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

3

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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 *C. racemosa* 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 *Posidonia oceanica* 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

44

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; Piazzini 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
60 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
64 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
67 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 *C.*
126 *racemosa*.
- 127 2. Within fragmented *Posidonia oceanica* meadows vulnerability differs among
128 structural substrate types such as the meadow margin and gaps of various sizes
129 without alive *P. oceanica*.
- 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
159 zone A), which was exploited in this study to test our third hypothesis.

160

161 2.2 *Field work*

162

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

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

172

173 In the first survey, three 50-m line transects were surveyed with SCUBA diving in
174 each of 23 sites. The selection of the 23 sites was based on the following
175 requirements: (1) good spatial coverage of the study area; (2) representative samples
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
180 depths between 5 and 13 m. The above restrictions caused a non-uniform spatial
181 distribution of the sampling sites in the study area. Specifically, the central regions of
182 zones B and Ia were not sampled as they were generally deep (reaching 70 m in zone
183 Ia), while the shallow regions (north part of zone B) had exclusively sandy bottoms
184 (all other habitat/substrate types were absent).

185

186 The line transects were defined with a nylon line, marked with water-resistant
187 numbered signs every five meters, that was deployed using a diving reel. After
188 deploying each line transect, the number of *C. racemosa* fronds within a 20x20 cm
189 quadrat was counted at each sign, i.e. eleven measurements were conducted along
190 each line. For each quadrat, the habitat type was also logged. Five different habitat
191 types were identified: unvegetated sandy bottoms (S); *Posidonia oceanica* meadows
192 (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 *P. oceanica* 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
215 to incorrect inference (Martin et al., 2005; Stasinopoulos and Rigby, 2007).

216

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 Nelder,
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 *a priori* specification of a set of candidate models,
231 model selection based on the principle of parsimony according to Akaike's
232 information criterion (AIC; Akaike, 1973), and the estimation of parameters and their
233 precision.

234

235 For data collected in the first survey, two categorical variables, habitat type (*habitat*)
236 and the corresponding management zone of the NMPZ (*zone*) were used as potential
237 predictor variables of the *C. racemosa* frond counts. Seven different GAMLSS, g_i , $i =$
238 0 to 6, were fitted (Table 1). Either only the mean response (models g_1 – g_3) or both the
239 mean response and the standard deviation (models g_4 – g_6) were modelled, with one or
240 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 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 j 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

264 For data collected in patches within *P. oceanica* meadows (second survey), two

265 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 ($\Delta_i \gg 10$).

285

286 The best models of the expected number of *C. racemosa* 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 ($\Delta_i \gg 10$). The habitat type was more important as predictor variable of *C.*
289 *racemosa* 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 zone in g_6 . In relation to habitat type (*habitat*) 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 ($\Delta_i \gg 10$) 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 *P. oceanica* beds, and was only recorded in a few spots of low *P.*
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)*

314

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 ($\Delta_i \gg 10$).

320

321 The best model of the expected number of *C. racemosa* fronds in the region of
322 patches within *P. oceanica* meadows was h_4 ($w_4 = 59.6\%$) (Table 2). Model h_6 also
323 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 ($\Delta_i \gg 10$). 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

334 *C. racemosa* was present in 50% of the quadrats in PM, 19.3% of those in Pa, and
335 only 4.5% of those in PO. The frequency of presence of the alga in PM was
336 significantly higher than the frequency of presence in Pa (chi-square test, $p < 0.001$).
337 The frond density in Pa (2.0–8.5 fronds in 20 x 20 cm quadrats; 95% CI) was not
338 significantly different ($p = 0.19$) than the frond density in PM (4.7–11.3 fronds) but
339 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 *C. racemosa* presence in *P. oceanica* meadows was low and the alga
362 was mostly restricted in the narrow margins of the seagrass meadows and in gaps
363 within fragmented meadows. As demonstrated by this study, *C. racemosa* average
364 density was high in the meadow margins and in patches, while it abruptly declined to

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
395 morte, low shoot density) vulnerability to *C. racemosa* invasion would be higher.
396 Scars created by anchoring in seagrass beds will also favour the distributional
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
403 respect, a ban of anchoring in seagrass beds, apart from being a management measure
404 for the protection of the meadow, is a measure against the further distributional
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
426 boats sailing in zones B and C and anchoring in zone C. As NMPZ is a semi-closed
427 bay, *C. racemosa* fragments that are produced within any of the protection zones are
428 likely to remain within the boundaries of NMPZ. Thus, the role of fishing gear and
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
434 margins of *P. oceanica* meadows. For the reasons stated above (role of fishing gear
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
439 of mobile fishing gear) and thus reduce favourable microhabitats, such as patches

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

444

445 Although the vulnerability of seagrass meadows to *C. racemosa* has been sufficiently
446 investigated, there is a lack of knowledge on the vulnerability of rocky bottoms. The
447 type of macroalgal assemblages (turf, encrusting, and erect) and the number of algal
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,
453 impacts to and competition with the benthic fauna, and the factors that favour
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
456 Ionian and the Aegean Sea, the extent of *C. racemosa* invasion on rocky habitats is
457 dramatic and the consequences largely unknown.

458

459 In conclusion: (1) we verified that vulnerability to *C. racemosa* invasion changes with
460 habitat and the most vulnerable habitat/substrate types are matte morte areas, the
461 margins of *P. oceanica* meadows, and rocky bottoms; (2) within fragmented
462 *Posidonia oceanica* meadows vulnerability differs among structural substrate types
463 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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474

475

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- 629
630

631 **Figure captions**

632

633 **Fig. 1:** Map of the study area. The sampling sites and the protection zones of the

634 National Marine Park of Zakynthos are indicated.

635

636 **Fig. 2:** Location (representing three different substrate types) of *C. racemosa* frond637 measurements within patches in fragmented *P. oceanica* meadows. Quadrats were638 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*) for643 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

645 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

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

651

652 **Fig. 5:** Estimated mean response and standard deviation of *C. racemosa* frond counts

653 in 20 x 20 cm quadrats in relation to the levels of the categorical predictor variable

654 *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

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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.

Model	Modeled distribution parameters	Predictor variables	df	AIC	Δ_i	w_i (%)
g_0	-	Null	2	2748.19	462.82	0.0
g_1	μ	<i>habitat</i>	6	2440.25	154.88	0.0
g_2	μ	<i>zone</i>	5	2744.40	459.03	0.0
g_3	μ	<i>habitat + zone</i>	9	2441.58	156.21	0.0
g_4	μ, σ	<i>habitat</i>	10	2285.39	0.03	49.7
g_5	μ, σ	<i>zone</i>	8	2712.07	426.70	0.0
g_6	μ, σ	<i>habitat + zone</i>	16	2285.37	0.00	50.3

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 h_i of the counts of *C. racemosa* fronds in 20 x 20 cm plots in the second survey (patches in *P. oceanica* 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	<i>location</i>	4	772.92	4.12	7.6
h_2	μ	<i>size</i>	3	826.80	58.00	0.0
h_3	μ	<i>location + size</i>	5	772.41	3.61	9.8
h_4	μ, σ	<i>location</i>	6	768.80	0.00	59.6
h_5	μ, σ	<i>size</i>	4	828.21	59.41	0.0
h_6	μ, σ	<i>location + size</i>	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.

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).

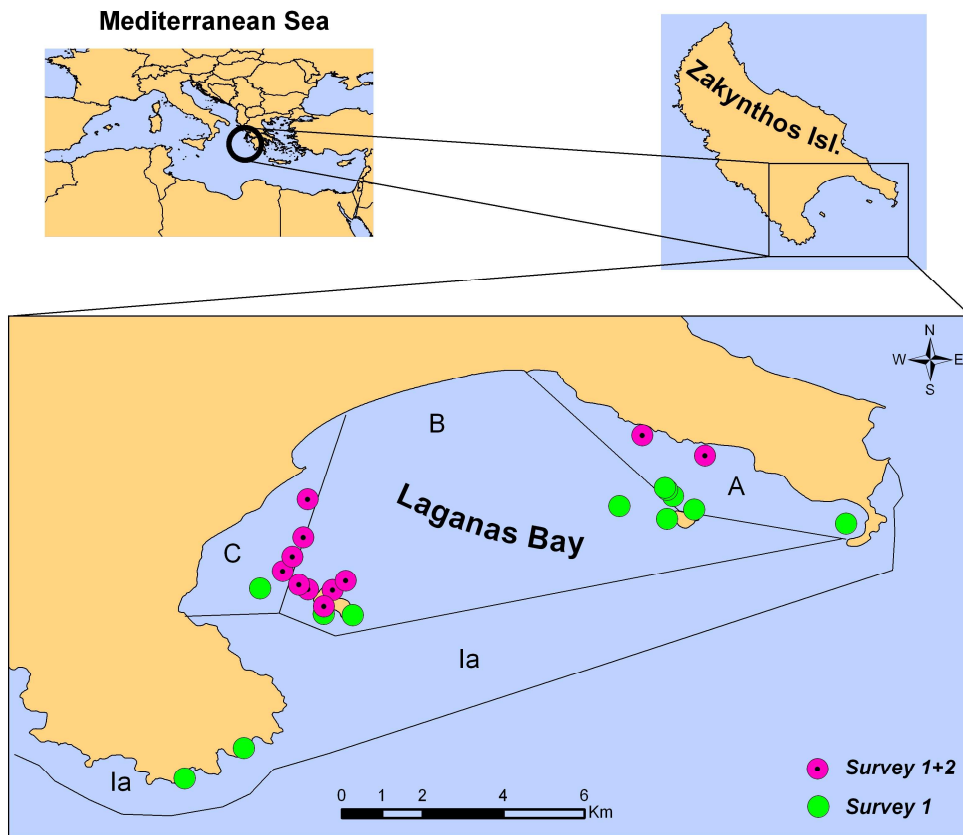
Model comparisons based on g_6		
Distribution	df	AIC
Negative Binomial	16	2285.4
Delaporte	17	2287.3
Sichel	17	2336.4
Poisson-inverse Gaussian	16	2415.8
Zero Inflated Poisson	16	3083.9
Poisson	8	5067.3

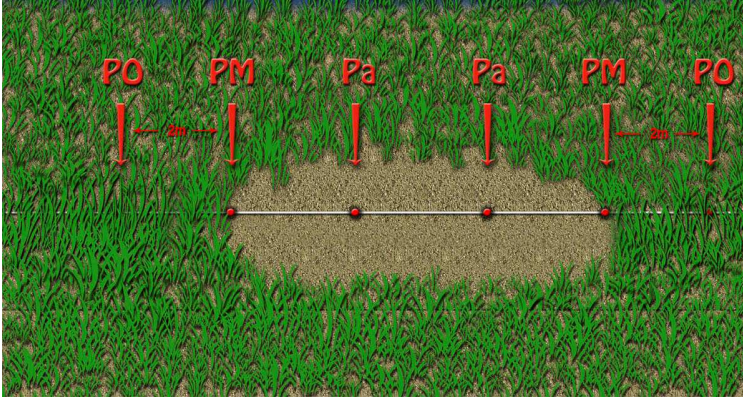
Model comparisons based on h_6		
Distribution	df	AIC
Negative Binomial	8	770.7
Delaporte	9	772.8
Sichel	9	778.0
Poisson-inverse Gaussian	8	839.8
Zero Inflated Poisson	8	916.8
Poisson	4	2249.2

Table 4: Survey 1: Expected counts of *C. racemosa* fronds in 20 x 20 cm quadrats, as predicted by model g_6 .

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

95% confidence intervals are given in parenthesis.

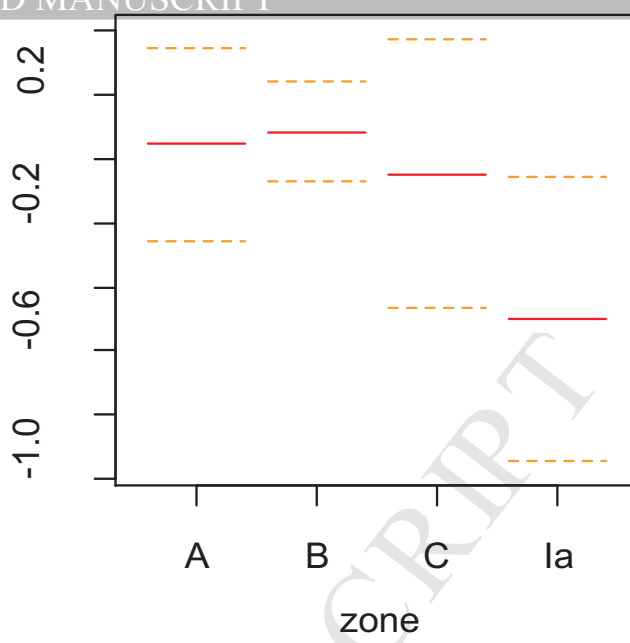
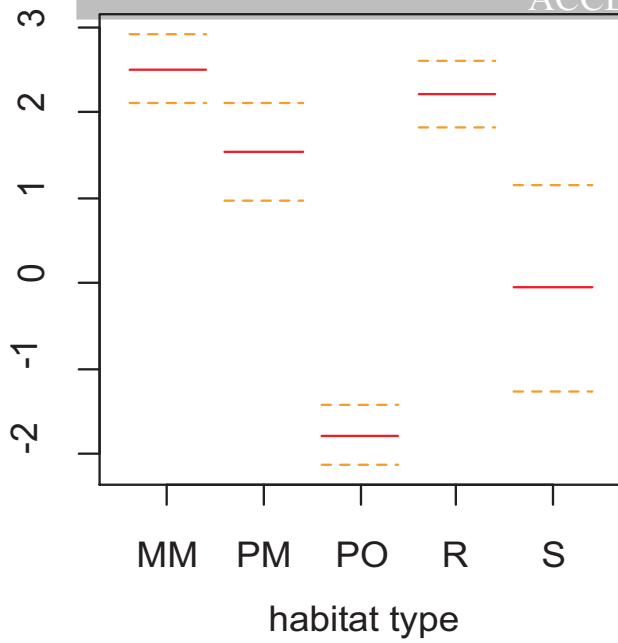




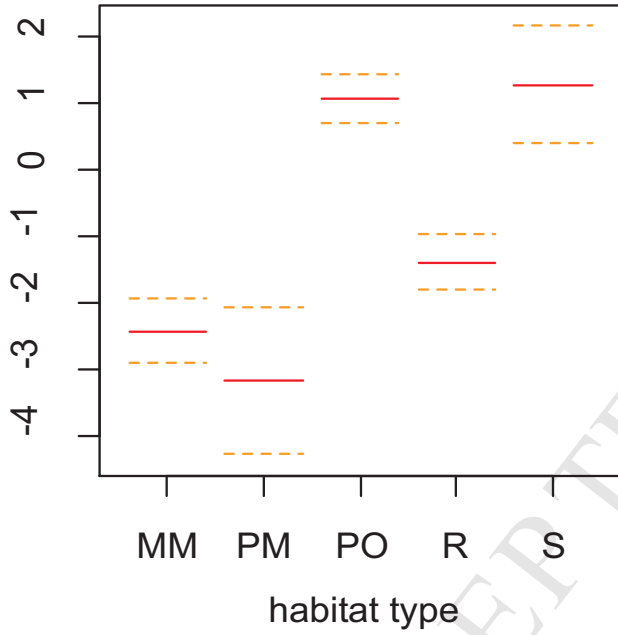
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mean

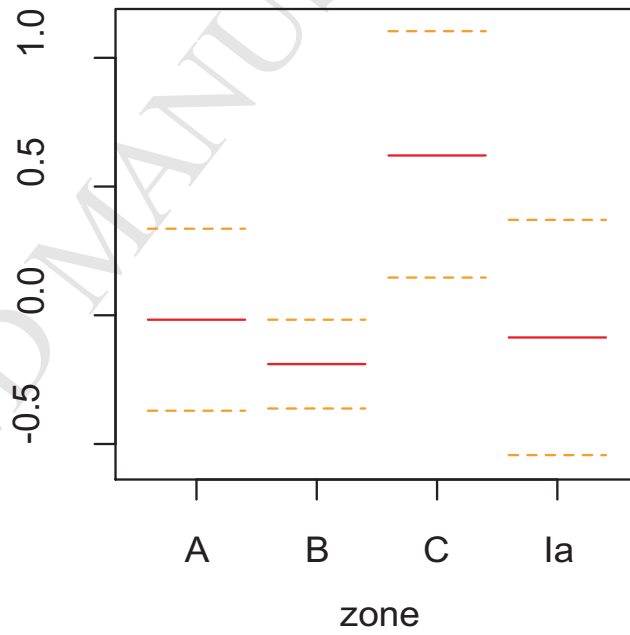
mean



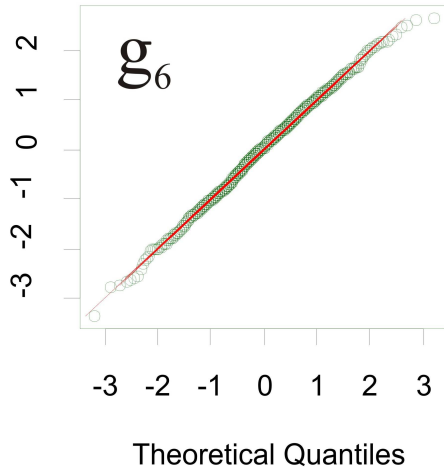
standard deviation



standard deviation



Normal Q-Q Plot



Normal Q-Q Plot

