometimes far from 411 the fishing site. In a similar way recreational boats may assist the dispersion of C. 412 racemosa by fragmenting its stolons during anchoring and even transferring such 413 fragments to the surface seawater layers from where longer dispersion is likely. 414 Currents may further disperse the fragments created by fishing gear or anchoring and

415 the alga may settle and get established in a very distant location. Even in zones of 416 absolute protection within MPAs, where both fishing and anchoring are prohibited, 417 such fragments may arrive with currents from neighbouring sites with no such 418 restrictions. In addition, the ability of *C. racemosa* to reproduce sexually renders any 419 protection measures in MPAs inefficient to prevent the introduction of the species 420 from other locations.

421

422 Commercial fishing with nets is allowed in all management zones of NMPZ and in all 423 neighbouring areas with only a six-month ban in zone A; anchoring is permitted 424 within zone C. Due to the existence of the marine park and the developed eco-touristic 425 industry focusing on turtle-watching, there is an increased number of recreational boats sailing in zones B and C and anchoring in zone C. As NMPZ is a semi-closed 426 427 bay, C. racemosa fragments that are produced within any of the protection zones are likely to remain within the boundaries of NMPZ. Thus, the role of fishing gear and 428 429 recreational boats to the further spread of the species in NMPZ cannot be avoided by 430 the existing protection measures. The operation of NMPZ for the last eleven years did 431 not seem to decelerate the spread of C. racemosa in Laganas Bay. On the contrary, the 432 species is found in the NMPZ with very high probabilities of presence within 433 randomly placed 20 x 20 cm quadrats on matte morte areas, rocky bottoms, and the margins of *P. oceanica* meadows. For the reasons stated above (role of fishing gear 434 435 and anchoring, ability of sexual reproduction, further expansion of existing stolons) 436 no direct effect of the protection measures to the spread of the species is anticipated in 437 the future, unless the protection measures will prove effective to improve the status of 438 P. oceanica meadows within NMPZ (mainly because of the ban of anchoring and use of mobile fishing gear) and thus reduce favourable microhabitats, such as patches 439

within meadows. However, the process of sea grass recovery is very slow and no
short-term effects are likely. If the management measures prove ineffective to protect
the *P. oceanica* meadows in the park and fragmentation increases in the future, *C. racemosa* will further spread covering all new matte morte areas.

444

Although the vulnerability of seagrass meadows to C. racemosa has been sufficiently 445 investigated, there is a lack of knowledge on the vulnerability of rocky bottoms. The 446 type of macroalgal assemblages (turf, encrusting, and erect) and the number of algal 447 448 species seem to affect the C. racemosa invasion, with substrates dominated by turfing 449 algae being more vulnerable (Ceccherelli et al., 2002). Turfs probably physically 450 assist the settlement of C. racemosa by entrapment of fragments of the alga and/or 451 enhancing the anchoring of stolons (Bulleri and Benedetti-Cecchi, 2008). However, 452 the extent of the invasion of C. racemosa on rocky bottoms, the invasion rates, impacts to and competition with the benthic fauna, and the factors that favour 453 454 successful settlement and high densities are issues that need further investigation. As 455 found in this study, but also based on our personal observations in other areas of the Ionian and the Aegean Sea, the extent of C. racemosa invasion on rocky habitats is 456 457 dramatic and the consequences largely unknown.

458

In conclusion: (1) we verified that vulnerability to *C. racemosa* invasion changes with
habitat and the most vulnerable habitat/substrate types are matte morte areas, the
margins of *P. oceanica* meadows, and rocky bottoms; (2) within fragmented *Posidonia oceanica* meadows vulnerability differs among structural substrate types
and is higher along the margins of patches with no apparent dependence on patch size;

464	and (3) the boundaries of the NMPZ do not seem to offer any protection against C .
465	racemosa invasion, which is explained by the dispersal mechanism of the species.
466	
467	
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- 630

631 Figure captions

632

Fig. 1: Map of the study area. The sampling sites and the protection zones of theNational Marine Park of Zakynthos are indicated.

635

636 Fig. 2: Location (representing three different substrate types) of *C. racemosa* frond

637 measurements within patches in fragmented *P. oceanica* meadows. Quadrats were

638 placed at the two intersections of the patch margin and the line (PM), within the P.

639 *oceanica* meadow at a 2 m distance from the margin of the patch (PO), and in two

- 640 randomly chosen spots within the patch (Pa).
- 641

642 Fig 3: Estimated values of the two categorical variables (*habitat type* and *zone*) for

643 model g_6 of *C. racemosa* frond counts within 20 x 20 cm quadrats. Graphs of the

644 mean response are given in the top panel and graphs of the standard deviation in the

bottom panel. Values are given in the response (log) scale and the corresponding 95%

646 confidence intervals are indicated with dotted lines. MM: 'matte morte'; PM: margins

647 of *P. oceanica* meadows; PO: *Posidonia oceanica* meadows; R: rocky bottoms; S:

648 unvegetated sandy bottoms.

649

Fig. 4: Normal QQ plots for models g_6 (full model) and g_3 .

651

Fig. 5: Estimated mean response and standard deviation of *C. racemosa* frond counts in 20 x 20 cm quadrats in relation to the levels of the categorical predictor variable *location*, based on model h_4 . Values are given in the response (log) scale and the

- 655 corresponding 95% confidence intervals are indicated with dotted lines. The three
- 656 levels of the predictor variable are defined in Fig. 2.
- 657

Model	Modeled distribution parameters	Predictor variables	df	AIC	Δ_{i}	$w_{i}\left(\%\right)$
g_0	-	Null	2	2748.19	462.82	0.0
<i>g</i> 1	μ	habitat	6	2440.25	154.88	0.0
g_2	μ	zone	5	2744.40	459.03	0.0
<i>g</i> ₃	μ	habitat + zone	9	2441.58	156.21	0.0
g_4	μ, σ	habitat	10	2285.39	0.03	49.7
g 5	μ, σ	zone	8	2712.07	426.70	0.0
g_6	μ, σ	habitat + zone	16	2285.37	0.00	50.3

Table 1: Survey 1: Summary of the parameterisation of the seven candidate models g_i of the counts of *C. racemosa* fronds in 20 x 20 cm plots.

For each model, the Akaike Information Criterion AIC, Akaike differences Δ_i , Akaike weights w_i , and degrees of freedom (df) are given. Models with substantial support ($\Delta_i < 2$) are given in bold. μ , σ are the mean and the standard deviation of the distribution of the response variable.

Table 2: Survey 2: Summary of the parameterisation of the seven candidate models <i>hi</i>
of the counts of C. racemosa fronds in 20 x 20 cm plots in the second survey (patches
in <i>P. oceanica</i> meadows).

Model	Modeled distribution parameters	Predictor variables	df	AIC	Δ_{i}	w _i (%)
h_0	-	Null	2	825.01	56.21	0.0
h_1	μ	location	4	772.92	4.12	7.6
h_2	μ	size	3	826.80	58.00	0.0
h_3	μ	location + size	5	772.41	3.61	9.8
h_4	μ, σ	location	6	768.80	0.00	59.6
h_5	μ, σ	size	4	828.21	59.41	0.0
h_6	μ, σ	location + size	8	770.71	1.91	23.0

For each model, the Akaike Information Criterion AIC, Akaike differences Δ_i , Akaike weights w_i , and degrees of freedom (df) are given. Models with substantial support ($\Delta_i < 2$) are given in bold. μ , σ are the mean and the standard deviation of the distribution of the response variable.

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Table 3: Comparisons among different error distributions of the response variable (count of *C. racemosa* fronds in 20 x 20 cm quadrats), based on the full models (g_6 for survey 1 and h_6 for survey 2).

Model comparisons based on g₆

Distribution	df	AIC
Negative Binomial	16	2285.4
Delaporte	17	2287.3
Sichel	17	2336.4
Poisson-inverse Gaussian	16	2415.8
Zero Inflated Poisson	16	3083.9
Poisson	8	5067.3

Model comparisons based on h₆

Distribution	df	AIC
Negative Binomial	8	770.7
Delaporte	9	772.8
Sichel	9	778.0
Poisson-inverse Gaussian	8	839.8
Zero Inflated Poisson	8	916.8
Poisson	4	2249.2

Table 4: Survey 1: Expected	counts of <i>C. racemosa</i>	fronds in 20 x 20 cm	ı quadrats, as
predicted by model g6.			

habitat type	zone A	zone B	zone C	zone Ia
MM	13.5	14.1	12.4	7.9
	(9.1-20.1)	(10.7-18.6)	(7.7-19.7)	(5.0-12.3)
PM	5.1	5.3	4.6	2.9
	(3.1-8.2)	(3.2-8.7)	(2.6-8.3)	(1.7-5.2)
PO	0.2	0.2	0.2	0.1
10	(0.1-0.4)	(0.1-0.4)	(0.1-0.4)	(0.1-0.2)
R	10.1	10.5	9.2	5.9
K	(6.7-15.1)	(8.2-13.5)	(5.6-15.0)	(3.9-8.7)
S	1.0	1.1	0.9	0.6
0	(0.3-3.9)	(0.3-3.9)	(0.2-3.7)	(0.2-2.3)

95% confidence intervals are given in parenthesis.

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