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1 **Influence of environmental patterns on gonadosomatic index and**
2 **early life stages of *Paracentrotus lividus* in Corsica**
3 **(Mediterranean Sea)**

4
5 **Sophie Duchaud**^{a, b}, **Sonia Ternengo**^{a, b}, **Eric D.H. Durieux**^{a, b}, **Benjamin Bianchini**^b,
6 **Marie Garrido**^c, **Antoine Aiello**^{a, b}, **Romain Bastien**^b, **Vanina Pasqualini**^{a, b*}

7 ^a *Université de Corse Pasquale Paoli, UMR CNRS 6134 Sciences Pour l'Environnement, 20250*
8 *Corte, Corse, France*

9 ^b *Université de Corse Pasquale Paoli, UMS CNRS 3514 Plateforme marine Stella Mare, 20620*
10 *Biguglia, Corse, France*

11 ^c *Environmental Agency of Corsica, Avenue Jean Nicoli, 20250 Corte, Corse, France*

12
13 * Corresponding author

14 *E-mail address: pasqualini_v@univ-corse.fr (Vanina Pasqualini)*

15
16 **Abstract**

17 Spatio-temporal patterns of the gonadosomatic index (GSI) and life cycle stages of the sea
18 urchin *Paracentrotus lividus* were studied at two Corsican near sites which differ in terms of
19 protection status. The results highlighted an annual cycle of the GSI with spring spawning
20 (between May and June) and presumed lesser autumn spawning (October or November). Spatial
21 patterns revealed homogeneity in larval densities between the sites whereas differences were
22 observed for settlers, recruits, sub-adults and adult stages. Temporal variability was detected
23 for all stages with highly variable patterns for larval stage and settlement. This study suggests
24 the presence of sporadic spawning and/or the arrival of allochthonous larvae to the sites. The

25 recruitment intensity was highly variable between the two studied years; in 2016, the peak
26 recorded was five-fold higher than in 2015. This study confirmed the importance of habitat
27 diversity on the density of small individuals. The site's protection status also influenced the
28 structuring of *P. lividus* indirectly as the highest densities were recorded at the site where
29 fishing was allowed. Finally, this work revealed the difficulty of observing the temporal
30 evolution of the *P. lividus* life cycle in the natural environment.

31

32 **Keywords:** *Paracentrotus lividus*; Spawning; Recruitment; Densities; Abiotic parameters;
33 Habitat.

34

35 **1. Introduction**

36

37 *Paracentrotus lividus* (Lamarck, 1816) (Echinoidea: Parechinidae) is a species that is
38 recognize for its major role in determining the structure of benthic communities such as algae
39 assemblages (e.g. Sala et al., 1998; Barnes et al., 2002) and its high-economic value (Palacín et
40 al., 1998). Given the organoleptic quality of its gonads, populations are often subjected to an
41 increase in consumer demand, leading to an impact on sea urchin abundance due to fishing
42 (Andrew et al., 2002; Gianguzza et al., 2006; Pais et al., 2007; Ceccherelli et al., 2011).
43 *Paracentrotus lividus* abundances are highly variable in time and space (Turon et al., 1995;
44 Sala et al., 1998) and are influenced by local factors, such as water temperature (Wing et al.,
45 2003), salinity (Fernandez et al., 2006), competition (Gianguzza et al., 2006), predation (Sala
46 and Zabala, 1996; Guidetti, 2004; Hereu, 2005), settlement (Tomas et al., 2004) and habitat
47 heterogeneity (Prado et al., 2012).

48 In the Mediterranean Sea, *P. lividus* is commonly observed in sublittoral zones (Lozano
49 et al., 1995) between 0 and 30 m deep (Mortensen, 1927), although abundances decrease below
50 a depth of 10 m (Chelazzi et al., 1997). It is widely present on rocky substrates or in seagrass
51 meadows. Previous studies have shown differences in population structure by habitat. For
52 example, the average size of an individual is larger in *Posidonia oceanica* meadows (Tomas et
53 al., 2004; Ceccherelli et al., 2009), but abundances in these meadows are lower than on rocky
54 substrates (Tomas et al., 2004; Ceccherelli et al., 2009; Boudouresque and Verlaque, 2013).
55 Habitat also influences the gonadal indices and settlement value. Ouréns et al. (2011)
56 highlighted that gonad development is higher in seagrass meadows than on rocky substrates
57 whereas Tomas et al. (2004) showed that settlement is higher on rocky substrates than in
58 seagrass meadows. It appears that *P. lividus* requires a habitat that provides both shelter and
59 food (Pinna et al., 2012). Habitat complexity also influences the population structure of this sea

60 urchin (Prado et al., 2012). Understanding the habitat preference of *P. lividus* is essential to its
61 management.

62 The life cycle of *P. lividus* is complex and includes relatively sedentary benthic juvenile
63 and adult stages, which are influenced by parameters occurring at small spatial scales (Keough,
64 1984). Conversely, planktonic larval stages depend on parameters occurring on a large spatial
65 scale (Grosberg and Levitan, 1992). Larvae are highly dependent on the hydrodynamic
66 conditions of the environment (Pedrotti and Fenaux, 1992; Farina et al., 2018). Variability of
67 their abundance appears to be related to variation in phytoplankton production (López et al.,
68 1998). Settlement abundance is also influenced by food availability (Fenaux et al., 1994), the
69 abundance of predators (Sala, 1997; Hereu, 2005), and the presence of shelter to protect them
70 from predation (Nishizaki and Ackerman, 2007). Small fish play a key role in reducing
71 settlement by feeding on small sea urchins (Hereu, 2005). The development of a larger test
72 diameter by individuals increases their defenses against predators (Tegner and Dayton, 1981;
73 Sala and Zabala, 1996; Sala, 1997). Recruitment rates are influenced by reproductive success,
74 larval supply, settlement, mortality and the migration of the post-metamorphic stage (Hunt and
75 Scheibling, 1997; Balch and Scheibling, 2000). As a result, a decrease in spawning sea urchin
76 stocks in fished areas reduces reproductive success (Pennington, 1985; Levitan, 1992; Levitan
77 and Sewell, 1998), recruitment rates and the size of the resulting population. Previous work has
78 already shown a decline in *P. lividus* abundance in Marine Protected Area compared to
79 neighboring unprotected areas (Sala and Zabala, 1996). This phenomenon could be linked to a
80 difference in the abundance of predatory fish (Garcia-Rubies and Zabala, 1990). Even if the
81 studies on GSI and early life stages of *P. lividus* are consequent in Mediterranean Sea (Hereu
82 et al., 2004; Tomas et al., 2004; Ouréns et al., 2011; Prado et al., 2012; Amri et al., 2017), the
83 studies on temporal evolution of the life cycle in the natural environment are again necessary
84 to understand the local pattern of this cycle.

85 This study described the density and spatio-temporal patterns of each life stage of *P.*
86 *lividus* in the two Corsican sites (northwestern Mediterranean Sea) which differ in terms of
87 protection status. This work aimed to: (i) identify the annual spawning period and the peaks of
88 larvae and settlers of two sites with different protection status (protected and unprotected); (ii)
89 study the influence of spatial, temporal and environmental factors (temperature, salinity and
90 habitat) on the density of the different life cycle stages of *P. lividus* and the GSI; (iii) establish
91 correlations between densities of different life cycle stages (larvae, settlers) and GSI.

92

93 **2. Materials and Methods**

94

95 *2.1. Study area, sampling strategy and environmental parameters*

96 The study area was located in NW Corsica (France, NW Mediterranean Sea; Fig. 1) and
97 included the sites of Albo and Nonza, approximately 10 km apart. Both sites are open to the sea
98 and may be exposed to high hydrodynamics, and consist of sloping and falling rocks, slab rocks,
99 boulders, pebbles, cobbles, and sand, with vegetal cover composed of different macroalgae and
100 *Posidonia oceanica* meadows. Their protection status differed: fishing was permitted in Albo
101 from mid-December to mid-April and prohibited in Nonza.

102 Initially, the monitoring of GSI in 2015 was carried out in order to determine the spring
103 spawning in Albo. This sampling was conducted weekly from 7 April 2015 to 19 May 2015.
104 The sites of Albo and Nonza presented differences in GSI. Thus, starting in August 2015, GSIs
105 were monitored on a monthly basis at both sites. Sampling frequency was intensified during
106 the main period of spawning (from 13 April 2016 to 20 July 2016, as recorded in 2015) and the
107 GSI was monitored weekly. From August 2016 until the end of the study (December 2016),
108 this monitoring was carried out monthly.

109 For the study of *Paracentrotus lividus* larvae, sampling was carried out from May 2015
110 to December 2016. In order to capture sudden changes in phytoplankton population, Beker et
111 al. (2001) recommend a weekly sampling frequency of plankton. Consequently, larval sampling
112 was carried out every week during a specific period (from 28 May to 17 July 2015 and from 13
113 April to 20 July 2016). Outside of these periods, sampling was conducted monthly.

114 In order to determine a precise date for spring spawning, the same strategy was applied
115 for GSI. Sampling of settlers was carried out weekly from 4 June to 17 July 2015 and from 13
116 April to 20 July 2016. Finally, counts of benthic stages were made in autumn 2015 and 2016.

117 Sea Surface Temperature (SST) and salinity were recorded using a multi-parameter
118 probe (Seabird SBE19) in Albo and Nonza at a depth between 1 m and 2 m. The measurements
119 were taken every month and every week in the spring-summer period following the sampling
120 described above.

121

122 2.2. Gonadosomatic index monitoring

123 *Paracentrotus lividus* individuals with test diameter larger than 5 cm (commercial size)
124 were collected in Albo and Nonza. In each date, 30 *P. lividus* individuals were weighed before
125 being dissected with a scalpel. The five gonads were carefully extracted and weighed (to the
126 nearest 0.01 g). The GSI was calculated using the following formula:

$$127 \quad GSI (\%) = \frac{\text{Wet-weight of gonads}}{\text{Total wet-weight of } P. \text{ lividus}} \times 100$$

128

129 2.3. Sampling of larvae and settlers

130 Larvae were collected with a zooplankton tow-net at a depth between 0 and 5 m during
131 20 min at an average of 2 km h⁻¹ using a standard 200 µm mesh-size WP2 net. The net container
132 was concentrated in order to obtain a final sample volume of 200 ml, which was preserved in
133 4% buffered formaldehyde. Echinoderm larvae counts were carried out by stereomicroscopy.

134 The settler sampling method was adapted from the work of Hereu et al. (2004). Artificial
135 structures were used, namely brushes with vegetable bristles, attached to a weighted rope and
136 surmounted by a subsurface buoy (Fig. 1). In order to obtain three replicates, each site was
137 subdivided into 3 sub-areas (a northernmost, a southernmost and an intermediate one) and 2
138 depths were selected for each sub-area (Fig. 1). At each sub-area, one collector line (ie. 4
139 brushes) was placed at 3 m and a second at 6 m (ie. 4 brushes). A total of 6 collector lines (ie.
140 24 brushes) were placed in Albo and 6 more (ie. 24 brushes) were deployed in Nonza during
141 each sampling.

142 Two lines were placed at each sub-area, at a depth of 3 m and 6 m, respectively, for one
143 week (Fig. 1). For collection, each brush was removed individually and placed in a labeled
144 plastic bag. To harvest settlers, brushes and bags were rinsed with fresh water on a 500- μ m
145 mesh sieve. Samples were concentrated in order to obtain a final sample volume of 100 ml and
146 were preserved in 70% ethanol. Settler counts were carried out by stereomicroscopy.

147

148 *2.4. Sampling of benthic stages, substrates and vegetal cover*

149 Counts of *P. lividus* (juveniles, sub-adults and adults) were made within the sub-areas
150 used for settler sampling. Enumeration of *P. lividus* test diameter (TD) > 2 cm was carried out
151 using quadrats of 1 m². The following size categories were used: juveniles (2 cm < TD \leq 3 cm),
152 sub-adults (3 cm < TD < 5 cm) and adults (5 cm \leq TD \leq 9 cm). For sea urchins \leq 2 cm, the
153 inventory was carried out on a more restricted area of the quadrat of a dimension of 0.25 m².
154 The term recruits will be used to refer to these individuals. A total of 180 randomly distributed
155 quadrats were counted per site, including 60 quadrats at a depth of 3 m, 6 m and 9 m,
156 respectively. The diameters of the tests without spines of *P. lividus* were recorded with a plastic
157 caliper to the nearest cm.

158 Vegetal cover and substrates were analyzed for each quadrat of 1 m² and 0.25 m² using
159 a photo-quadrat. The proportion in terms of substrates and vegetal cover was estimated by
160 image processing using a predetermined scale. The following classification was applied:
161 sloping and falling rocks, slab rocks, boulders, pebbles and cobbles, and sand. For vegetal
162 cover, the classification used was that described by Ruitton et al. (2000): encrusting substratum
163 (crustose species), turfy substratum (saccate cushion-shaped and filamentous species, usually
164 ≤ 1 cm in height), shrubby substratum (sheet-shaped, jointed calcareous and thick leathery-
165 shaped species, from 1 to 10 cm in height) and arborescent substratum (coarsely-branched
166 species, usually > 10 cm in height). A last class was added: “*Posidonia oceanica*”. For the study
167 of recruits within the 0.25 m² quadrats, an inventory of the shelters present was carried out and
168 four categories were defined: rocky shelter, vegetal shelter, rocky and vegetal shelter, and
169 absence of shelter.

170

171 2.5. Statistical analyses

172 The spatial and temporal variability were tested with a two-way ANOVA (Date and
173 Site) for the GSI and with a one-way ANOVA (Site) for the larval phase, whereas the
174 recruitment variation was evaluated using a three-way ANOVA (Date, Site and Depth). The
175 data from subsites were pooled for the settlers. Density variability of recruits by size classes
176 and by categories of shelters was studied using a MANOVA test. The MANOVA test was also
177 used to test the spatio-temporal variability of benthic stages densities (recruits, sub-adults and
178 adults) obtained using the quadrat method. ANOVA tests were performed on variables detected
179 as significant during the MANOVA test. All ANOVA tests were followed by Tukey HSD
180 multiple pairwise analyses.

181 Associations between GSI, densities of *P. lividus* stages and abiotic drivers were
182 assessed using Pearson’s pairwise correlations. The relationship between vegetal cover and

183 rocky substrates on *P. lividus* size classes was investigated by Principal Component Analysis
184 (PCA). When normality (Kolmogorov-Smirnov test) and heteroscedasticity (Cochran's test)
185 were non-compliant, data were log-transformed. When the transformed data did not comply
186 with the hypothesis, the level of significant was reduced to $\alpha = 0.01$ (Underwood, 1997). All
187 statistical analyses were carried out using XLSTAT software v. 19.01.

188

189 **3. Results**

190

191 *3.1. Spatio-temporal patterns*

192 For the study of GSI, 1710 individuals were dissected (960 individuals in Albo and 750
193 individuals in Nonza). Sea urchin test diameter was between 5.1 cm and 8.2 cm (average of
194 5.49 cm). Total body weight was between 25.5 g and 158.8 g (average of 80.15 g). The highest
195 GSI values in Albo were found in May 2015 and 2016 (Fig. 2a). The lowest values were
196 observed in November 2015 and 2016. In Nonza, the highest value of the GSI was recorded in
197 April 2016 and the lowest in December 2015 (Fig. 2a).

198 A spatio-temporal variability of the GSI was highlighted by two-way ANOVA test
199 (Table 1a). *Post hoc* tests highlighted significant decreases in Albo, between 12 May and 19
200 May and between 27 May and 6 June for the years 2015 and 2016, respectively (Fig. 3a and
201 Fig. 3b). In Nonza, a significant decrease was observed between 18 May and 27 May 2016 (Fig.
202 3b). In the autumn, significant differences were detected between October and November for
203 the year 2015 and 2016 in Albo, and between November 2015 and December 2015 in Nonza
204 by *post hoc* tests (Fig. 2a).

205 Considering the larval stage, two spring-peaks were observed in Albo on 10 June 2015
206 and 17 July 2015 (Fig. 2b and Fig. 3c). In Nonza, a peak was detected on 8 July 2015 (Fig. 2b
207 and Fig. 3c). There were no larvae at either site on 17 and 24 June 2015 (Fig. 3c). In 2016,

208 spring peaks were recorded on 6 July for Albo and Nonza (Fig. 2b and Fig. 3d). A few larvae
209 were counted during autumn and winter 2015 and 2016 (Fig. 2b). Statistical analyses did not
210 reveal any spatial variability between Albo and Nonza (Table 1b).

211 For both sites and both years, the highest values of the settler stage larvae were detected
212 in the first half of June (Fig. 2c, Fig. 3e and Fig. 3f). The average density of sea urchins settled
213 was highly variable between the two years. Statistical tests revealed spatial and temporal
214 variability for settlers (Table 1c). In 2016, *post hoc* tests highlighted two significantly different
215 peaks from the other dates: on 6 June and 28 June. In addition, a significantly higher average
216 density was detected in Nonza compared to Albo (Table 1c). However, no significant difference
217 was found between depths.

218 Concerning recruits, juveniles, sub-adults, and adults, the average densities for all
219 classes combined, was 0.99 individual.m⁻² in 2015 and 0.94 individual.m⁻² in 2016, in Albo. In
220 Nonza, the average densities for all classes combined were 0.53 individual.m⁻² and 0.47
221 individual.m⁻² (respectively) for the years 2015 and 2016. For both sites, the lowest average
222 densities were observed for the class]2-3]cm, in 2015 and 2016 (Fig. 4). The highest average
223 densities were reported for the small size classes [0-1]cm and]1-2]cm for both sites and for
224 both years (Fig. 4). The MANOVA test highlighted spatial variability in density among sites
225 and depths, and for “Site”, “Depth” and “Site x Depth” factors (Table 2). *Post hoc* tests showed
226 that densities were significantly higher in Albo than in Nonza for all size classes with an
227 exception for the class [0-1]cm where no significant difference was detected.

228

229 3.2. Relationship with environmental factors

230 Salinity varied according to the same trends over the two years at the two sites, with
231 slightly lower values in autumn and winter, particularly in Nonza (Fig. 5a). For the SST, a
232 seasonal trend was also observed at the two sites and for the two years studied (Fig. 5a). Weekly

233 measurements showed a decrease in salinity and SST in June 2015 (Fig. 5b). The relationships
234 between the different life cycle stages and environmental parameters were highlighted. Positive
235 correlations were recorded between the SST and the GSI and between the SST and the larval
236 stage (Fig. 6). For the GSI, a negative correlation was observed with the settler stage. No
237 relationship was detected between the GSI and the larval stage or between the larval stage and
238 the settler stage (Fig. 6).

239 Principal Component Analysis was performed to understand the relationship between
240 the substrate and vegetation cover, and the densities of recruits, juveniles, sub-adults and adults.
241 For *P. lividus* recruits, the first two axes of PCA explained 46.74% of the total variance (Fig.
242 7a). Axis 1 separated slab rocks from other rocky substrates and *P. oceanica* and arborescent
243 substratum from other vegetal covers. Axis 2 differentiated sediments (sand, pebbles and
244 cobbles) from bedrocks (boulders, slab rocks, slopping and falling rocks), and the substrates
245 with vegetal covers of intermediate to low heights. The class [0-1]cm was positively correlated
246 with boulders (0.380, $P < 0.05$), whereas the class]1-2]cm was positively correlated with the
247 turfy substratum (0.365, $P < 0.05$). Both classes were negatively correlated with *P. oceanica* (-
248 0.360, $P < 0.05$; -0.354, $P < 0.05$, respectively). For sub-adults and adults, the two axes of PCA
249 explained 50.12% of the total variance (Fig. 7b). The distinctions made by axes 1 and 2 are the
250 same as those described in the previous PCA. The class]2-3]cm was positively correlated with
251 the turfy substratum (0.483, $P < 0.05$). The classes]2-3]cm and]3-5[cm were negatively
252 correlated with *P. oceanica* (-0.388, $P < 0.05$; -0.474, $P < 0.05$, respectively).

253 Concerning the shelters, the MANOVA test showed an influence of shelter on *P. lividus*
254 and ANOVAs highlighted its effect on both size classes (Table 3). For the size class [0-1]cm,
255 densities were significantly higher in the presence of rocky shelters and mixed shelters (rocky
256 and vegetal shelters) than in vegetal shelters. For the class]1-2]cm, densities were significantly
257 higher in rocky shelters than in vegetal shelters, or in substrates without shelter.

258

259 **4. Discussion**

260

261 *4.1. Gonadosomatic index variation*

262 The temporal variability of the GSI allows determination of the reproductive cycle and
263 the spawning period (Ouréns et al., 2011). Our results showed that the pattern of the GSI could
264 be regular from one year to the next and, this phenomenon was observed since 2013 in this area.
265 This assumption are consistent with that described by Lozano et al. (1995) on Spanish
266 Mediterranean coasts, but it contrasted with the results obtained by Ouréns et al. (2011) and
267 Gianguzza et al. (2013) which showed that determination of the reproductive cycle in the
268 Mediterranean is complex. Indeed, these authors highlighted a spatio-temporal variability of
269 the GSI, which complicates the understanding of the reproductive cycle in the Mediterranean
270 basin. More recently, de la Uz et al. (2018) observed a pattern similar to that found on our study
271 on the west coast of Asturias (Spain) with a single spawning period between May and June.
272 Our study also revealed the presence of a single spawning period in the same period and for the
273 both study sites. This was consistent with works of Régis (1978) and Lozano et al. (1995)
274 carried out in the Mediterranean. In Albo, our results described a smaller decrease during
275 November. Some authors have explained this decrease by the existence of an autumn spawning,
276 which is lower than that occurring in spring (Fernandez, 1998; Sellem and Guillou, 2007;
277 Ouréns et al., 2011; Machado et al., 2019), but other works consider that these declines are
278 caused by a decrease of nutritive storage and not by gamete release (King et al., 1994; Lozano
279 et al., 1995). Gonads are organs that can be used to store nutrients and in unfavorable
280 conditions, sea urchins can use them, which can influence the GSI independently of
281 reproduction (Lozano et al., 1995). Recent histological studies tend to confirm the second
282 hypothesis because the authors described a phenomenon of resorption of non-evacuated mature

283 gametes during October and November (Sellem and Guillou, 2007). However, other authors
284 have reported the presence of two spawning events in the Mediterranean Sea (Fenaux, 1968;
285 Leoni et al., 2003). Considering the results of the present study and the observation of gonads
286 at different stages of maturation during dissections, the hypothesis of a smaller second
287 spawning in autumn seemed plausible. No spatial variability was detected, which contrasted
288 with previous work describing the high variability on a small spatial scale (King et al., 1994;
289 Sánchez-España et al., 2004). The difference in terms of protection status between the two sites
290 had no influence on the GSI. Within the unprotected site, harvesting is prohibited from mid-
291 April to mid-December. This period includes spawning period and recruitment. Machado et al.
292 (2019) suggest that the establishment of a no-harvesting period during the spawning and
293 recruitment months would limit the effect of sea urchin harvesting. This could explain the lack
294 of correlation between the degree of protection and the GSI.

295

296 *4.2. Spatio-temporal patterns*

297 The present study highlighted different patterns on larval density during spring in both
298 years. The second peak observed in 2015 could be explained by the existence of sporadic
299 spawning, as has been already described for the species *Diadema antillarum* (Levitan, 1988).
300 Boudouresque and Verlaque (2013) indicated that spawning could occur almost all year round
301 regardless of the number of annual peaks, habitat or inter-annual variability, that could reflect
302 a strategy to spread larval losses over time. Populations could have a high reproductive
303 capacity, for example in the zones where there are a low wave exposure (Lozano et al., 1995;
304 Guettaf et al., 2000; Sellem and Guillou, 2007; Gianguzza et al., 2013). Furthermore, Hereu et
305 al. (2004) supposed that larvae could establish locally or more heterogeneously depending on
306 local conditions such as topography or orientation and wave exposure. Local water circulation
307 ensures larval supply to coastal populations (López et al., 1998; Prado et al., 2012). As a return

308 of larvae was observed after their disappearance, it can be assumed that the Albo and Nonza
309 sites were supplied by local and allochthonous larvae. Albo and Nonza are in close proximity
310 and no spatial variability was observed between the two sites. These results were concordant
311 with Prado et al. (2012), which demonstrate that larval densities were determined by regional
312 scale factors (> 100 km). Given the duration of their planktonic phase, ranging from 20 to 40
313 days (Fenaux et al., 1985), larvae had a high dispersal potential (Cowen et al., 2006), which
314 ensured the presence of new recruits into receiving sites.

315 Concerning recruit, sub-adult and adult stages, spatial heterogeneity is a characteristic
316 feature of *P. lividus* population structure (Pais et al., 2007; Ceccherelli et al., 2009, 2011) and
317 its spatial distribution can be influenced by several factors, such as recruitment rate (Tomas et
318 al., 2004), migration (Palacín et al., 1998; Crook et al., 2000), competition (Guidetti, 2004) or
319 predation (Gianguzza et al., 2006). In the present study, the predation pressure and the level of
320 protection of sites may explain the fact that the densities recorded in Albo were higher than in
321 Nonza. Fishing is prohibited in Nonza while Albo is not subject to any restrictions. Previous
322 work has already shown a decline in abundance in reserves compared to neighboring
323 unprotected areas (Sala and Zabala, 1996) that could be linked to a difference in the abundance
324 of predatory fish between a protected site and an unregulated site (Garcia-Rubies and Zabala,
325 1990). In addition, a study on genetic diversity showed that the current impact of harvesting on
326 *P. lividus* populations in Corsica seems to be limited (Duchaud et al., 2018) and could explain
327 the fact that this species was more abundant on the unprotected site of Albo. Although the
328 harvest of *P. lividus* is allowed in Albo, this site is regulated by quotas and a restriction period.
329 However, as harvesting data are limited for the Corsican region, the interpretation of
330 demographic trends according to this parameter remains complicated. Finally, the difference in
331 terms of habitat between the two sites should be taken in consideration because in Nonza, large

332 rock slabs were dominant and thus offer few shelters for small individuals particularly
333 vulnerable to predation.

334

335 *4.3. Abiotic factors and correlations among the different stages of life cycle*

336 The abiotic factors study highlighted an influence of SST on the densities of larvae,
337 which was consistent with previous work (Pétinay et al., 2009). In addition, the larval release
338 of *P. lividus* in late spring appeared to occur when the SST exceeded 18°C (López et al., 1998;
339 Hereu et al., 2004) that were similar to data obtained in the present work for both sites and both
340 years. In general, larvae are susceptible to drastic changes in abiotic parameters and have the
341 ability to prolong their planktonic stage when environmental parameters become unfavorable
342 (Lozano et al., 1995; Amri et al., 2017). Nevertheless, in this study, the influence of temperature
343 on the GSI was not highlighted. However, spawning did not appear to be possible until the
344 animal received stimuli (Byrne, 1990; Spirlet et al., 1998; González-Irusta et al., 2010; Vadas
345 et al., 2015). For example, Pearse et al. (1988) indicated that endogenous factors, light intensity,
346 and the presence of gametes or pheromones in the water column can trigger a spawning event.
347 Fenaux (1968), Byrne (1990) and Pedrotti (1993) have described that spring spawning is
348 triggered by an increase of temperature to a certain value and that autumn spawning is provoked
349 by a decrease in that temperature value. Byrne (1990) and Spirlet et al. (1998) highlighted that
350 spawning was triggered when the temperature reached 13°C whereas for González-Irusta et al.
351 (2010) and de la Uz et al. (2018), this phenomenon occurred at 15°C. In Albo and Nonza, the
352 data revealed that when temperature was around 18°C, gametes were released and the autumn
353 GSI values decreased. Overall, it is accepted that temperature influences gonadal development
354 (Saravanan et al., 2016) by acting on the initiation and duration of the reproductive period
355 (Soualili and Guillou, 2009). In addition, temperature has a direct relationship (Byrne, 1990;
356 Catoira, 1995; Spirlet et al., 1998; González-Irusta et al., 2010; Ouréns et al., 2013) and, only

357 water temperatures exceeding 24-26°C seemed to affect gonad growth and nutrient
358 accumulation (Shpigel et al., 2004). Although in the present study statistical analysis did not
359 reveal any correlation between salinity and larval density, the absence of larvae in the
360 environment appeared to coincide with a significant decrease in salinity. Monitoring of salinity
361 seems important in the *P. lividus* study because the rapid decrease in salinity seems to induce
362 high mortality rates on sea urchins (Fernandez et al., 2006).

363 This study showed the difficulty of observing the evolution of the *P. lividus* life cycle
364 over time. A spawning phenomenon followed by a larvae peak and then a settler peak was
365 expected. However, data highlighted the presence of settlers before the larvae arrival and the
366 spawning phenomenon. This would support the hypothesis that sites are supplied by
367 allochthonous larvae and/or by sporadic spawning events as larvae can disperse over long
368 distances (Cowen et al., 2006). This study also showed a limitation of the method used for
369 sampling larvae. When *P. lividus* larvae were differentiated from those of other echinoderms,
370 referenced densities were very low even during the spawning peak, while settlement
371 abundances were higher. It is therefore difficult to derive conclusions about the existence of
372 autumn spawning by sampling larvae, although studies have shown that it was possible to
373 determine the number of annual spawning events with larval counts (Pedrotti and Fenaux, 1992;
374 Pedrotti, 1993; López et al., 1998) and with benthic post-settlement larval counts (Verlaque,
375 1984; Fenaux, 1987; Sala and Zabala, 1996). In addition, our results were consistent with those
376 of López et al. (1998) which indicated that, given the high variability of planktonic data, studies
377 of benthic stages provided a better representation of events.

378 Although previous studies showed that recruitment abundance patterns were correlated
379 with reproductive success, availability in the planktonic stage, post-metamorphic migration and
380 mortality (Hunt and Scheibling, 1997; Balch and Scheibling, 2000), no correlation between
381 spawning intensity (GSI) and the abundance patterns of larvae, settlers and recruits was

382 observed at the study sites. Nevertheless, these results were consistent with previous studies
383 describing high variability in the recruitment rate (Hereu et al., 2004) and in reproductive
384 success (Calderón et al., 2012). Mortality rates for young benthic stages are known to be very
385 high of about 75% in the first six months (Sala and Zabala, 1996) and 99% in the first year after
386 settlement (López et al., 1998). Survivors can escape predation by reaching shelters (Sala and
387 Zabala, 1996).

388

389 *4.4. Habitats and shelters*

390 The habitat study revealed that recruitments were more abundant in rocky habitats.
391 Although the arrival of settlers occurs in both rocky and vegetal habitats, recruitment seems to
392 be limited within the seagrass (Karlson and Levitan, 1990). Prado et al. (2012) suggested that
393 the low settler abundances found in vegetal habitats would be due to the low effectiveness of
394 trapping sea urchins in the leaf canopy. The vegetal cover study showed that individuals from
395 the class [0-1]cm were very scarce in *P. oceanica* and that individuals from the class]1-2]cm
396 were more numerous within the turfy substrate, suggesting that these individuals had acquired
397 an adult diet. This was consistent with the results of Verlaque (1984) who observed that the diet
398 of individuals ≥ 1 cm was relatively similar to that of adults. The low densities observed on the
399 encrusting substratum could be explained by the absence of shelters and crevices conferred by
400 this type of substrate. Prior studies showed that predators of young *P. lividus* settlers were more
401 abundant in erect algae and almost absent in barren grounds (Bonaviri et al., 2010), that could
402 justify the low densities of recruits recorded in strictly vegetal shelters and highlighted the
403 preference for boulders, which give them more appropriate shelters underneath where recruits
404 could hide during the day. Verlaque (1984) assumed that the presence of recruits in shelters,
405 such as fissures, macroalgae or pebbles, may reflect an anti-predator behavior against high-
406 predation pressure. However, population dynamics was not only induced by the exposed or

407 protected nature of the habitat and consideration should be given to the state of population
408 stability (Turon et al., 1995). For the classes]1-2]cm and]2-3]cm, preferences for turfy
409 substratum were observed, but these individuals seemed to avoid the encrusting substratum and
410 *P. oceanica*. These results could be explained by the high presence of predators in macroalgae
411 forests (Bonaviri et al., 2010). In addition, the strong presence of predators would confirm data
412 on the bimodal structure of the population; when predation is high, habitat complexity is
413 fundamental because it increases shelter availability, which influences population structure
414 (Hereu, 2005; Pais et al., 2007; Ceccherelli et al., 2009). The complexity of the substrate also
415 acts as a stimulus for metamorphosis (Hereu, 2005), which is important for the settlement of
416 *P. lividus* (Oliva et al., 2016). Increasing habitat complexity increases shelter availability and
417 provides protection against predation and hydrodynamism (Sala and Zabala, 1996; Hereu,
418 2005; Clemente and Hernández, 2008); individuals settling in cryptic microhabitats have higher
419 chances of survival (Scheibling and Robinson, 2008). The present work highlighted difference
420 in abundance patterns of size classes of *P. lividus* according to habitat traits. This present study
421 clearly demonstrates the importance of substrate heterogeneity on the structure of *P. lividus*
422 populations, particularly through the presence of shelters for the stages most sensitive to
423 predation.

424

425 **5. Conclusions**

426 This study highlighted a regular annual cycle of the *P. lividus* GSI with spring spawning
427 occurring between May and June and presumed smaller autumn spawning. Variability in larval
428 phase and recruitment patterns were observed. The first suggested a high resilience capacity of
429 *P. lividus*; the second appeared to be related to the presence of major spawning associated with
430 sporadic, weaker episodes and a supply of allochthonous larvae. The predation, the protection
431 status and the presence of habitats could explain the lack of success concerning the recruitment.

432 These results revealed different spatio-temporal patterns according to the stage studied;
433 therefore, if management actions are envisaged, the variability of spatial and temporal scales
434 should be considered.

435 This work also demonstrated the difficulty of observing the temporal evolution of the
436 *P. lividus* life cycle in the natural environment. Lack of correlation between densities of the
437 different stages complicated stock prediction. The importance of habitat diversity was
438 highlighted, particularly for small individuals that are extremely sensitive to predators. Since
439 this study did not reveal the presence of autumn spawning, only continued monitoring of
440 gonadosomatic indices, combined with histological studies, will confirm this trend. Longer-
441 term monitoring would provide a better understanding of the links between abiotic drivers, the
442 different life stages of *P. lividus* and the GSI. As this work highlighted the complexity of
443 assessing larvae in marine environment, future work should focus on modelling planktonic
444 stages. Studying local processes could help to determine larvae origin, which is fundamental to
445 the development of management plans.

446 **Declaration of competing interest**

447 The authors declare that they have no known competing financial interests or personal
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449

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458

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709

1 **Figure captions**

2

3 **Fig. 1.** Location of both study sites in Corsica (NW Mediterranean Sea, France) and details of
4 settlers experiments.

5

6 **Fig. 2.** Monthly variation in the average gonadosomatic index (a), the average density of larvae
7 (b), the average density of settlers (c) for Albo and Nonza sites, throughout the study period
8 (April 2015-December 2016). In some months the sampling was done weekly, the graph shows
9 an average of the results with the standard error. Shaded months represent non-sampled dates.
10 The term “ind” is used to refer to individuals.

11

12 **Fig. 3.** Weekly variation in the average gonadosomatic index $\pm SE$ respectively, for the spring-
13 summer 2015 season (a) and the spring-summer 2016 season (b), the average density of larvae
14 respectively, for the spring-summer 2015 season (c) and the spring-summer 2016 season (d),
15 the average density of settlers respectively, for the spring-summer 2015 season (e) and the
16 spring-summer 2016 season (f), for Albo and Nonza sites. Shaded dates represent non-sampled
17 dates. The term “ind” is used to refer to individuals.

18

19 **Fig. 4.** Average density of *P. lividus* by size classes for Albo and Nonza sites for 2015 (a), and
20 2016 (b). The term “ind” is used to refer to individuals.

21

22 **Fig. 5.** Variation in average Sea Surface Temperature (SST) $\pm SE$ and salinity values $\pm SE$
23 throughout the study period (April 2015-December 2016) by month (a), for the spring-summer
24 seasons 2015 (b), and 2016 (c), for Albo and Nonza sites. The black arrow marks a significant
25 decrease in salinity following an important rainfall event.

26

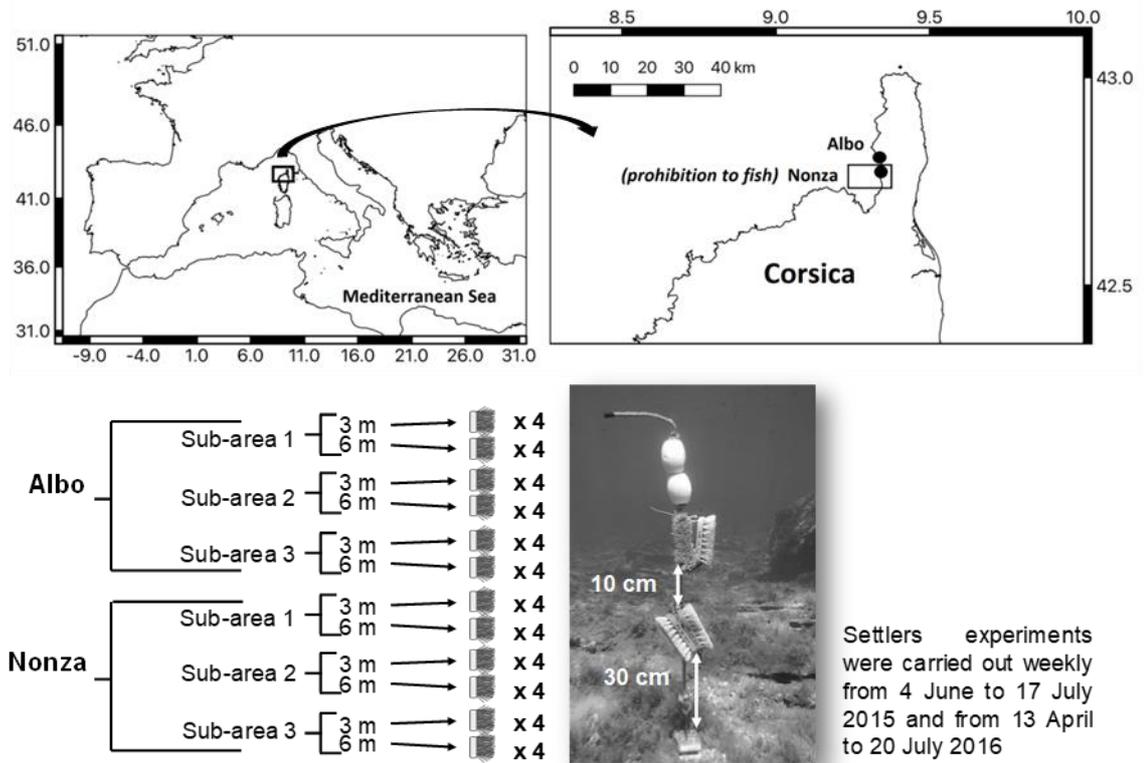
27 **Fig. 6.** Pair-plots and Pearson correlations for abiotic drivers, gonadosomatic index and life
28 cycle stages. Average densities are expressed in individuals per site and significant values are
29 shown in bold. Terms are abbreviated as follow: SST: Sea Surface Temperature, NS: not
30 significant.

31

32 **Fig. 7.** Principal Component Analysis (PCA) of relationships between vegetal cover, rocky
33 substrates and *P. lividus* densities by size classes, for recruits (individuals ≤ 2 cm) (a), for
34 juveniles, sub-adults and adults (individuals > 2 cm) (b). Factors are abbreviated as follow:
35 Enc: encrusting vegetal cover, Tur: turfy vegetal cover, Shr: shrubby vegetal cover, Arb:
36 arborescent vegetal cover, *P. oce*: *Posidonia oceanica*, S&f: slopping and falling rocks, Slr:
37 slab rock, Bou: boulders, P&c: pebbles and cobbles, San: Sand.

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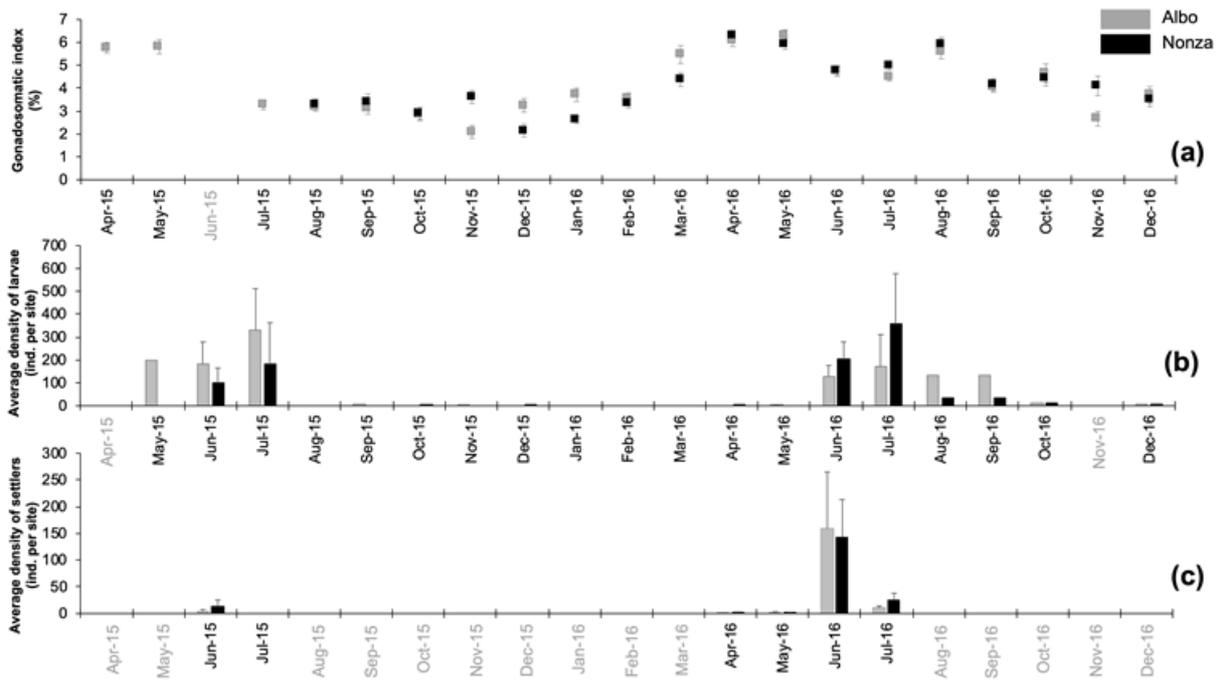
39 **Fig. 1.**



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42 **Fig. 2.**

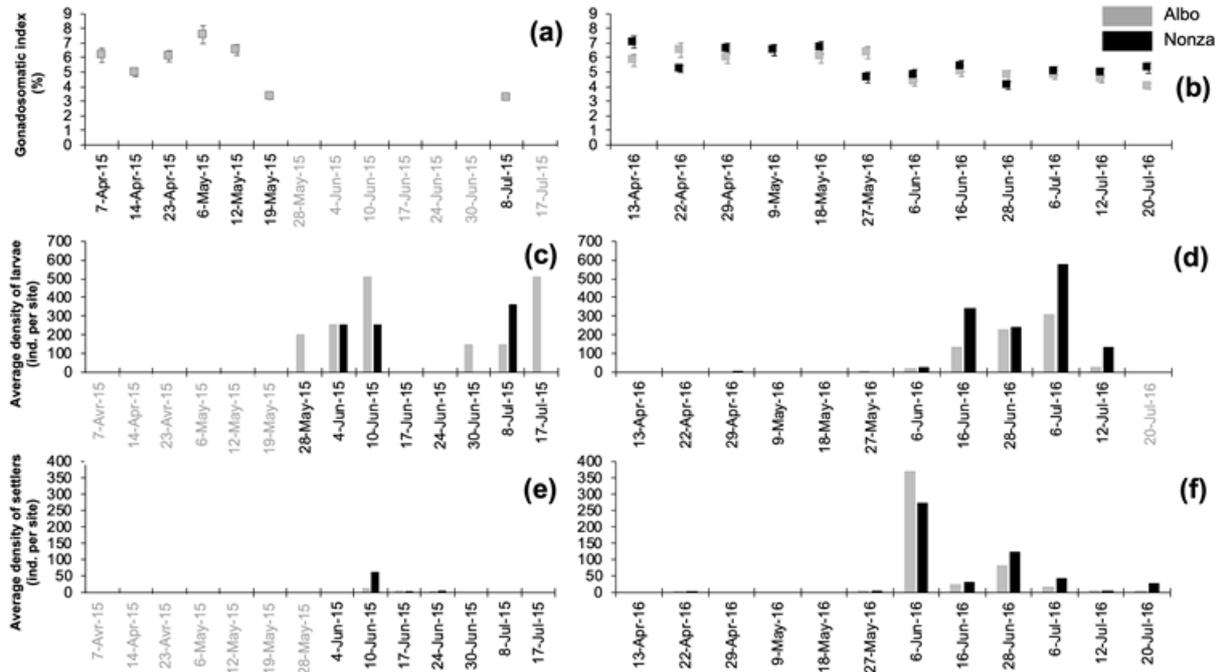


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46 **Fig. 3.**



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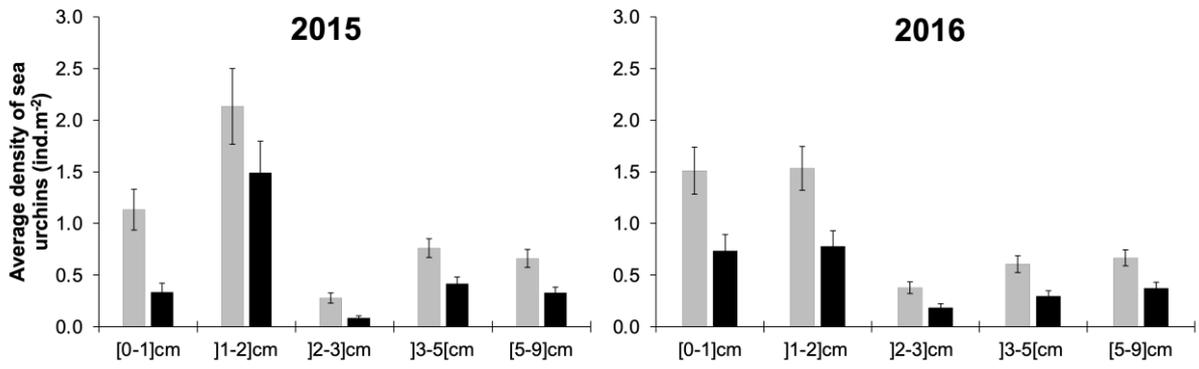
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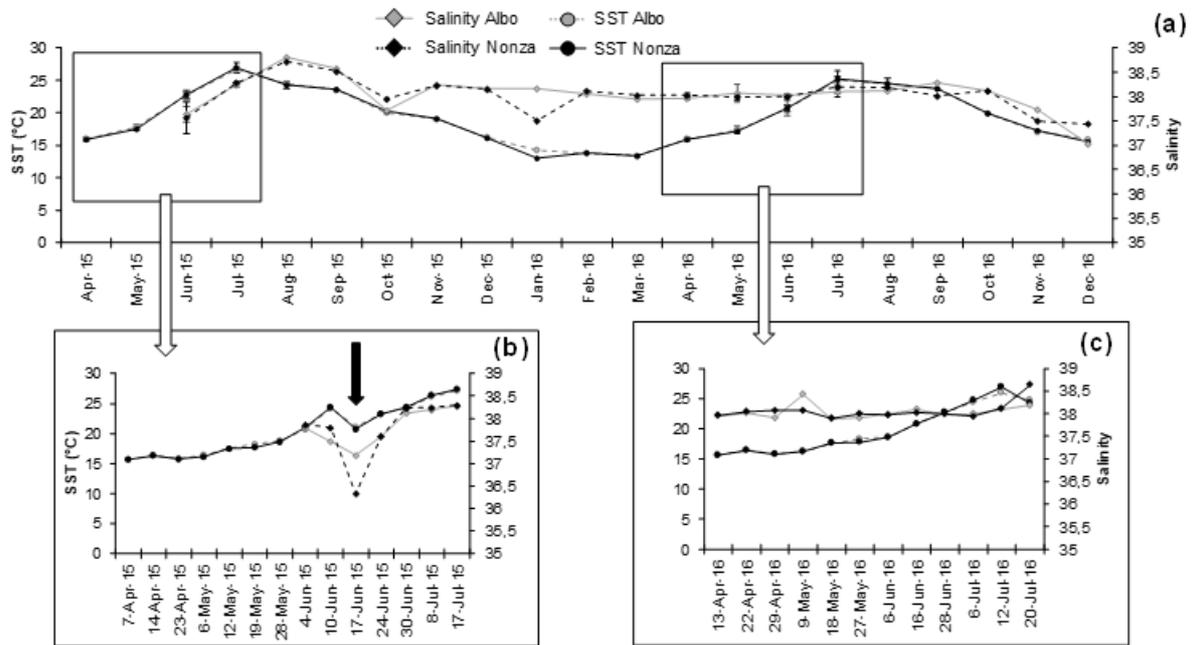
52 **Fig. 4.**



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55 **Fig. 5.**

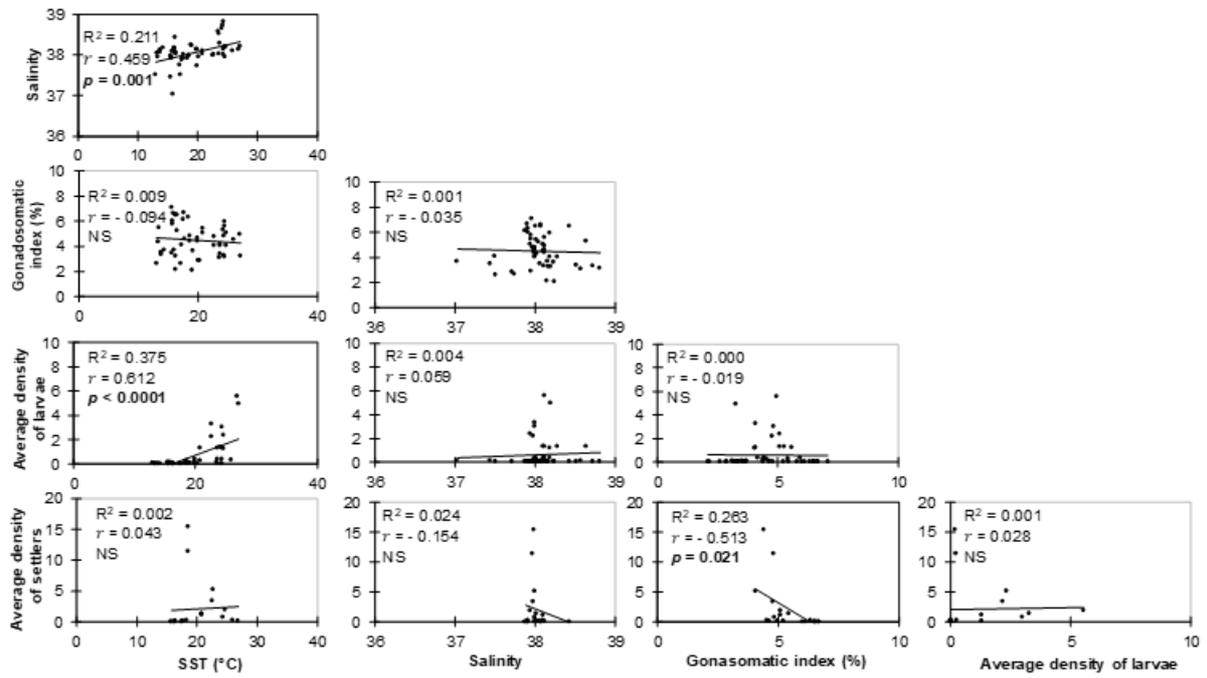


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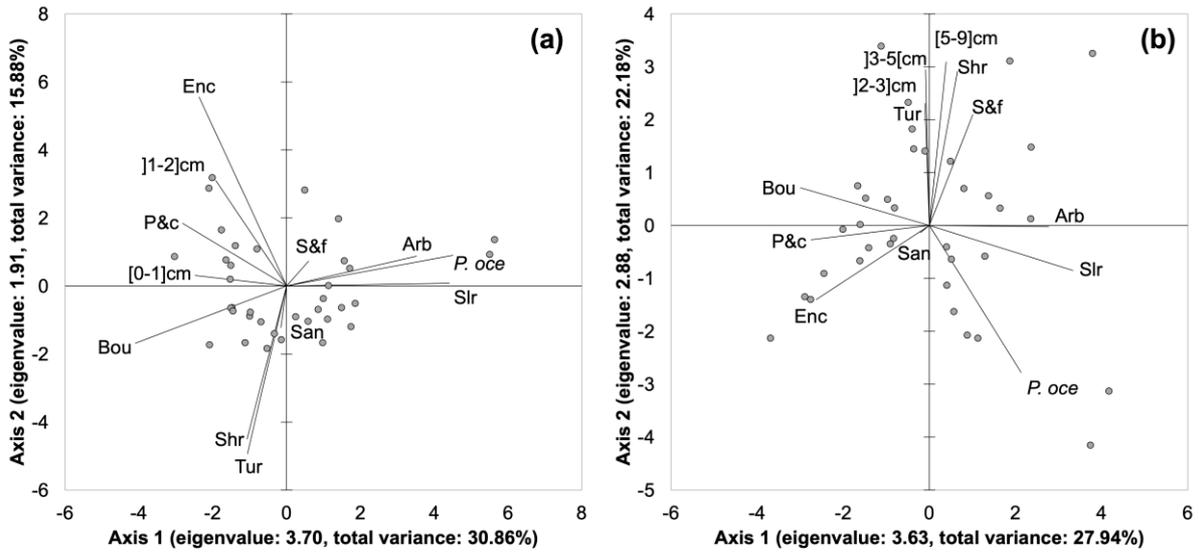
59 **Fig. 6.**



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62 **Fig. 7.**



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64

1 **Tables**

2

3 **Table 1** Results of ANOVAs investigating the spatio-temporal variability of the gonadosomatic
4 index (a), the larval stage (b), the settler stage (c). Terms are abbreviated as follow: df: degrees
5 of freedom; MS: Mean Square, F: F statistic.

	<i>df</i>	MS	F	<i>P</i> -values
(a) Gonadosomatic index				
Date	24	3.490	30.974	< 0.0001
Site	1	0.050	0.446	0.504
Date x Site	24	0.434	3.849	< 0.0001
(b) Larvae				
Site	1	4.834	0.835	0.364
(c) Settlers				
Date	17	12.886	83.737	< 0.0001
Site	1	1.082	7.029	0.009
Depth	1	0.557	3.621	0.060
Date x Site	17	0.464	3.016	0.000
Site x Depth	1	0.548	3.560	0.062

6

7

8 **Table 2** Results of MANOVA investigating the spatio-temporal variability of benthic stages
9 densities (F: F statistic).

	F	<i>P</i> -values
Date	3.927	0.002
Site	10.453	< 0.0001
Depth	7.026	< 0.0001
Date x Site	0.219	0.954
Site x Depth	2.832	0.002

10

11

12 Table 3 Results of statistical analyses investigating the influence of shelter recruit densities,
 13 MANOVA for all size classes (a), ANOVAs for each class (b). Terms are abbreviated as follow:
 14 df: degrees of freedom; MS: Mean Square, F: F statistic.

(a) MANOVA				
Type of shelter	F	<i>P</i> -values		
Type of shelter	5.092	< 0.0001		
(b) ANOVA				
Type of shelter	<i>df</i>	MS	F	<i>P</i> -value
[0-1]cm				
Type of shelter	3	0.817	8.237	< 0.0001
]1-2]cm				
Type of shelter	3	0.798	4.845	0.002

15

16