

Short-term variation of abundance of the purple sea urchin, *Paracentrotus lividus* (Lamarck, 1816) subject to harvesting in northern Portugal

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3

4 ABSTRACT

5 *Paracentrotus lividus* is a common and intensely harvested sea urchin at several European
6 locations, including the Mediterranean Sea and the Atlantic coast of the Iberian Peninsula. The
7 increasing human pressure on this resource due to the growing demand and market value of sea
8 urchin gonads as seafood raises concerns on the ecological sustainability of present fisheries,
9 which are showing a technological improvement and an expansion towards previously non-
10 harvested areas. We examined the abundance of *P. lividus* of both commercial and non-
11 commercial size before, during and after the harvesting season (from October to April) in the
12 rocky shallow subtidal habitat along the northern Portuguese coast. The abundance of
13 commercial (≥ 50 mm in test diameter) *P. lividus* individuals increased in the harvesting season,
14 but drastically dropped by about 90% in the after-harvesting period. Such a pattern was
15 consistent among three rocky shores spanning about 65 km of coast. The multivariate
16 population structure and most size classes of non-commercial sea urchins did not differ
17 depending on the period. The only exception was Class 4 (test diameter between 30 and 40
18 mm), which was more abundant in the harvesting than in the before- and, further, the after-
19 harvesting period, but only at one shore. Very small (Class 1, test diameter below 10 mm)
20 urchins were never found. The present findings suggest that human harvesting may cause
21 considerable reductions in the abundance of target *P. lividus*, but that such an effect would not
22 be evident concomitantly with harvesting, but in the subsequent period. Even if just under a
23 precautionary principle, protection strategies focused on sea urchin populations and the
24 harvesting period are advisable to contribute to maintain a sustainable local fishery of *P.*

25 *lividus* populations that are likely to be negatively affected also by other natural and
26 anthropogenic perturbations.

27

28 **1. Introduction**

29 The purple sea-urchin *Paracentrotus lividus* Lamarck, 1816 (Echinodermata, Echinoidea)
30 is one of the most harvested invertebrate species in the Iberian Peninsula and at other European
31 locations due to the high market price of its gonads (roe) as seafood (Ceccherelli et al., 2011;
32 Fernández-Boán et al., 2012; Bertocci et al., 2014; Ouréns et al., 2014, 2015; Furesi et al.,
33 2016). As a consequence, in the last decade commercial fisheries not only have expanded
34 geographically, but have also shown a technological switch from traditional harvesting
35 methods (e.g., use of hooked poles in intertidal habitats) to more modern, intensive and
36 effective means, including hookah diving (Fernández-Boán et al., 2012). This led to the
37 overexploitation of populations of this species (Pais et al., 2012), in some cases associated with
38 the eventual collapse of their fisheries (Andrew et al., 2002; Williams, 2002; Boudouresque
39 and Verlaque, 2007; Micael et al., 2009; Fernández-Boán et al. 2012; Ouréns et al. 2013). In
40 addition, *P. lividus*, analogously to other sea urchin species and when occurring at large
41 density, plays an important ecological role as a grazer and bioengineer due to its capacity to
42 trigger the transition from complex macroalgal communities to barren areas dominated by
43 encrusting coralline algae (Hereu et al., 2004; Jacinto et al., 2013; Ouréns et al., 2013).

44 Increasing concerns on the economic and ecological impacts of the depletion of *P. lividus*
45 populations in the Iberian Peninsula and elsewhere have led to the recent implementation of
46 management measures, including reductions of fleet size and number of given licenses, limits
47 to the number of catches, and the setting of a minimum legal size of captured individuals
48 (Gianguzza et al., 2006; Fernández-Boán et al., 2012; Bertocci et al., 2014). Very unlikely,
49 however, such measures are combined with the knowledge of the natural patterns of
50 distribution of sea urchins in both space and time and of their actual or potential drivers. For

51 example, *P. lividus* can show a patchy distribution in intertidal habitats where individuals
52 smaller than those found in the subtidal environment tend to be associated in large densities
53 with rockpools or depressions of the substrate (González-Irusta et al., 2010, Domínguez et al.
54 2015). Hydrodynamic forces related to wave-exposure, the timing of food availability,
55 behavioural responses implying the vertical migration of the largest individuals, and selective
56 predation are other described processes shaping the distribution of *P. lividus* (Ouréns et al.,
57 2013). Although beyond the specific goals of this study, knowing natural patterns of
58 distribution of target populations, of their driving processes, such as reproductive potential,
59 larval dispersal and stock-recruitment interactions (e.g., Butler et al., 2011; Ehrhard and
60 Fitchett, 2010; Cochrane and Chakalall, 2011; Loi et al., 2017), and of the actual fishing-driven
61 mortality per unit of effort is also needed to assess and model the sustainability of invertebrate
62 fisheries (e.g., Babcock et al., 2015).

63 In the north-western Iberian Peninsula, the professional harvesting of *P. lividus* occurs
64 typically from October to April, corresponding to the period of maturity of the gonads and their
65 highest market price (Montero-Torreiro and García Martínez, 2003; Fernández-Boán et al.,
66 2012; Bertocci et al., 2014). In northern Portugal in particular, the commercial harvesting of
67 this species has started only recently to fulfill the market demand of nearby regions, such as
68 Galicia (Spain), where overexploitation resulted into drastic reductions of local stocks (FAO,
69 2004). Nevertheless, previous studies reporting a reduced abundance of *P. lividus* along
70 stretches of coast subject to intense harvesting compared to reference (non- or much less
71 harvested) stretches, and the general lack of a positive effect of an implemented marine
72 protected area raise concerns about the impact of sea urchin harvesting in northern Portugal
73 (Bertocci et al., 2012a, 2014). These are also exacerbated by the perception, also supported by
74 some empirical evidence, that stretches of shore that had remained, until a few years ago,
75 virtually unvisited by professional harvesters of sea urchins, are now getting subject to intense
76 pressure. This is the case, for instance, of the Vila Chã shore, which was considered as a

77 reference site by Bertocci et al. (2014), but that has made front page news both in January 2016
78 and December 2017 due to the requisition of large amounts of illegally caught *P. lividus* (see
79 www.amn.pt/Media/Paginas/DetailheNoticia.aspx?nid=271 and
80 www.gnr.pt/ultimahora.aspx?linha=7826).

81 Under such circumstances, it became relevant to compare the overall abundance and the
82 size-class distribution of *P. lividus* before, during and after the harvesting season at multiple
83 rocky shores along the northern Portuguese coast. Specifically, assuming a realized impact of
84 harvesting on target urchins, we examined the hypotheses that (i) the abundance of *P. lividus* of
85 commercial size (≥ 50 mm, test diameter) decreased from before to during and, further, to after
86 the harvesting season, (ii) the total abundance and the abundance of single size classes of non-
87 commercial *P. lividus* individuals did not differ before, during and after the harvesting season,
88 and (iii) such patterns were consistent among three locations interspersed along ~65 km of
89 coast. Although within the impossibility of separating the potential effect of other processes
90 that are likely to vary over the same time scale and that could affect the patterns of distribution
91 and abundance of sea urchins besides harvesting, testing such hypotheses was aimed at
92 assessing whether the direction of changes in the examined response variables was consistent
93 with a potential impact of harvesting. Even just under a precautionary principle, this evidence
94 would have suggested the opportunity of implementing management programs to ensure the
95 sustainability of sea urchin populations at the studied shores.

96

97 **2. Materials and methods**

98 *2.1. Study system*

99 The study was carried out at three rocky shores (hundreds m long), interspersed within ~65
100 km of the mostly sandy northern Portuguese coast (Fig. 1; see also Araújo et al., 2005; Bertocci
101 et al., 2012a, 2014 for details on environmental characteristics of this region). The professional
102 exploitation of *P. lividus* along this coastline is mostly performed from mid-autumn (October-

103 November) to early spring (April) using artisanal means and, in principle, according to a
104 number of laws aimed at preventing overexploitation through limiting the usable tools, the
105 amount of catchable urchins per person per day and the minimum commercial size (see
106 Bertocci et al., 2014 for details). Nevertheless, the high market value of *P. lividus* roe and its
107 increasing demand in nearby regions has been recently associated with an increased pressure
108 on this resource due to illegal behaviour (e.g., use of hookah diving, overrun of the allowed
109 weight and nighttime harvesting) and the expansion of activities to locations that were not
110 subject to intense or any harvesting until a few years ago. The three sampled locations, in
111 particular, are, from north to south, Praia da Areosa (41.710724°N, 8.862913°W), Praia Norte
112 (41.695683°N, 8.852985°W) and Praia Congreira (41.295160°N, 08.737073°W), near the cities
113 of Areosa, Viana do Castelo and Vila Chã, respectively. The first two locations are well known
114 for being subject to intense harvesting of sea urchins, while the third has been only recently
115 indicated so by anecdotal information and police actions reported on the news. Such shores,
116 however, are comparable for a number of physical factors that are reported as potentially
117 relevant for shaping the patterns of distribution and abundance of sea urchins, including the
118 (typically granitic) nature of the substrate (Guidetti et al., 2004), (almost horizontal) slope
119 (Bulleri et al., 1999), (north to south) orientation (Jacinto et al., 2011), and (easy) accessibility
120 (Ceccherelli et al., 2011).

121

122 2.2. *Sampling design and collection of data*

123 Each shore was sampled, in the shallow subtidal habitat (0-5 m depth), at each of two
124 dates in the period before, during and after the harvesting season of *P. lividus* (July and August
125 2016, October and November 2016, and May and June 2017, respectively). At each date, two
126 different, randomly chosen, areas (~ 10 x 10 m, tens m apart) were sampled within each shore.
127 At each date and shore, the sampling was performed in a few hours, during daytime and at low
128 tide, by snorkelling divers visiting the shores in three consecutive days.

129 At each date of sampling, the number of *P. lividus* individuals of commercial size was
130 counted in each of five quadrats (1 x 1 m, some metres apart) selected at random on suitable
131 habitat (rocky reefs or large boulders) within each area and shore. Such estimates were
132 collected directly underwater using a reference ruler to identify the sea urchins individuals
133 meeting the legal catch size. For smaller *P. lividus*, all individuals were collected from each of
134 five quadrates (50 x 50 cm) that were selected based on the same criteria adopted for
135 commercial sea urchins, and put into separate cloth bags for transportation to the nearby beach.
136 There, all collected bags were initially kept in the water, then the urchins from each replicate
137 were distributed on a scaled (to the nearest mm) tray and digitally photographed before their
138 release to the sampled areas. The photographs were subsequently checked in the laboratory,
139 using an image analysis software (ImageJ), and each individual in each replicate was assigned
140 to one of five size classes (test diameter), following Bertocci et al. (2014): Class 1 ≤ 10 mm;
141 $10 \text{ mm} < \text{Class 2} \leq 20 \text{ mm}$; $20 \text{ mm} < \text{Class 3} \leq 30 \text{ mm}$; $30 \text{ mm} < \text{Class 4} \leq 40 \text{ mm}$; $40 \text{ mm} <$
142 $\text{Class 5} \leq 50 \text{ mm}$. The choice of a larger sampling resolution for commercial, compared to non-
143 commercial, *P. lividus* individuals was aimed at obtaining more representative estimates of the
144 abundance of large sea-urchins which were perceived as being relatively more sparsely
145 distributed (authors' personal observation).

146

147 2.3. Analyses of data

148 The abundance of commercial individuals, the total abundance and the abundance of each
149 of four (from Class 2 to Class 5, Class 1 excluded as not found in any sample) size classes of
150 non-commercial individuals of *P. lividus* were analysed with four-way analysis of variance
151 (ANOVA) including the following factors: 'Period' (three levels, fixed), 'Date' (two levels,
152 random, nested within 'Period'), 'Shore' (three levels, random, crossed with 'Period' and
153 'Date'), and 'Area' (two levels, random, nested within all other factors). Five 1 x 1 m or 50 x
154 50 cm quadrats provided the replicates for these analyses. When relevant in some analyses, one

155 or more terms were eliminated from the linear model either to test for the effect of ‘Period’, or
156 to obtain a more powerful test of other sources. This procedure followed the logic described in
157 Winer et al. (1991) and Underwood (1997). Before each ANOVA, the assumption of
158 homoscedasticity was verified with Cochran’s *C* test, log-transforming the data when
159 necessary. When heterogeneous variances could not be stabilised by transformation,
160 untransformed data were analysed and results were considered robust if non-significant or
161 significant with $p < 0.01$ (instead of 0.05), to compensate for increased probability of type I
162 error (Underwood, 1997). The Student-Newman-Keuls (SNK) test was used for relevant *post-*
163 *hoc* comparisons of levels of significant factors.

164 The multivariate composition (presence and relative abundance of four size classes) of non-
165 commercial *P. lividus* was analysed with permutational multivariate analysis of variance
166 (PERMANOVA, Anderson, 2001) based on Bray-Curtis untransformed dissimilarities and on
167 the same four-way model as that of univariate analyses.

168

169 **3. Results**

170 Irrespective of the shore, the abundance of *P. lividus* of commercial size showed a two-fold
171 increase from the period before to the harvested period, which was then followed by a drastic
172 drop (Table 1 and Fig. 2). The main effect of ‘Period’ was detected in spite of the significant
173 variation between areas and the interaction between dates and shores (Table 1).

174 The multivariate structure of *P. lividus* of non-commercial size varied only with
175 combinations of sampled dates and shores, but not depending on the period (Table 2).
176 Similarly, the total abundance and the abundance of almost all size classes did not vary
177 significantly with the period of sampling neither in interaction with the shore nor as main effect
178 (Table 3 and Fig. 3 A, B, C and E). Both the total abundance and Class 3 were significantly
179 different just among shores (Table 3 and Fig. 3 A and C, respectively), while Class 2 did not
180 show any significant result (Table 3 and Fig. 3 B) and Class 5 varied with combinations of

181 dates and shores (Table 3 and Fig. 3 E). The only exception was the abundance of Class 4,
182 which was affected by the 'Period x Shore' interaction (Table 3). Specifically, these urchins
183 were comparably abundant among the three examined periods at both Praia da Areosa and
184 Praia Congreira, while, at Praia Norte, they decreased from the harvesting period to the period
185 before and, even more, to the period after (Fig. 3 D). Class 5, however, displayed a non-
186 significant trend towards a lower abundance in the after-harvesting period, compared to the
187 other two periods, at Praia Norte, and in both the harvesting and the after-harvesting period,
188 compared to the before-harvesting one, at Praia Congreira (Fig. 3 E).

189

190 **4. Discussion**

191 Our results indicated that the abundance of *P. lividus* of commercial size almost
192 doubled, on average, in the harvesting season compared to the preceding period, while it
193 dropped by about 90% in the after-harvesting period. Such a pattern was consistent among the
194 sampled shores. Therefore, the original hypothesis predicting a progressive reduction of
195 commercial sea urchins from before to during and to after the harvesting season was not fully
196 supported. The present finding suggests that the abundance of large-size individuals may have
197 naturally increased from the pre-harvesting to the harvesting period, but that a drastic reduction
198 possibly due to intense human removal became apparent only at a later time. Indeed, a number
199 of biotic and abiotic processes can affect the distribution of *P. lividus* in space and time,
200 including the availability of food (Andrew, 1993), predation (Sala and Zabala, 1996; Guidetti,
201 2004; Hereu et al., 2005), competition (Guidetti et al., 2004), recruitment (Lozano et al., 1995;
202 Tomas et al., 2004), migration (Palacín et al., 1997; Crook et al., 2000) and habitat
203 heterogeneity (Hereu et al., 2005; Domínguez et al., 2015). Although none of these processes
204 were specifically examined in the present study, their likely similarity among shores that were
205 comparable for the type, slope, heterogeneity and exposure of the substrate, depth, spatial
206 extent, degree of (non) protection and fishing activities on potential predators was consistent

207 with the lack of among-shores variation in the abundance of commercial *P. lividus* individuals.
208 At the same time, they could have increased in abundance in parallel with the year-round
209 variation in the process of growth and gonad maturation of sea urchins, possibly reaching a
210 peak during the harvesting season. Under such circumstances, extant harvesting was apparently
211 unable to produce a concomitant reduction of large-size urchins as, instead, it was observed in
212 the period after the end of the harvesting season. This observation agrees with the widely
213 reported negative impact of human harvesting on *P. lividus* populations (Guidetti et al., 2004;
214 Gianguzza et al., 2006; Pais et al., 2007; Addis et al., 2009; Ceccherelli et al., 2011; Bertocci et
215 al., 2014). Unfortunately, most of these studies were not suited to examine the responses of *P.*
216 *lividus* to professional or recreational removal over time scales encompassing the entire fishing
217 season of this species. The only exception was the work by Pais et al. (2012), which included a
218 before vs. after fishing season comparison of the biomass and size of *P. lividus* at both
219 protected and harvested sites in north-western Sardinia. Such a study, however, suggested that
220 the long-term and existing overall impact of sea urchins fishery likely overwhelmed the
221 potential impact of the single fishing season. In our study, the correlative evidence available
222 and the lack of shores that could be reasonably considered not subject to sea urchin harvesting,
223 does not allow to fully tease apart the alternative that the drop in the abundance of commercial
224 urchins observed in the after-harvesting period was not only, or mainly, due to the actual effect
225 of harvesting, but due to other processes naturally variable over that time scale. Nevertheless,
226 harvesting-related effects look plausible for several reasons. First, previous studies carried out
227 in the same system, although in the intertidal habitat, did not show any reduction in the
228 abundance of large-size *P. lividus* from rocky shores that were relatively free of (at least
229 intense) harvesting (Bertocci et al., 2012a, 2014). Second, a number of processes have been
230 described as potential drivers of the widely reported variation of *P. lividus* at temporal and
231 spatial scales comparable to those examined here (e.g., Pais et al., 2007; Ceccherelli et al.,
232 2009). These include, for example, the local availability of refuges (Benedetti-Cecchi and

233 Cinelli, 1995; Sala et al., 1998; Ruitton et al., 2000; Barnes and Crook, 2001), hydrodynamics
234 (Chelazzi et al., 1997) and presence of potential competitors (Domínguez et al., 2015). Such
235 processes, however, should affect, either directly or indirectly, both large and small sea urchin
236 individuals. The fact that this did not occur in the present study, where only commercial size
237 urchins showed a consistent effect of 'Period', further points at an actual effect of harvesting
238 on these animals. Third, it could be hypothesized that high abundances of large-sized *P. lividus*
239 should rely on large amounts of available algal food, especially after the spawning season. In
240 fact, some species of sea urchins tend to reduce their food consumption with the beginning of
241 the maturation of gonads and, even more, during the spawning season, to increase it again later
242 on, when the gonads start to recover from spawning (Lawrence, 2013). Our after-harvesting
243 period corresponded not just to the after-spawning period, but also to the period when the
244 abundance of seaweeds, including very palatable green algae of the genus *Ulva*, are typically
245 more abundant on local rocky shores (e.g., Bertocci et al., 2012b). It seems, therefore, unlikely
246 that such processes were associated with the observed drastic drop in the abundance of
247 commercial *P. lividus* if this was not primarily due to the intense harvesting occurred in the
248 preceding months.

249 In agreement with our initial hypotheses, non-commercial *P. lividus* did not generally vary
250 in abundance with the examined period, irrespective of whether this was tested in interaction
251 with shore or as main effect. The only exception was provided by Class 4 urchins, which
252 progressively decreased in abundance from the harvesting to the before-harvesting and the
253 after-harvesting period at Praia Norte only. A similar, though not-significant, pattern, however,
254 was shown by Class 5. This result may suggest that, in spite of the legal size limit, some
255 relatively large individuals of *P. lividus* are still harvested, particularly at Praia Norte. As
256 reported by Bertocci et al. (2014), this could be due to the weak enforcement of the current
257 legislation, coupled with the economic advantage still provided by such sized urchins.
258 Moreover, the harvesting pressure could be relatively higher at Praia Norte due to its proximity

259 to the city of Viana do Castelo, the human population of which is larger than that of the small
260 cities nearby the other two sampled shores.

261 The total abundance of non-commercial *P. lividus*, as well as that of Class 3, varied among
262 shores irrespective of the sampled period. Several processes could explain the variability of sea
263 urchins at relatively small spatial scale, especially where this is not erased by more pervasive
264 effects of human activity (Pais et al., 2007; Ceccherelli et al., 2009, 2011). These include, for
265 example, microhabitat availability (Jacinto et al., 2013; Domínguez et al., 2015), behavioural
266 responses (Hereu, 2005), sediment input (Walker, 2007), larval supply and settlement ability
267 (Miller and Emlet, 1997). Discussing such processes in detail is beyond the goals of the present
268 study, but our findings highlight the need for future, ideally manipulative, experiments
269 specifically designed to elucidate cause-effect relationships between the intended physical and
270 biological drivers and the observed temporal and spatial patterns of abundance of non-
271 commercial *P. lividus*. Instead, it was interesting to find a complete lack of Class 1 (test
272 diameter below 10 mm) *P. lividus* individuals in all collected samples. This observation is
273 consistent with the general lack of small-sized *P. lividus* reported by Pais et al. (2007) in the
274 Mediterranean Sea. Once again, the underlying processes were not tested and could not be
275 identified by the present study, but some hypotheses can be proposed. These may include, for
276 example: (i) the lack, or very low rates, of recruitment and settlement of sea urchins at the
277 examined shore during the time spanned by the study; (ii) the preference of small-sized
278 individuals for habitats different than the shallow subtidal one sampled; (iii) the intense and
279 continuous removal of small urchins by predators preferring them over larger-sized
280 individuals; (iv) the increased predation pressure on small urchins due to the harvesting of
281 large individuals within the spines of which they can find protection (Boudouresque and
282 Verlaque, 2007). Testing such, not mutually exclusive, alternatives requires larger-scale and
283 longer-term specifically designed research (Tomas et al., 2004).

284 Indeed, the present findings are necessarily limited to the examined system and temporal
285 extent. Therefore, caution should be taken when attempting to extrapolate these results to
286 broader contexts. Nevertheless, our previous considerations on fishery-targeted *P. lividus*, the
287 accumulation of evidence of negative effects of human harvesting on sea urchin populations
288 from several locations and geographic regions, and the documented worldwide increasing
289 human pressure, and consequent impacts, on several species of sea urchins, attribute a great
290 importance to present results for the possible and likely urgent implementation of further
291 management and protection strategies of such species and populations. For example, our
292 results may suggest to implement protection measures (e.g., temporary and rotating closure to
293 harvesting of single shores or smaller areas within shores) directly focused on local populations
294 of large-size *P. lividus*, within the harvesting season. The first criterion could allow to avoid
295 the indirect, through trophic cascades, negative effect of protection observed in cases where
296 protection is primarily directed at fished populations of sea urchins predators (e.g., Guidetti,
297 2006). The second option would overcome ecological problems associated with the possible
298 assumption that the relatively larger abundance of commercial *P. lividus* during the harvesting
299 season was an indicator of a virtually irrelevant and sustainable human pressure on the target
300 populations. Even under the previously discussed limitations in our ability to univocally
301 attribute the observed patterns to the actual effect of harvesting, and not neglecting the
302 ecological role played by sea urchins which, when excessively abundant, can have negative
303 consequences on affected organisms and overall biodiversity (e.g., Ling et al., 2010; Filbee-
304 Dexter and Scheibling, 2014; Franco et al., 2015), such protection strategies are advisable just
305 for a precautionary principle. They could considerably contribute to maintain a sustainable
306 local fishery of *P. lividus* populations, possibly avoiding drops, not only and not necessarily
307 mainly due to human harvesting, in their abundances up to so drastic levels that their
308 subsequent recovery may be unlikely and their ecological and economic collapse virtually
309 inevitable (Uthicke et al., 2009). It is worth underlying, however, that assessing the realized

310 impact and sustainability vs. non-sustainability of the examined fishery would also necessarily
311 require long-term studies involving multiple consecutive harvesting seasons, comparisons
312 between harvested and not harvested shores and empirical data on the natural spatial and
313 temporal variability of the factors that can modulate the recovery rates of harvested sea urchins
314 (e.g., Turon et al., 1995; López et al., 1998; Tomas et al., 2004; Yeruham et al., 2015). In this
315 respect, *P. lividus* stocks depleted due to natural events, such as an extreme reduction of
316 salinity, have shown the ability to recover in a few years due to their high population dynamics
317 and recruitment potential (Fernandez et al., 2006). Moreover, although the individual
318 production of gametes is higher for commercial compared to smaller *P. lividus*, relatively
319 higher numbers of non-commercial, but still fertile, size classes may guarantee the self-
320 supporting capacity of the population even under a strong harvesting pressure on large
321 individuals (Loi et al., 2017). Nevertheless, our ability to understand the large set of biological
322 and ecological drivers of sea urchins dynamics and the complex interactions among them and
323 with the effects of harvesting is likely to improve slower than the increase of the global
324 demand of sea urchin roes. Therefore, our advice on applying a precautionary principle to the
325 examined *P. lividus* fishery is consistent with approach proposed worldwide for virtually all
326 fisheries (FAO, 1996).

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Table 1. Analysis of variance (ANOVA) on commercial *P. lividus* individuals (≥ 50 mm, test diameter) sampled at two dates and three shores in the period before, during and after the harvesting season. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant ($p > 0.05$).

Source of variation		df	MS	<i>F</i>	Denominator for <i>F</i>
Period	= P	2	57.47	68.65**	D(P) ^a
Date(Period)	= D(P)	3	0.84	0.19	D(P) x S
Shore	= S	2	24.34	5.50 *	D(P) x S
P x S		4	1.15	0.26	D(P) x S
D(P) x S		6	4.43	6.55***	Area(D(P) x S)
Area(D(P) x S)		18	0.68	1.89 *	Residual
Residual		144	0.36		
Cochran's test		$C = 0.129$, ns			
Transformation		$\text{Ln}(x+1)$			

^aTested over the D(P) MS after elimination of the P x S term that was not significant at $p > 0.25$.

Table 2. Permutational multivariate analysis of variance (PERMANOVA) on non-commercial *P. lividus* individuals (four size classes < 50 mm, test diameter) sampled at two dates and three shores in the period before, during and after the harvesting season. Significant effects are indicated in bold.

Source of variation		df	MS	pseudo- <i>F</i>	p	No. unique permutations	Denominator
Period	= P	2	4250.9	0.95	0.570	997	$D(P)+20\sigma^2_{P \times S}+30\sigma^2_{D(P)}$
Date(Period)	= D(P)	3	4233.4	0.81	0.743	997	D(P) x S
Shore	= S	2	12796.0	2.44	0.004	998	D(P) x S
P x S		4	5811.3	1.11	0.374	999	D(P) x S
D(P) x S		6	5246.9	1.72	0.003	998	Area(D(P) x S)
Area(D(P) x S)		18	3047.6	0.96	0.611	996	Residual
Residual		144	3174.9				

Table 3. ANOVA on the total and each of four size classes of non-commercial *P. lividus* ($10 \leq$ Class 2 < 20, $20 \leq$ Class 3 < 30, $30 \leq$ Class 4 < 40, and $40 \leq$ Class 5 < 50 mm) sampled at two dates and three shores in the period before, during and after the harvesting season. Individuals smaller than 10 mm (test diameter, ‘Class 1’) are not included as they were not found in any sample. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant ($p > 0.05$).

Source of variation	df	Total		Class 2		Class 3		Class 4		Class 5	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Period = P	2	47.17	1.57 ^a	0.74	3.41 ^b	0.28	1.31 ^a	0.52	no test	12.95	2.42 ^a
Date(Period) = D(P)	3	30.06	2.26	0.17	0.77	0.21	3.03	1.21	27.30***	5.36	0.48
Shore = S	2	134.84	10.13 *	0.82	3.79	0.50	7.19 *	4.91	110.49***	25.32	2.28
P x S	4	21.82	1.64	0.31	1.45	0.05	0.76	0.31	6.86 *	9.14	0.82
D(P) x S	6	13.31	1.31	0.22	1.63	0.07	0.32	0.04	0.12	11.11	5.97**
Area(D(P) x S)	18	10.13	1.36	0.13	0.71	0.21	1.42	0.36	1.64	1.86	0.70
Residual	144	7.44		0.19		0.15		0.22		2.64	
Cochran's test		C = 0.113, ns		C = 0.265**		C = 0.132, ns		C = 0.096, ns		C = 0.110, ns	

Transformation	None	None	Ln(x+1)	Ln(x+1)	None
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^aTested over the D(P) MS after elimination of the P x S term that was not significant at $p > 0.25$.

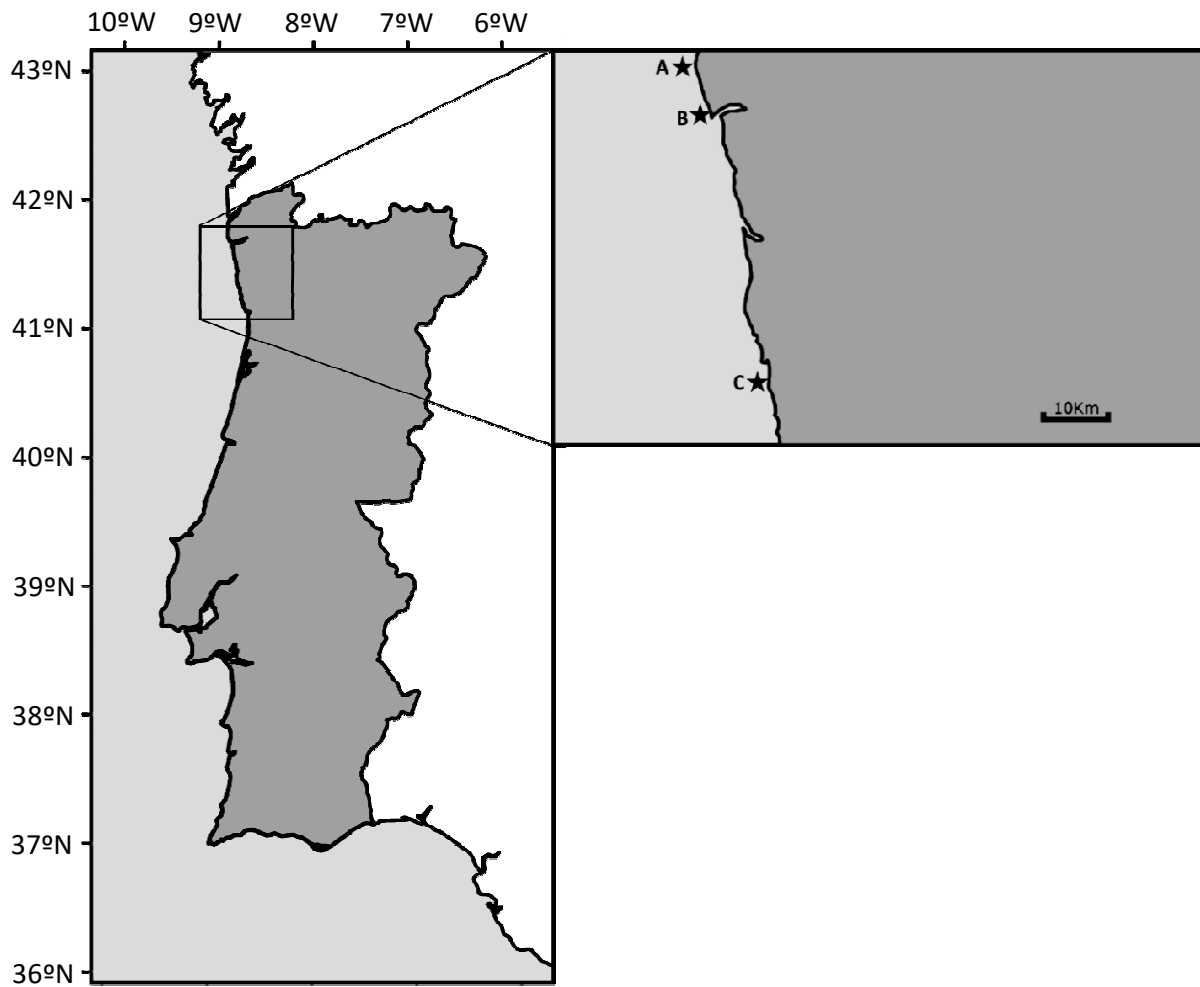
^bTested over the D(P) x S MS after elimination of the P x S and the D(P) terms that were not significant at $p > 0.25$.

FIGURE CAPTIONS

Figure 1. Map of the study area along the northern Portuguese coast, showing the three sampled locations (A = Praia da Areosa, B = Praia Norte, C = Praia Congreira).

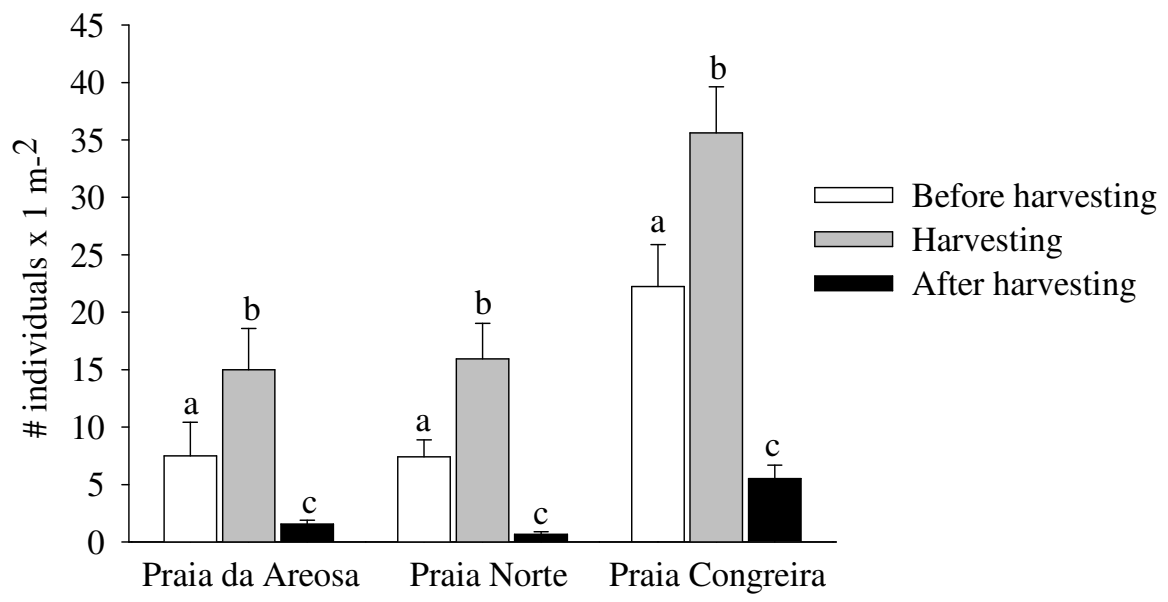
Figure 2. Mean (+SE) abundance of *P. lividus* of commercial size (≥ 50 mm, test diameter) at each of three shores sampled in the period before, during and after the harvesting season. Data averaged over five replicate quadrats, two areas and two dates of sampling. Different letters above bars indicate levels that differ significantly at $p < 0.05$ (SNK test).

Figure 3. Mean (+SE) total abundance and abundance of each of four size classes of non-commercial *P. lividus* ($10 \leq \text{Class 2} < 20$, $20 \leq \text{Class 3} < 30$, $30 \leq \text{Class 4} < 40$, and $40 \leq \text{Class 5} < 50$ mm) at each of three shores sampled in the period before, during and after the harvesting season. Data averaged over five replicate quadrats, two areas and two dates of sampling. Different letters above bars indicate levels that differ significantly at $p < 0.05$ (SNK tests, only within-shore comparisons are appropriate).

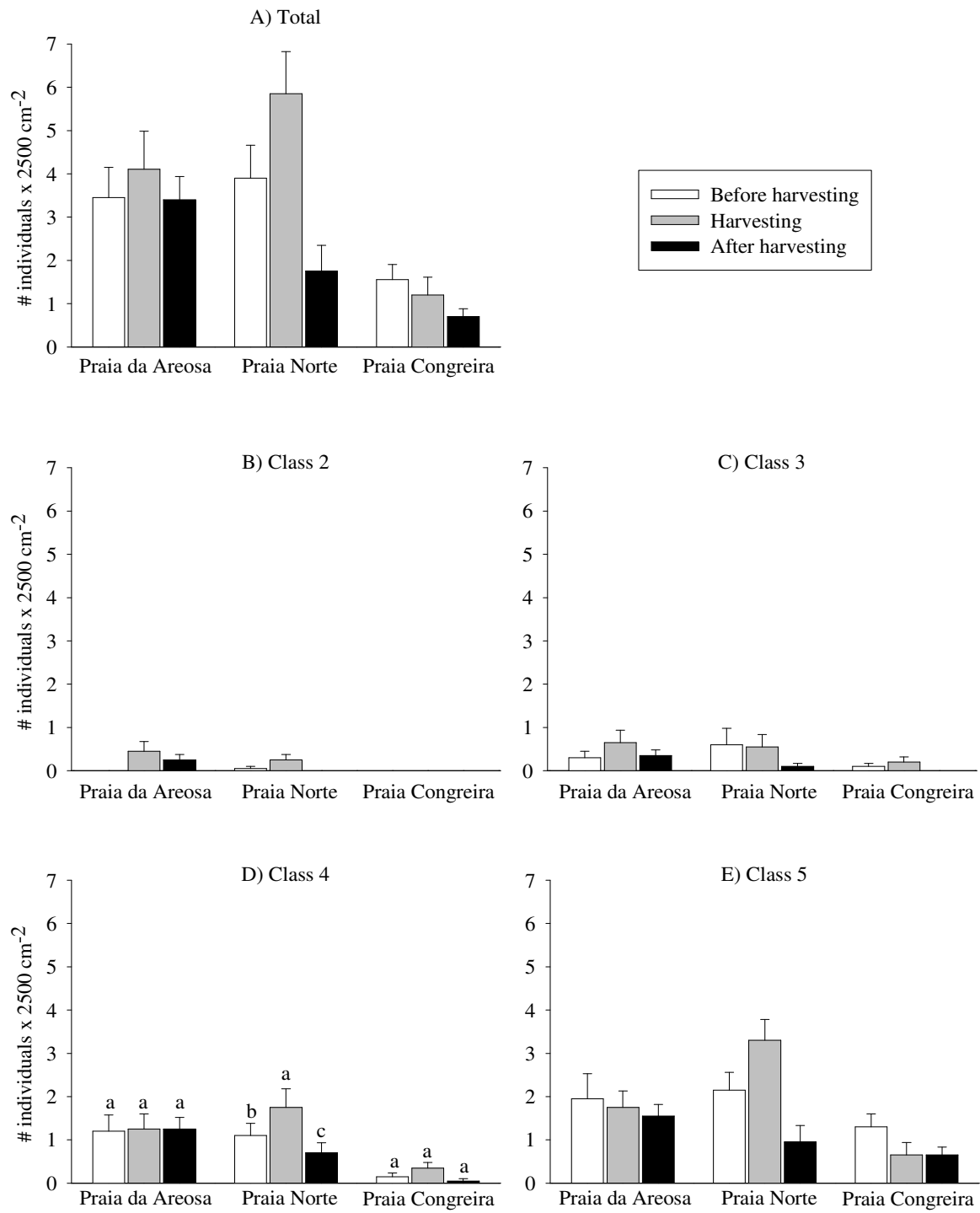


Bertocci et al. Figure 1

Commercial size *P. lividus*



Bertocci et al. Figure 2



Bertocci et al. Figure 3