

Resilience of the seagrass *Posidonia oceanica* following pulse-type disturbance

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Abstract

Understanding the response of species to disturbance and the ability to recover is crucial for preventing their potential collapse and ecosystem phase shifts. Explosive submarine activity, occurring in shallow volcanic vents, can be considered as a natural pulse disturbance, due to its suddenness and high intensity, potentially affecting nearby species and ecosystems. Here, we present the response of *Posidonia oceanica*, a long-lived seagrass, to an exceptional submarine volcanic explosion, which occurred in the Aeolian Archipelago (Italy, Mediterranean Sea) in 2002, and evaluate its resilience in terms of time required to recover after such a pulse event. The study was carried out in 2011 in the sea area off Panarea Island, in the vicinity of Bottaro Island by adopting a back-dating methodological approach, which allowed a retrospective analysis of the growth performance and stable carbon isotopes ($\delta^{13}\text{C}$) in sheaths and rhizomes of *P. oceanica*, during a 10-year period (2001-2010). After the 2002 explosion, a trajectory shift towards decreasing values for both the growth performance and $\delta^{13}\text{C}$ of rhizomes was observed. The decreasing trend reversed in 2004 when recovery took place progressively for all the analysed variables. Full recovery of *P. oceanica* occurred 8 years after the explosive event with complete restoration of all the variables (rhizome growth performance and $\delta^{13}\text{C}$) by 2010. Given the ecological importance of this seagrass in marine coastal ecosystems and its documented large-scale decline, the understanding of its potential recovery in response to environmental changes is imperative.

Keywords: aquatic plant ecology; ecosystem function and service; plant development and life-history

36 traits; CO₂ vent; recovery; perturbation; hydrothermal activity; stable isotope; lepidochronology

37

38 **1. Introduction**

39 The concept of resilience has become of crucial importance for the conservation and protection of
40 natural ecosystems. Resilience is an inherent property of ecosystems determined by the physical
41 components and functional capacity of ecological processes (Stringham *et al.*, 2003). Two different
42 definitions of resilience are commonly adopted nowadays, generally referred to as ecological
43 resilience and engineering resilience. Ecological resilience (or stochastic resilience) is the ability of a
44 system to absorb repeated disturbances and retain the same fundamental structures and functions, thus
45 implying internal reorganization (Holling, 1973). In contrast, engineering resilience (or deterministic
46 resilience), which we deal with in this paper, is defined as the time required by a system to return to its
47 equilibrium state after disturbance (Pimm, 1984). Within the framework of resilience, another
48 ambiguity concerns the distinction between the concepts of disturbance and perturbation. Here, we
49 refer to the term disturbance to indicate an event disrupting ecosystem functioning and/or structure
50 due to an external agent (White and Pickett, 1985), and perturbation as the deviation, or displacement,
51 from the original state of the ecosystem at any level of organization, due to such disturbance (Odum *et al.*,
52 1979). Two main types of disturbance can occur and differently affect ecosystems, i.e. pulse and
53 press disturbance. Pulse disturbances are relatively discrete sudden events of usually short duration
54 (Bengtsson, 2002), expected to produce reversible damages allowing the system to restore the original
55 state (Sheffer *et al.*, 2001). They may be intrinsic of natural ecosystem dynamics and in such cases
56 species affected by pulse disturbances adapt to them, or may be triggered by anthropic activities
57 (Bengtsson, 2002). On the other hand, press disturbances, also known as chronic, are continuous
58 events, often of anthropogenic origin. Under press disturbances, only certain species may be able to
59 adapt and recover after their occurrence (Bengtsson, 2002). Therefore, the characteristics of the
60 disturbance (i.e. intensity, duration, spatial extent, timing and recurrence) affecting an ecosystem are
61 likely to influence its resilience (O'Brien *et al.*, 2018). In particular, the type, frequency and intensity
62 of the disturbance determine the response of the ecosystem (Lake, 2000) potentially including rapid-
63 onset (e.g. disease), chronic changes (e.g. habitat loss) or transitory (e.g. drought) environmental
64 changes (Oliver *et al.*, 2015). Therefore, understanding the responses of ecosystems after disturbance
65 and their ability to recover is critical for preventing potential phase shifts (Chemello *et al.*, 2018), and
66 securing vital ecosystem services, with important implications for biodiversity management (Bunse,
67 2013).

68 Seagrass meadows are key elements of marine coastal environments as they are responsible for the
69 creation and maintenance of valuable ecosystems supporting highly complex and biodiverse climax

70 communities (Mazzella and Buia, 1986; Orth, 1992; Hemminga and Duarte, 2000). Seagrasses, in
71 fact, are habitat-structuring species, providing habitats to many species; they represent a basal organic
72 matter source in complex food webs (Vizzini, 2009) and a long-term store of sedimentary carbon
73 (Fourqurean *et al.*, 2012). Furthermore, they protect the shoreline from erosion and maintain high
74 water quality by reducing sediment re-suspension (Hemminga and Duarte, 2000). Despite their high
75 value, seagrasses have suffered large-scale declines at alarming rates in response to increasing
76 stressors mainly imputable to human activities and the consequent environmental changes they induce
77 (Orth *et al.*, 2006; Waycott *et al.*, 2009; Marbà *et al.*, 2014). All these severe impacts can affect the
78 overall capacity of seagrasses to recover from disturbance; thus, an insight into the recovery process of
79 such declines is crucial. Recovery of seagrass after a disturbance is species/genus-specific and
80 dependent on local environmental conditions, demographic history and the existence of a large and
81 diverse number of genotypes at meadow scale (Salo *et al.*, 2015; Tuya *et al.*, 2018). The capacity to
82 recover is influenced by the availability of sexual or asexual propagules, which includes fast growth
83 rates (Macreadie *et al.*, 2014a), persistence of the rhizomes (Jarvis *et al.*, 2014) and potential transport
84 of propagules (seeds and vegetative fragments) from neighbouring meadows (McMahon *et al.*, 2014;
85 Stafford-Bell *et al.*, 2015). A study conducted on tropical seagrasses in north Queensland (Australia)
86 showed that deep water seagrass species (i.e. *Halophila* spp.) are able to quickly re-colonise after
87 storm events, while shallow species fail to recover mainly because of the lack of seed reserves
88 (Rasheed *et al.*, 2014). It has been argued that, while fast-growing pioneering species of seagrass, such
89 as *Halophila* spp., are relatively quick to respond to disturbances, damages to large slow-growing
90 species, such as the Mediterranean *Posidonia oceanica*, are viewed with particular concern since they
91 rely mainly on vegetative clonal growth and their colonization is likely to occur over centuries
92 (Duarte, 1995; González-Correa *et al.*, 2005). A survey carried out in New South Wales (Australia)
93 demonstrated the slow rate of recovery of a damaged *Posidonia australis* bed that took over 25 years
94 to recolonise an area of 0.4 ha (Meehan and West, 2000). Recovery of *P. oceanica* in an area affected
95 by illegal trawling (SE Spain, Mediterranean Sea) was found to be possible after eliminating the cause
96 of the impact and, given the low rates of vegetative growth, 100 years would have been necessary for
97 full meadow recovery (González-Correa *et al.*, 2005). However, it is evident that the ability of
98 seagrass to recover and the rate of recovery are largely dependent on the nature of the disturbance, its
99 duration and spatial extent (O'Brien *et al.*, 2018).

100 Explosive submarine activity, occurring in shallow volcanic vents, can be considered as a natural
101 pulse disturbance, due to its suddenness and high intensity, potentially affecting seagrass communities
102 due to abrupt changes in the physical and chemical features of seawater and sediments, with possibly
103 large functioning effects (Vizzini *et al.*, 2010). In fact, it has been suggested that shallow submarine

104 volcanic vents may serve as natural laboratories for evaluating biological response to extreme
105 environmental conditions at ecosystem level (Hall-Spencer *et al.*, 2008; Vizzini *et al.*, 2017). Evidence
106 from temporally stable volcanic vents has revealed variations in seagrass abundance, photosynthesis
107 and growth (Hall-Spencer *et al.*, 2008; Apostolaki *et al.*, 2014; Vizzini *et al.*, 2019), even though the
108 results of different studies are contradictory, thus highlighting the complexity of biological responses
109 to naturally altered environmental conditions. A study conducted in the shallow waters of the active
110 volcanic arcs of the Aeolian Islands (Italy, Mediterranean Sea) showed the effects of a sudden and
111 large hydrothermal event on the growth and carbon stable isotope ($\delta^{13}\text{C}$) interannual variations of the
112 seagrass *Posidonia oceanica* (L.) Delile (Vizzini *et al.*, 2010) detecting a reduction in plant
113 productivity. However, while it was possible to measure the resistance to this disturbance through
114 retrospective analysis, the short time frame after the submarine gas explosion examined by Vizzini *et*
115 *al.* (2010) (4 years) did not allow the assessment of the plant's resilience, which thus remains
116 unexplored. Given that this long-lived seagrass is able to store time series data (i.e. several decades) in
117 its tissues concerning functional trait dynamics, plants exposed to a pulse disturbance represent a
118 unique opportunity to gain a better understanding of their recovery/response mechanisms to abrupt
119 environmental changes. For this reason, in this study, we returned to the same hydrothermal vent, ten
120 years after the submarine gas explosion, in order to reconstruct a longer growth profile than that
121 previously studied, evaluate the ability of the plant to recover after such a pulse event and estimate its
122 resilience in terms of time required to return to the equilibrium state after disturbance.

123

124 **2. Materials and Methods**

125 *2.1 Study area and sampling procedure*

126 The study was carried out in July 2011 off the eastern coast of Panarea Island, in the Aeolian
127 Archipelago (Italy, Mediterranean Sea) where several islets are present. Before the explosion, *P.*
128 *oceanica* had been reported as dominant benthic species showing high percentages of covering in the
129 islet area (Acunto *et al.*, 1995; Ministero dell' Ambiente AA.VV 2002).

130 The hydrothermal and geological features of the study area are described in detail in Vizzini *et al.*
131 (2010). In this area, in November 2002, in coincidence with a low magnitude seismic event (Saccorotti
132 *et al.*, 2003), a sudden and huge degassing phenomenon was observed on the sea surface (Fig. 1). The
133 exceptional and unanticipated submarine gas explosion occurred near the islet of Bottaro (Caliro *et al.*,
134 2004) where a crater, c. 20 x 14 m wide and 10 m deep, was formed on the sea bottom (Capaccioni *et*
135 *al.*, 2005) and the most active degassing phase lasted several months (Aliani *et al.*, 2010).

136 In particular, gas emissions (vertical gas flux expressed in L d^{-1}) recorded at Bottaro islet prior to the
137 disturbance (Italiano and Nuccio, 1991) and from November 2002 to April 2004 (Aliani *et al.*, 2010)

138 are summarized in Table 1. In November 2002, the submarine fluid discharges were an emulsion
 139 characterized by a CO₂-dominated continuous gas phase (up to 65,000 mmol/mol) with suspended
 140 sediments, colloidal sulfur, and water condensate micro droplets acidified by dissolution of
 141 compounds such as SO₂ (up to 900 mmol/mol), HCl (up to 13,000 mmol/mol) and HF (up to 170
 142 mmol/mol) (Capaccioni *et al.*, 2007).



144
 145 Fig. 1. Submarine gas explosion recorded near the Islet of Bottaro in
 146 November 2002. Photograph courtesy of the National Institute of
 147 Geophysics and Volcanology (INGV).

148
 149 Table 1. Literature data on vertical gas fluxes (L d⁻¹) at the site of interest due to the
 150 2002 explosive event near the islet of Bottaro from the 1980s to April 2004.

Year	Area	Ascending gas flux (L d ⁻¹)	Reference
1980s	Panarea	0.09 x 10 ⁸	Italiano and Nuccio, 1991
1980s	Bottaro	0.02 x 10 ⁸	Italiano and Nuccio, 1991
November 2002	Bottaro	4.40 x 10 ⁸	Aliani <i>et al.</i> , 2010
December 2002	Bottaro	2.60 x 10 ⁸	Aliani <i>et al.</i> , 2010
September 2003	Bottaro	0.30 x 10 ⁸	Aliani <i>et al.</i> , 2010
December 2003	Bottaro	0.10 x 10 ⁸	Aliani <i>et al.</i> , 2010
April 2004	Bottaro	0.02 x 10 ⁸	Aliani <i>et al.</i> , 2010

151
 152 Two sampling sites were selected at different distance from the crater generated by the explosive
 153 event (Fig. 2). The first one (hereafter disturbed site) was located on the north-western side of Bottaro
 154 islet, a few meters from the new crater; the second site (hereafter control site) was at a distance of
 155 about 1 km from Bottaro islet, on the north-eastern side of Dattilo islet, where hydrothermal activity
 156 was not recorded. Only one control was chosen in the area, since Vizzini *et al.* 2010 detected very low
 157 variability in growth performance between controls in response to disturbance after the underwater

158 explosion. At each site, 20 orthotropic single (unbranched) shoots were haphazardly collected by
 159 SCUBA divers at a depth range of 5-8 m and transported to the laboratory in polyethylene bags for
 160 further analysis.

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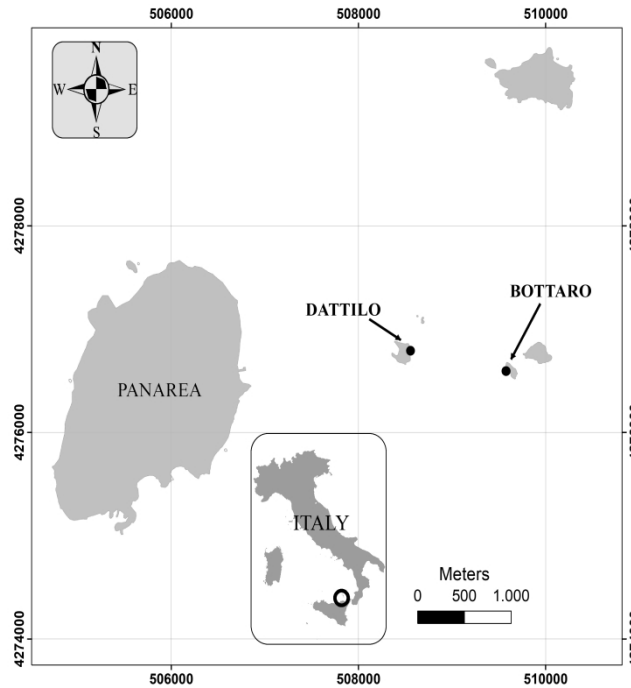


Fig. 2. Study area with sampling sites (●): disturbed site (Bottaro islet) and control site (Dattilo islet).

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165 2.2 *Lepidochronological analysis*

166 Orthotropic rhizomes from the collected shoots were analyzed by lepidochronology (Pergent, 1990) in
 167 order to provide a reliable estimate of seagrass growth performance (annual vertical growth) (Pergent-
 168 Martini *et al.*, 2005). This technique is based on the observation of cyclic variations in the thickness of
 169 *P. oceanica* sheaths and in the isolation of rhizome segments corresponding to a 1-year period
 170 (lepidochronological year). Fragment dating was performed starting from the rhizome apex
 171 (corresponding to the sampling year) downward and by back-dating the sequence of cycles with their
 172 corresponding rhizome fragments. For each segment, the length was measured to estimate the growth
 173 of the rhizomes. Thus, for each orthotropic shoot, the history of growth performance (mm year^{-1}) was
 174 reconstructed.

175

176 2.3 *Isotopic composition*

177 After backdating, isotopic analysis was conducted on a sub sample composed by four orthotropic
 178 shoots collected at each site, since low variability for $\delta^{13}\text{C}$ was previously estimated between shoots at
 179 site level (Vizzini *et al.*, 2010).

180 For each dated rhizome fragment, the sheaths were pooled by annual cycle. Each sample was oven-
 181 dried at 60°C to constant weight, powdered using a micro mill and weighed (c. 2.5 mg) in a tin
 182 capsule. Carbon stable isotope ratios were analyzed using an Isotope Ratio Mass Spectrometer (IRMS;
 183 Thermo Scientific Delta Plus XP, Bremen, Germany) coupled to an Elementar Analyser (EA; Thermo
 184 Scientific 1112, Bremen, Germany). All stable isotope values were reported as parts per thousand (‰)
 185 and differences (δ) from the standard (Vienna Pee Dee Belemnite-limestone, V-PDB), according to
 186 the equation $\delta^{13}\text{C} = [(R_A - R_r) / R_r] \times 10^3$, where R_A and R_r are the ratios $^{13}\text{C}/^{12}\text{C}$ in the sample and in
 187 the standard, respectively. Isotopic precision was less than 0.1‰ based on the external standard
 188 IAEA-CH-6.

189

190 2.4 Statistical analysis

191 Growth performance and $\delta^{13}\text{C}$ in sheaths and rhizomes were regressed over time by segmented
 192 regression (Muggeo, 2003; Muggeo, 2008; Muggeo *et al.*, 2013). This type of statistical analysis is
 193 used for modeling abrupt changes in a dependent variable as a consequence of changes in the
 194 continuous explanatory variable, in this case time. In particular, the relationships between the response
 195 and one or more explanatory variables are piecewise linear, represented by two or more straight lines
 196 connected at unknown points (values), usually referred to as breakpoints. Therefore, the goal of this
 197 semi-parametric procedure is to verify the existence of breakpoints for the considered variables and
 198 estimate their position at the same time. The estimated breakpoint of the segmented regression was
 199 used to assess the resilience profile.

200

201 2.5 Measures of perturbation and resilience

202 Perturbation was estimated by considering the displacement induced by the disturbance (submarine
 203 gas explosion) on rhizome elongation and $\delta^{13}\text{C}$ in sheaths and rhizomes. The magnitude of
 204 perturbation was calculated as the percentage deviation (D) from initial conditions using the equation
 205 $D = [(I - P) / I] \times 100$, proposed by Jones and Schmitz (2009), where P is the value of the investigated
 206 variables after disturbance and I indicates the value prior to disturbance. The recovery time or return
 207 time (expressed in years) of *P. oceanica* after the disturbance was used as a direct measure of
 208 resilience and considered as the time required by the plant to restore the pre-disturbance values for
 209 rhizome elongation and $\delta^{13}\text{C}$ in sheaths and rhizomes, according to Pimm (1984). P, I and recovery
 210 time were estimated by using breakpoints obtained by the segmented regression.

211

212 3. Results

213 Rhizome elongation, $\delta^{13}\text{C}$ in sheaths and $\delta^{13}\text{C}$ in rhizomes all demonstrated negative deviations (34.6,

214 37.5 and 24.7 %, respectively) from the pre-disturbance values.

215 In the time frame 1999-2010 (the earliest and the latest lepidochronological years dated, respectively),
216 segmented regression analysis showed the existence of breakpoints for both rhizome elongation and
217 carbon isotope values ($\delta^{13}\text{C}$) in the sheaths and rhizomes of *P. oceanica* at the disturbed site.
218 Regarding rhizome elongation, segmented regression analysis detected three breakpoints in
219 lepidochronological years 2002, 2004 and 2009, respectively (Fig. 3A). The first breakpoint was
220 detected in correspondence with the year of gas explosion occurrence (2002), corresponding to a
221 rhizome elongation value of 15.9 mm y^{-1} . Since 2002, a trajectory shift towards a decreasing trend was
222 observed until 2004 (second breakpoint) when rhizome elongation reached an estimated value of 10.4
223 mm y^{-1} . From 2004 an opposite trend was detected and elongation values progressively increased until
224 2009 (third breakpoint) when rhizome growth was almost completely restored to its initial value (15.1
225 mm y^{-1}). Return time for rhizome elongation was equivalent to 7 years. The analysis carried out on the
226 rhizomes from the control site estimated the presence of breakpoints in 2000, between 2006 and 2007
227 and in 2008-2009, but with no dramatic variation of the growth trajectory (Fig. 3B).

228 With regard to $\delta^{13}\text{C}$ in sheaths, at the disturbed site the analysis estimated three breakpoints
229 corresponding to lepidochronological years 2002-2003, 2004 and 2006-2007 (Fig. 4A), and $\delta^{13}\text{C}$
230 values of -16.8 ‰ , -23.0 ‰ and -18.7 ‰ , respectively. After the explosion, an initial drop in $\delta^{13}\text{C}$ was
231 observed in correspondence with the first breakpoint in the lepidochronological years 2002-2003. The
232 decreasing trend continued until 2004 (second breakpoint) when sheath $\delta^{13}\text{C}$ reached the lowest value
233 (-23.0 ‰). Between 2006 and 2007 (third breakpoint), a partial recovery of sheath $\delta^{13}\text{C}$ occurred ($-$
234 18.7 ‰) although, in total, 8.5 years were necessary to completely restore pre-disturbance values ($-$
235 16.3 ‰ in 2011).

236 Finally, the analysis implemented on rhizome $\delta^{13}\text{C}$ detected three breakpoints corresponding to
237 lepidochronological years 2001-2002, 2004 and 2010, and $\delta^{13}\text{C}$ values of -16.3 ‰ , -20.4 ‰ and -15.6
238 ‰ , respectively (Fig. 5A). The first breakpoint was detected between 2001 and 2002; a trajectory shift
239 towards a decreasing trend was observed until 2004 (second breakpoint) when $\delta^{13}\text{C}$ values reached
240 their minimum (-20.4 ‰). From 2004, an inversion in the trend was observed and $\delta^{13}\text{C}$ values
241 progressively increased to fully restored values (-15.6 ‰) in 2010 (third breakpoint). Return time for
242 rhizome $\delta^{13}\text{C}$ was equivalent to 8 years.

243 At the control site, the segmented regression analysis did not detect any breakpoint for either sheath or
244 rhizome $\delta^{13}\text{C}$ (Fig. 4B and 5B).

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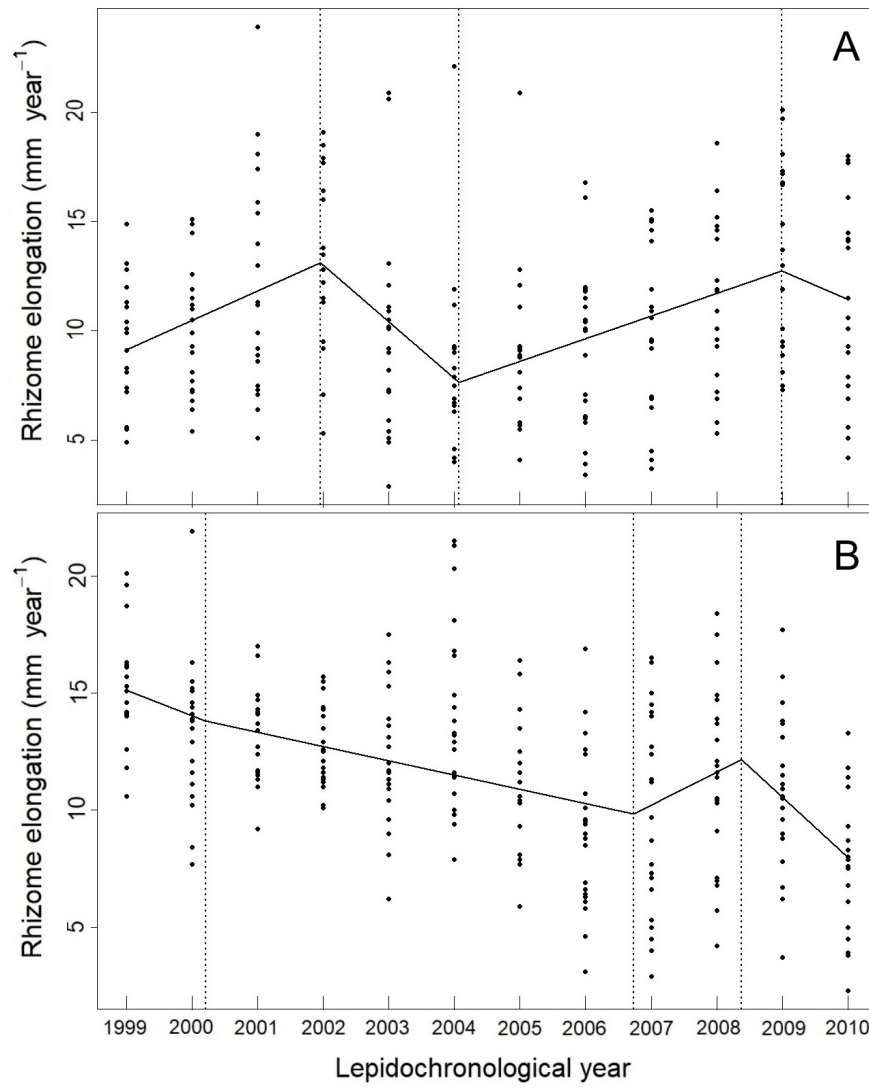


Fig. 3. Segmented regression for *P. oceanica* rhizome elongation at the disturbed (A) and control (B) sites. Solid lines represent the best fitting segmented regression model for rhizome elongation and year; vertical dashed lines indicate breakpoint positions.

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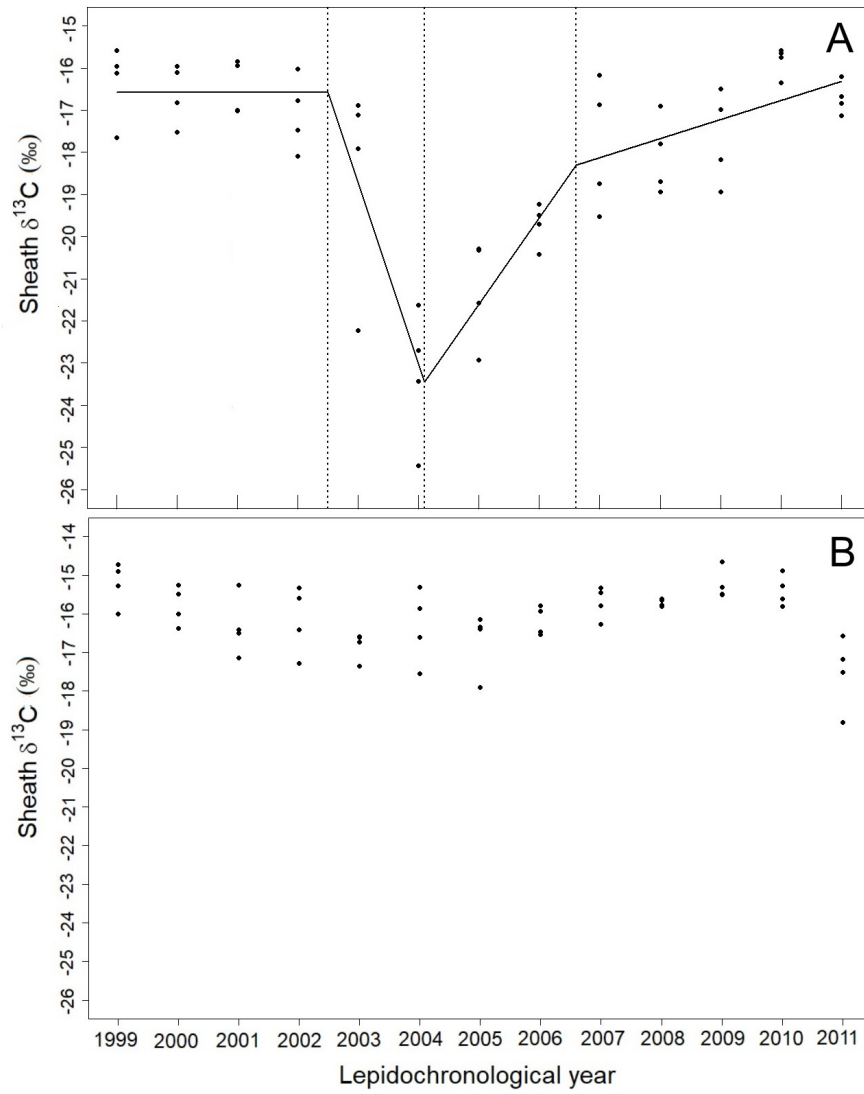


Fig. 4. Segmented regression for $\delta^{13}\text{C}$ in *P. oceanica* sheaths at the disturbed (A) and control (B) sites. Solid lines represent the best fitting segmented regression model for sheath $\delta^{13}\text{C}$ and year; vertical dashed lines indicate breakpoint positions.

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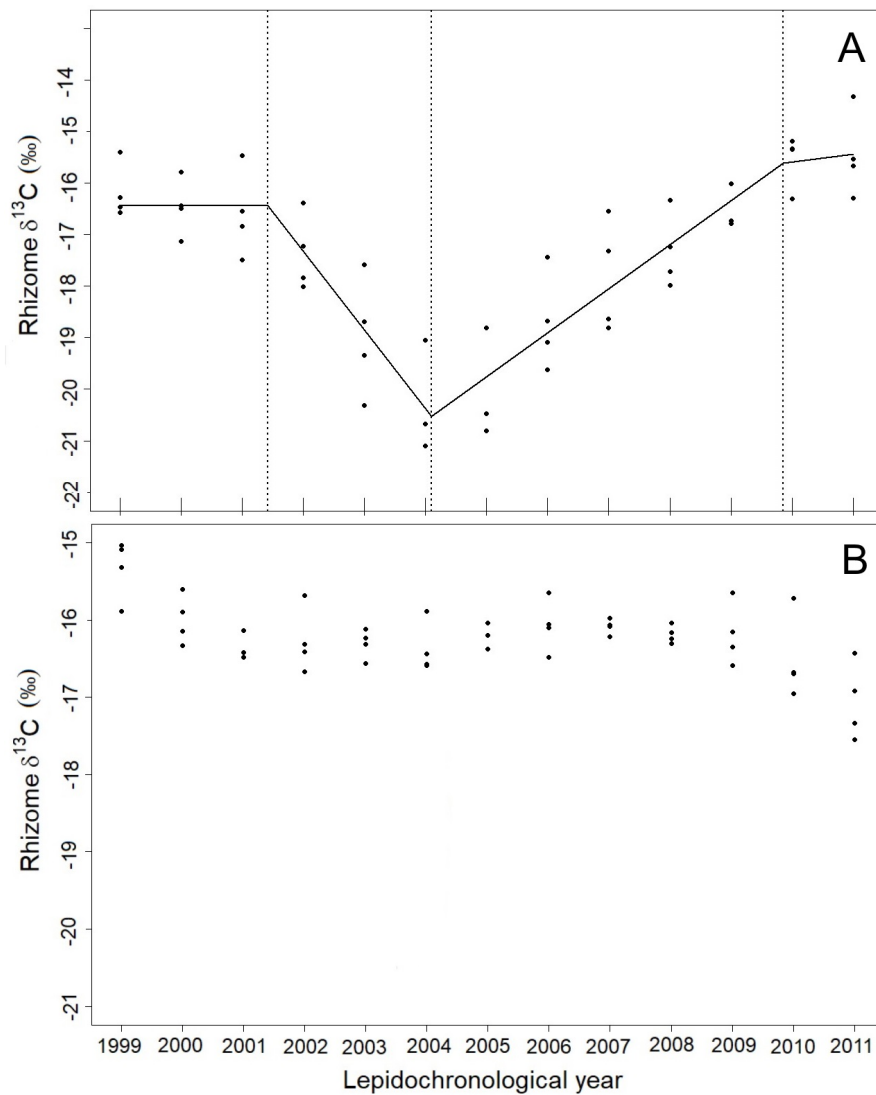


Fig. 5. Segmented regression for $\delta^{13}\text{C}$ in *P. oceanica* rhizomes at the disturbed (A) and control (B) sites. Solid lines represent the best fitting segmented regression model for rhizome $\delta^{13}\text{C}$ and year; vertical dashed lines indicate breakpoint positions.

4. Discussion

This study showed that explosive volcanic submarine activity is able to adversely affect the seagrass *P. oceanica*, resulting in a sequence of trajectory shifts in growth performance and carbon stable isotope composition ($\delta^{13}\text{C}$) across time. By examining these patterns, we reconstructed, for the first time, perturbation and recovery time within the framework of the resilience scenario for *P. oceanica* following this kind of pulse disturbance. Segmented regression analysis did not reveal substantial variations in growth performance and $\delta^{13}\text{C}$ trajectories until 2002, at both the disturbed and control site. At this threshold time, disruption of the equilibrium state was observed, resulting in a trajectory shift towards decreasing values for all the variables at the disturbed site. These findings are consistent with a previous study, conducted at the same site, revealing a reduction in *P. oceanica* growth

276 performance and pronounced ^{13}C -depletion in both sheaths and rhizomes, in response to the same
277 submarine explosion (Vizzini *et al.*, 2010). However, previous studies have shown that seagrasses
278 might benefit from enrichment in CO_2 in terms of biomass and shoot density (Hall-Spencer *et al.*,
279 2008), reproductive output, below-ground biomass and vegetative proliferation of new shoots under
280 natural light-replete conditions (Palacios and Zimmerman, 2007). In our study, harsh environmental
281 conditions (e.g. light limitation due to turbidity and high temperature) caused by the submarine gas
282 explosion resulted in a decrease in the rhizome elongation rate, opposing to the expected positive
283 effect of the CO_2 increase. Moreover, the decline in growth with a consequent reduction of the plant's
284 demand for carbon and the peculiar environmental settings (increased availability of volcanic ^{13}C -
285 depleted inorganic carbon) resulted in much lower $\delta^{13}\text{C}$ signatures in plant tissues as an effect of the
286 higher discrimination against the heavy isotope (^{13}C).

287 Actually, segmented analysis implemented on rhizome $\delta^{13}\text{C}$ detected the first disruption between
288 lepidochronological years 2001 and 2002, thus suggesting that those rhizome segments were still
289 growing during the sudden 2002 gas explosion. In fact, rhizomes are metabolically active structures
290 undergoing continuous modifications. Therefore, it is likely that rhizome segments from a specific
291 lepidochronological year extend their growth to the following years (Peirano, 2002). The decreasing
292 trend for rhizome growth and $\delta^{13}\text{C}$ (in both sheaths and rhizomes) reversed in 2004 when the plant
293 recovery process progressively took place for all the analysed variables. One plausible explanation for
294 such an inverted trend may be the restoration of the pre-crisis abiotic conditions observed at the
295 disturbed site several months after the pulse disturbance (Aliani *et al.*, 2010). Between November
296 2002 and September 2003, the intensity of the gas eruption decreased progressively reaching a value
297 of $0.3 \times 10^8 \text{ L d}^{-1}$ (15-fold lower than that recorded in November 2002) and a further decrease took
298 place until April 2004 when the vent was erupting at $0.02 \times 10^8 \text{ L d}^{-1}$ (220-fold lower than that
299 recorded in November 2002), indicating a recovery towards normal conditions.

300 Such decrease in submarine emissions, i.e. reduced release of volcanic CO_2 and increased light
301 availability, probably allowed the plant to progressively re-establish its physiological mechanisms of
302 growth. It is worth noting that the health status of *P. oceanica* at the disturbed site prior to the
303 explosive event can be easily predicted as good and typical of undisturbed sites, according to the
304 reference growth charts approach proposed by Tomasello *et al.* (2016). This method allows the
305 reconstruction of the past growth and production history of *P. oceanica* involving different growth
306 performance measures (speed of growth and primary production of rhizomes). In our case study,
307 rhizome growth rate, at the time of the disturbance (2002), reached 15.9 mm y^{-1} that corresponds to a
308 growth performance over the median value expected for Sicilian meadows at the same depth
309 (Tomasello *et al.*, 2016). Therefore, it can be speculated that the pre-existing optimal growth

310 conditions of the plant have facilitated complete recovery of the damaged meadows after the gas
311 explosion supporting the concept that the status of the ecosystem exposed to disturbance may affect its
312 resilience capacity (Unsworth *et al.*, 2015).

313 It has been argued that disturbance characteristics such as type, intensity, duration, spatial extent and
314 timing can affect seagrass degradation and resilience trajectories (O'Brien *et al.*, 2018). Pulse
315 disturbances, being relatively discrete events with a short duration (Bengtsson, 2002), are expected to
316 produce more reversible damages allowing the system to settle back to the original state after the
317 disruptive event (Sheffer *et al.*, 2001). However, in the current study, the relatively rapid restoration of
318 the environmental conditions in the impacted area after the submarine gas explosion did not coincide
319 with the recovery of *P. oceanica*, which lasted much longer (about 8 years). Specifically, the time
320 required by rhizomes to re-establish the pre-disturbance elongation values, after a perturbation of
321 34.6%, corresponds to 7 years, although it is reasonable to state that recovery may have occurred a
322 year earlier. The elongation values measured in 2009 (last break point) are, in fact, underestimated
323 since the elongation of the rhizomes at the 2-3 last lepidochronological years was still ongoing at the
324 time of collection (Peirano, 2002).

325 The time taken by rhizomes to restore the original $\delta^{13}\text{C}$ values after a perturbation of 24.7%
326 corresponds to 8.5 years and, consistently, $\delta^{13}\text{C}$ values for sheaths with a perturbation of 37.5% were
327 restored in 8 years. This “delayed” recovery is indicative of hysteresis in the return trajectory, which
328 often occurs (Duarte *et al.*, 2009) and may be explained by the plant’s life history strategy. Several
329 authors have proposed that large long-lived species, such as *P. oceanica*, respond more slowly to
330 change (i.e. long recovery times), while smaller, short-lived pioneering species recover more quickly
331 (Duarte *et al.*, 1997; Orth *et al.*, 2006; Kendrick *et al.*, 2012; Kilminster *et al.*, 2015; Roca *et al.*,
332 2016). Moreover, the timing of the disturbance (i.e. the period of the year when the disturbance
333 occurred) may play a key role in determining seagrass trajectory and response to environmental
334 changes (O'Brien *et al.*, 2018). Specifically, the submarine gas explosion occurred in the beginning of
335 the winter season (November), thus coinciding with the *P. oceanica* life span phase in which the plant
336 suffers a negative carbon balance due to winter light conditions that, generally, do not permit net
337 carbon gains. Under these circumstances, the plant mainly exploits the carbohydrate reserves stored in
338 the rhizomes gained during the previous summer period (Alcoverro *et al.*, 2001). This metabolic
339 strategy allows the plant to reallocate carbon resources from below-ground compartments to support
340 leaf growth under unfavorable light conditions (Marbà *et al.*, 2002; Alcoverro *et al.*, 2001)
341 contributing, together with low growth performance (i.e. reduced carbon demand), to the protraction
342 of ^{13}C -depleted values in 2003 and 2004 due to the use of recycled and ^{13}C -depleted carbon (Marbà *et al.*,
343 2002). It is likely that persisting insufficient light availability, induced by the explosion, led to a

344 more negative carbon balance, thus limiting the development of a well-structured leaf canopy that is
345 necessary for optimal carbon fixation and storage in the following summer and leaf re-growth in the
346 following winter. Indeed, the minimum growth and isotopic ratios were recorded two years after the
347 disturbance (2004), which supports the concept that this mechanism may result in the propagation of
348 disturbance across the years with severe effects on seagrass recovery (Alcoverro *et al.*, 2001) and that
349 rhizome growth in *P. oceanica* displays time serial autocorrelation (Lovison *et al.*, 2011).

350 Nevertheless, the key finding of this study is that *P. oceanica* demonstrated the ability to fully recover
351 in about 8 years after the explosive event occurred in 2002, completely restoring its parameters
352 (rhizome elongation, $\delta^{13}\text{C}$ of sheaths and rhizomes) by 2010. It should be noted that an increasing
353 number of studies, conducted on recovery in the marine realm, have shown that, overall, more than
354 10% but less than 50% of depleted species have experienced some recovery, although rarely to former
355 conditions (see the review by Lotze *et al.*, 2011). However, a considerable part of the degraded
356 ecosystems seems to remain irreversibly in a damaged state for a long time (Lotze *et al.*, 2011), thus
357 showing that recovery is not a common process. Of course, recovery trajectories depend on the nature
358 of the disturbance and can change among different ecosystems (Duarte *et al.*, 2015). Limited recovery
359 from trawling has been documented for *P. oceanica* after eliminating the cause of the impact with
360 heavily impacted meadows showing a very slow recovery compared to undisturbed meadows in terms
361 of rhizome growth, rhizome production and shoot balance (González-Correa *et al.*, 2005).

362 Here, we demonstrated that, at shoot level, *P. oceanica* may settle back to the original conditions after
363 pulse disturbance through its capacity to successfully adapt to disruptive environmental changes
364 without any regime shifts. This study increases the observational evidence, so far relatively scant,
365 about the resilience processes of coastal ecosystems and contributes to the debate on implicit paradigms
366 in the ecosystem recovery (*sensu* Duarte *et al.*, 2015). We showed that the trajectory of *P. oceanica*
367 recovery from the submarine gas explosion presented hysteresis as it differed from the trajectory of
368 degradation. This is due to the differential thresholds and time scales of *P. oceanica* degradation and
369 recovery phases (i.e. non-linear disturbance-response pathways). Therefore, the results of this study
370 oppose the paradigm that degradation and recovery follow similar but opposite trajectories and
371 support the conceptual model proposed by Duarte *et al.* (2015). Furthermore, although it is widely
372 accepted that partial (as opposed to full) recovery prevails in coastal ecosystems (Duarte *et al.*, 2015;
373 Lotze *et al.*, 2011), our study shows the opposite by presenting an example of fully reversible
374 degradation.

375 In conclusion, this case study represents a unique opportunity to show the response of *P. oceanica*, a
376 long-living species, to extreme environmental changes and to outline the capacity to record and
377 recover from explosive hydrothermal submarine activity. The findings of this study may have

378 important implications for the management and conservation of *P. oceanica* meadows, since they
379 provide insights that may help in predicting seagrass response to environmental change and preventing
380 its potential collapse. This study contributes to filling knowledge gaps as regards recovery at plant
381 level, helping to implement adequate methods and metrics for measuring deviations from baseline
382 conditions in order to provide crucial information and guidance for management and policy actions.

383

384 **Acknowledgements**

385 The authors thank A.E. Aleo for help with stable isotope analysis, F. Luzzu and A. Savona for field
386 survey and V. Pampalone for map editing.

387

388 **Funding**

389 This work was supported by the Interreg Italia-Malta Programme 2014-2020 (PROJECT BESS).

390

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Simona Noè: Writing- Original draft preparation, Reviewing and Editing; **Carmelina Bellavia:** Methodology, Investigation; **Sebastiano Calvo:** Writing- Reviewing and Editing, Resources; **Antonio Mazzola:** Writing- Reviewing and Editing, Resources; **Maria Pirrotta:** Investigation, Writing- Reviewing and Editing; **Mariangela Sciandra:** Formal analysis, Visualization; **Salvatrice Vizzini:** Conceptualization, Writing- Reviewing and Editing, Supervision; **Agostino Tomasello:** Conceptualization, Methodology, Writing- Reviewing and Editing, Supervision, Resources.