

Intensive sea urchin harvest rescales *Paracentrotus lividus* population structure and threatens self-sustenance (#82410)

1

First submission

Guidance from your Editor

Please submit by **2 Mar 2023** for the benefit of the authors (and your token reward) .



Structure and Criteria

Please read the 'Structure and Criteria' page for general guidance.



Raw data check

Review the raw data.



Image check

Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the [materials page](#).

5 Figure file(s)

3 Table file(s)

5 Raw data file(s)

3 Other file(s)



Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. BASIC REPORTING
2. EXPERIMENTAL DESIGN
3. VALIDITY OF THE FINDINGS
4. General comments
5. Confidential notes to the editor






 You can also annotate this PDF and upload it as part of your review

When ready [submit online](#).





Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your [guidance page](#).




BASIC REPORTING

-  Clear, unambiguous, professional English language used throughout.
-  Intro & background to show context. Literature well referenced & relevant.
-  Structure conforms to [Peerj standards](#), discipline norm, or improved for clarity.
-  Figures are relevant, high quality, well labelled & described.
-  Raw data supplied (see [Peerj policy](#)).

EXPERIMENTAL DESIGN

-  Original primary research within [Scope of the journal](#).
-  Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
-  Rigorous investigation performed to a high technical & ethical standard.
-  Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

-  Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
-  All underlying data have been provided; they are robust, statistically sound, & controlled.
-  Conclusions are well stated, linked to original research question & limited to supporting results.



The best reviewers use these techniques

Tip

Example

Support criticisms with evidence from the text or from other sources

Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.

Give specific suggestions on how to improve the manuscript

Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).

Comment on language and grammar issues

The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 - the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.

Organize by importance of the issues, and number your points

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

Please provide constructive criticism, and avoid personal opinions

I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

Comment on strengths (as well as weaknesses) of the manuscript

I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

Intensive sea urchin harvest rescales *Paracentrotus lividus* population structure and threatens self-sustenance

Nicole Ruberti¹, Gianni Brundu², Giulia Ceccherelli³, Daniele Grech², Ivan Guala², Barbara Loi², Simone Farina^{Corresp. 4, 5}

¹ Department of Architecture, Design and Planning, University of Sassari, Sassari, Italy

² IMC- International Marine Centre, Torre Grande (OR), Italy

³ Department of Chemical Physical Mathematical and Natural Science, University of Sassari, Sassari, Italy

⁴ Department of Integrative Marine Ecology (EMI), Stazione Zoologica Anton Dohrn-National Institute of Marine Biology, Ecology and Biotechnology, Genoa Marine Centre, Genoa, Italy

⁵ National Research Council, Institute for the study of Anthropic Impacts and Sustainability in the Marine Environment (CNR-IAS), Torre Grande, Italy

Corresponding Author: Simone Farina
Email address: simone.farina@szn.it

The harvest of the edible sea urchin *Paracentrotus lividus* is intensively practiced in some regions of the Western Mediterranean Sea. The removal of the largest individuals can determine an overall reduction in population size and a size class truncation that can lead to a drastic drop the self-sustenance. The aim of this study is to evaluate the reproductive cycle and reproductive potential across five years of a population in one the main harvest hotspots of Sardinia (Italy). The breeding stock consists of commercial and under-commercial size individuals and for this reason they were sampled on a monthly basis to estimate their GonadoSomatic Index. The reproductive potential of the population - Total Gamete Output - was calculated across the five-year period in relation with the variation of the density of the major breeding stock. Moreover, during the last year, the reproductive cycle and reproductive potential were also estimated in a well-conserved population of the nearby Marine Protected Area, as a reference control. No variation in GonadoSomatic Index and Individual Gamete Output was found over the five years nor when compared with the ones of protected population in the last year. However, the intensive harvesting drastically rescaled the population body-size: although density of the commercial size class was stable on minimum values, density of the under-commercial size-class halved from the beginning to the end of the monitoring. Accordingly, the proportional decrease of their gamete output contribution led to loss 40% of the reproductive potential of the whole population in the five-year period. On the basis of these results, if harvest pressure would continue, the local population in ten years will not be able to contribute to the recruitment. Interestingly, whilst the Total Gamete Output decreased as consequence of the drastic decrease of the major population breeding stock, the inter-annual trends of

GonadoSomatic Index and Annual Gamete Output slightly decreases and increases respectively. These patterns suggest that a potential compensatory response as reproductive investment of the survivors in gonad production rate or spawning intensity in front to the lack of the largest sea urchins need to be investigated. Definitely, this work brings clear evidence of the direct effect of the size-selective harvesting in the rapid loss of the population self-sustenance. Furthermore, it lays new prospective for future research of the indirect effects of the rescaling population body-size in functional traits of key herbivores species such as *P. lividus* in Mediterranean Sea that could become important both for the sustainable exploitation and ecosystems conservation management.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38

Intensive sea urchin harvest rescales *Paracentrotus lividus* population structure and threatens self-sustenance

Nicole Ruberti¹, Gianni Brundu², Giulia Ceccherelli³, Daniele Grech², Ivan Guala², Barbara Loi², Simone Farina^{4,5}

¹ University of Sassari, Department of Architecture, Design and Planning, Via Piandanna 4, 07100 Sassari, Italy

²IMC - International Marine Centre, Loc. Sa Mardini, Torre Grande, 09170, Oristano, Italy.

³ University of Sassari, Department of Chemical Physical Mathematical and Natural Science, Via Vienna 2, 07100, Sassari, Italy.

⁴ Department of Integrative Marine Ecology (EMI), Stazione Zoologica Anton Dohrn–National Institute of Marine Biology, Ecology and Biotechnology, Genoa Marine Centre, 16126 Genoa (Italy).

⁵ National Research Council, Institute for the study of Anthropic Impacts and Sustainability in the Marine Environment (CNR-IAS), Loc. Sa Mardini, 09170 Torre Grande, OR (Italy)

Corresponding author: simone.farina@szn.it

39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83

Abstract

The harvest of the edible sea urchin *Paracentrotus lividus* is intensively practiced in some regions of the Western Mediterranean Sea. The removal of the largest individuals can determine an overall reduction in population size and a size class truncation that can lead to a drastic drop the self-sustenance. The aim of this study is to evaluate the reproductive cycle and reproductive potential across five years of a population in one the main harvest hotspots of Sardinia (Italy). The breeding stock consists of commercial and under-commercial size individuals and for this reason they were sampled on a monthly basis to estimate their GonadoSomatic Index. The reproductive potential of the population - Total Gamete Output - was calculated across the five-year period in relation with the variation of the density of the major breeding stock. Moreover, during the last year, the reproductive cycle and reproductive potential were also estimated in a well-conserved population of the nearby Marine Protected Area, as a reference control. No variation in GonadoSomatic Index and Individual Gamete Output was found over the five years nor when compared with the ones of protected population in the last year. However, the intensive harvesting drastically rescaled the population body-size: although density of the commercial size class was stable on minimum values, density of the under-commercial size-class halved from the beginning to the end of the monitoring. Accordingly, the proportional decrease of their gamete output contribution led to loss 40% of the reproductive potential of the whole population in the five-year period. On the basis of these results, if harvest pressure would continue, the local population in ten years will not be able to contribute to the recruitment. Interestingly, whilst the Total Gamete Output decreased as consequence of the drastic decrease of the major population breeding stock, the inter-annual trends of GonadoSomatic Index and Annual Gamete Output slightly decreases and increases respectively. These patterns suggest that a potential compensatory response as reproductive investment of the survivors in gonad production rate or spawning intensity in front to the lack of the largest sea urchins need to be investigated. Definitively, this work brings clear evidence of the direct effect of the size-selective harvesting in the rapid loss of the population self-sustenance. Furthermore, it lays new prospective for future research of the indirect effects of the rescaling population body-size in functional traits of key herbivores species such as *P. lividus* in Mediterranean Sea that could become important both for the sustainable exploitation and ecosystems conservation management.

84
85
86
87
88
89
90
91
92
93
94
95
96

1. Introduction

97
98

Fishing is the most widespread human exploitative activity in the marine environment, and it is size-selective by definition (Longhurst, 2006). Worldwide fishery is based on removing individuals above a minimum legal size (Jackson et al., 2001) and in theory, juveniles can grow large enough to reproduce at least once before being harvested, guaranteeing their own replacement (Law, 2000). However, nowadays fishing is so intense (Baum et al., 2003; Myers & Worm, 2003; Pauly et al., 1998) that affects many aspects of the biology of a target species, such as demography, life history and ecology (Fenberg & Roy, 2008).

105
106
107
108
109
110
111
112
113

One of the main effects of the size-selective harvest is the deep change in demographic structure of the population. Specifically, the continuous removal of the largest individuals rather than the smallest ones can determine an overall reduction in population abundance and body-size (Fenberg & Roy, 2008). Thus, under heavy size-selective harvest, an age-size truncation of the populations occurs, leading to a multitude of consequences (Festa-Bianchet, 2003; Heino & Godo, 2002). This phenomenon is critical for the self-sustenance of populations that need relying totally on the youngest specimens and that eventually results in a serious decline of the population growth rate (Enberg, Jørgensen & Mangel, 2010). Effectively, it is widely demonstrated that in general large individuals give the greatest contribution to successful

114 offspring and the size and quality of larvae of some exploited marine fish have been shown to be
115 positively correlated with maternal length and age (Berkeley, Chapman & Sogard, 2004; Trippel,
116 1995; Vallin & Nissling, 2000). Thus, the removal of the largest and oldest individuals generally
117 decreases the population ability to replenish itself.

118 Moreover, the body-size is central to ecology from the organismal physiology to the
119 functioning of communities and ecosystems (Peters, 1983). The intensive size-selective
120 harvesting can cause alterations in the growth rate and in the timing of maturation of the
121 youngest specimens (Hamilton et al., 2007). The decrease in mean size and abundance of the
122 target fishes can also generate negative effects on non-target species through the food web
123 interactions (Audzijonyte et al., 2013), for example reducing the predator-prey interactions and
124 causing the proliferation of preys (e.g. Pinnegar et al., 2000). This mechanism is widely
125 demonstrated in the tri-trophic interactions fish, sea urchins and macrophytes in temperate reefs.
126 Overfishing depletes populations of predatory fish and the substantial loss of the large predators
127 that exert a top-down control mechanism determines an unregulated increase in sea urchin
128 population densities (Guidetti, Boero & Bussotti, 2005; McClanahan & Shafir, 1990; Micheli et
129 al., 2005; Sala et al., 2012; Sala, Boudouresque & Harmelin-Vivien, 1998; Shears & Babcock,
130 2003).

131 The indirect impact of the size-selective harvesting on the ecosystems largely depends on
132 the functional role and competitive dominance of the target species (Kaiser & Jennings, 2001).
133 For example, heavy size-selective harvest of sea urchin predatory fishes generates cascading
134 effects pushing the system beyond the resilience tipping points (Ling et al. 2015) and facilitates a
135 shift from vegetated coastal marine ecosystem to a bare rocky area - barrens – hosting low
136 biodiversity (e.g., Bianchelli & Danovaro 2020).

137 In the last decades the lower-trophic-level fisheries intensified the exploitation on
138 remaining commercial species, including invertebrates (e.g., Anderson et al., 2011), among
139 which sea urchins represent a relevant economic resource (Andrew et al., 2002). Sea urchin
140 fisheries further worsen the health of the ecological system. In the extreme cases, in addition to
141 low density and biomass of predatory fishes due to overfishing, the intensive sea urchin
142 harvesting leads to the abrupt decline of these herbivores and, ultimately, determining the
143 collapse of their populations (e.g., Johnson et al. 2012).

144 Since the gonads are proportional to the sea urchin size and are more mature and
145 developed in the largest individuals (Mita et al., 2007), the size-selective harvesting of the largest
146 sea urchins can gradually compromise the population fertility (Brewin et al., 2000; Byrne, 1990;
147 Guettaf, San Martin & Francour, 2000). Many studies demonstrated strong correlations between
148 the reproductive potential of the harvested populations and the harvesting pressure (Levitan &
149 Sewell, 1998; Levitan, Sewell & Chia, 1992; Pennington, 1985; Tegner & Dayton, 1977).
150 Populations under heavy harvesting pressure are often destined to collapse unless they receive
151 enough larval supply from the outside (Dubois et al., 2016).

152 Furthermore, the sea urchin species commercially harvested are led to such a strong
153 reduction in population density that consequent changes in the community structure of
154 macrophytes ecosystems have also been observed (Steneck et al., 2002; Vadas & Steneck, 1995;
155 Villouta, 2000). Moreover, the size-selective harvesting of the edible sea urchin species can
156 increase the individual growth rate, size, and abundance of others non-harvested sea urchin
157 species because of release from competitive pressure, for example *Arbacia lixula* is favored by
158 the removal of *Paracentrotus lividus* (Guidetti, Terlizzi & Boero, 2004).

159 The edible sea urchin *P. lividus* (Lamarck 1816) is the most exploited species in the
160 Mediterranean Sea for its appreciated gonads but, at the same time, it is an indispensable
161 functional herbivore in controlling macroalgal communities through the grazing activity (Boada
162 et al., 2017; Guarnieri et al., 2014; McClanahan & Sala, 1997; Prado et al., 2007). In some
163 regions of the Western Mediterranean Sea, the intensive harvest of *P. lividus* locally re-scaled
164 population body-size determining an evident cut-off of the population structure above the
165 commercial size-class of 50 mm (test diameter without spines; TD) and with the depletion of the
166 major breeding stock (Couvray et al., 2015; Gianguzza et al., 2006; Guidetti, Boero & Bussotti,
167 2004).

168 In Sardinia (Italy), despite regional decrees regulating quotas, fishing calendar and the
169 minimum size, *P. lividus* is extensively harvested all-year-round since the early 2000s
170 (Ceccherelli et al., 2011; Pais et al., 2012, 2007; Pieraccini, Coppa & De Lucia, 2016). The
171 intensive exploitation (given by the sum of authorized and illegal harvesting) has dramatically
172 reduced the sea urchin density in many coastal areas (Ceccherelli et al., 2021). In some cases, the
173 loss of the largest and oldest individuals, as the major breeding stock of the population, is
174 shifting all the reproduction activity onto the shoulders of the youngest fertile sea urchins (Loi et
175 al., 2017). Thus, monitoring the gamete production of the overexploited populations can be
176 crucial to manage the local fishery sustainability but also to prevent the population collapse. The
177 spatial and temporal variation of the gamete production can be assessed through the analysis of
178 the annual reproductive cycle (Brewin et al., 2000). The reproductive cycle is generally
179 evaluated through the estimation of the GonadoSomatic Index, as fluctuations in gonad size and
180 spawning periods (Gianguzza et al., 2013; Shpigel et al., 2004; Spirlet, Grosjean & Jangoux,
181 1998), and from which the reproductive potential of a population (the total gamete output)

182 depends on (Brewin et al., 2000). The variation of the reproductive cycle is strictly associated to
183 environmental factors changes, such as sea surface temperature (Beddingfield & McClintock,
184 1998; Levitan, 1991; Levitan, Sewell & Chia, 1992; Spirlet, Grosjean & Jangoux, 2000; Spirlet,
185 Grosjean & Jangoux, 1998), but also wave height or food quality (Brady & Scheibling, 2006;
186 Byrne, 1990; Gianguzza et al., 2013; Lozano et al., 1995; Minor & Scheibling, 1997; Sellem &
187 Guillou, 2007). Overall, the largest *P. lividus* adults represent at the same time the major
188 breeding stock of the population and the target commercial size-class ($TD \geq 50$ mm), whilst the
189 smaller fertile individuals, the under-commercial size-class ($40 \leq TD < 50$ mm), are still
190 important contributors for the self-sustenance of the population (e.g. Loi et al., 2017) and
191 represent the future stock of fishing. These fertile size-classes can produce more than one cohort
192 of mature gametes in a single breeding season (Mita et al., 2007) and their reproductive cycle
193 generally has one or two seasonal peaks (Boudouresque & Verlaque, 2001; Ouréns, Fernández &
194 Freire).

195 The aim of this study is to estimate the variability across five years of the reproductive
196 cycle and the reproductive potential of *P. lividus* in one of the main harvest hotspots of Sardinia
197 (Italy). The reproductive cycle was evaluated through the estimation of the GonadoSomatic
198 Index and the potential relation of the Sea Surface Temperature and Sea Wave Height with the
199 spawning events was explored. Whilst, the reproductive potential was calculated as the Total
200 Gamete Output produced by the whole population, as it is strictly related to the density of the
201 fertile sea urchins (commercial and under-commercial size-classes). Finally, during the last year
202 of sampling, the reproductive cycle and the reproductive potential were also compared with those
203 of a well-conserved population of the nearby Marine Protected Area as control reference.
204 Although the reproductive cycle is expected no differing across the years, the reproductive

205 potential of the whole population is expected to drastically decline due to the phenomenon of the
206 rescaling population body-size.

207

208 **2. Material and Methods**

209

210 *2.1. Study site*

211

212 This study was conducted at Su Pallosu Bay (40.0489° N, 8.4161° E), located in the north
213 of the Peninsula of Sinis (Sardinia, Western Mediterranean), a high natural density area of sea
214 urchins that has been overexploited by fishermen for many years (e.g. Fois et al., 2020; Farina et
215 al., 2020; Coppa et al., 2018; Guala, Simeone & Baroli, 2009; Pais et al., 2007). The favourable
216 environmental conditions, such as the shallow calcareous plateau with *Posidonia oceanica*
217 patches (De Falco et al., 2008) and the low predatory fish density (Marra et al., 2016), seem to
218 support a high sea urchin colonization (Oliva et al., 2016). Moreover, the low current speed
219 determining recirculation cells of water surface in the Bay (Farina et al., 2018) is probably
220 favourable for the reproduction success of the local sea urchin population (Ouréns et al., 2013).
221 Su Pallosu Bay is considered one of the main harvest hotspots (harvest **locality**, H hereafter) in
222 Sardinia (Fig.1). In this area, and along the entire coast of the island, the professional sea urchin
223 harvesting is officially open from November to April and it is allowed with scuba diving.
224 Nowadays the daily catches amount to 1500 per fisherman or 3000 per boat, while the minimum
225 catch size is above 5 cm diameter size (RAS, Autonomous Region of Sardinia, decree no.
226 2524/DecA/102 of 7 October 2009).

227 In the last year of sampling, a control population was selected at Cape Seu (39.8980° N,
228 8.4010° E) in the nearby Marine Protected Area ("Penisola del Sinis - Isola di Mal di Ventre",
229 established in 1997; Fig.1), where the harvesting is strongly restricted (Control **locality**, C from

230 now on) in terms of number of fishing licenses (only residents), areas, modality (only free diving
231 is admitted) and catch quotas per day (Farina et al. 2020; Ceccherelli et al., 2022).

232 The study area is far from urbanizations, harbours, aquaculture activities and rivers and,
233 accordingly, there was no anthropogenic influence on the dissolved nutrient concentration on
234 macroalgal composition and abundance over the years (Loi et al., 2017).

235 The annual average of the Sea Surface Temperature (SST) ranged between 17.5° C and
236 19° C with colder open waters and warmer coastal waters (Cucco et al., 2006). The wind-waves
237 are generated on a wide fetch by the prevailing winds that, in the form of severe winter storms,
238 can produce intense Sea Wave Height (SWH) of up to 5m (Simeone et al. 2016). Data of the
239 daily SST (C°) were extrapolated from NOAA dataset and free downloaded from “Asia-Pacific
240 Data Research Centre” webpage (<http://apdrc.soest.hawaii.edu/las/v6/dataset?catitem=1233>).
241 Data of the hourly SWH (m) were free downloaded from Copernicus Marine Environmental
242 Monitoring Service
243 ([https://resources.marine.copernicus.eu/?option=com_csw&task=results&pk_vid=20be7e57367a](https://resources.marine.copernicus.eu/?option=com_csw&task=results&pk_vid=20be7e57367a57a51616599440425bbc)
244 [57a51616599440425bbc](https://resources.marine.copernicus.eu/?option=com_csw&task=results&pk_vid=20be7e57367a57a51616599440425bbc)). The monthly mean SST and SWH were calculated choosing an
245 intermediate point between the two sampling sites and that represents the trend of the SST and
246 SWH in each locality during the sampling periods.

247 248 2.2. *GonadoSomatic Index and Annual Gamete Output*

249
250 Sea urchins were monthly sampled across five years from 2013 to 2019 at the H locality
251 and in 2018-19 at the C locality. The estimated GonadoSomatic Index (GSI) from May of one
252 year to June of the year after representing a sampling period of a complete annual reproductive
253 cycle. Thus, GSI was monthly estimated for five sampling periods (P1-P5) at the H locality and

254 for the last sampling period (P5) at the C locality and for both commercial and under-commercial
255 size-classes.

256 The sea urchins were collected by scuba diving at two sites few hundred meters apart and
257 over a rocky bottom at the bathymetry of 5 ± 1 m (mean depth at which the harvesters usually
258 work). Depending on the year, 12 to 20 individuals were sampled for each site, both for the
259 commercial (CS, test diameter $TD \geq 50$ mm) and the under-commercial size-class (US, $40 \leq TD$
260 < 50 mm). Size and wet weights of urchins were measured, while the gonads were removed and
261 weighted and the GSI was estimated for each sampled individual as:

262

263
$$[\textit{gonad wet weight} / \textit{total wet weight}] \times 100 \quad (\text{Lawrence et al., 1965})$$

264 Since 1:1 sex ratio is usually observed, female and male were pooled together to obtain a
265 single mean of GSI value per month (monthly mean GSI; e.g. Loi et al., 2017). The annual mean
266 GSI was also estimated for the whole population as the average of the monthly mean GSI values
267 for each sampling period. The highest and the lowest peaks of the monthly mean GSI recorded
268 over a sampling period correspond to the time before the beginning (pre-spawning) and after the
269 end (post-spawning) of a spawning event.

270 The mean individual gamete output (IGO) was then calculated as the difference between
271 the monthly mean pre-spawning GSI and the monthly mean post-spawning GSI in units of
272 gamete wet weight per urchin per spawning event ($\text{g g}^{-1} \text{se}^{-1}$). The sum of the all-year-round
273 differences (IGOs) represents the Annual Gamete Output (AGO), which is the reproductive
274 contribution of each fertile size-class per year ($\text{g g}^{-1} \text{yr}^{-1}$).

275

276 2.3. *Population reproductive potential*

277

278 Sea urchin population structure was estimated during the first P1 and the last P5 sampling
279 periods (2013-14 and 2018-19) at the H locality, and in the last sampling period P5 (2018-19) at
280 the C locality. Density and size frequency distribution of sea urchins were estimated in both of
281 sites of the localities by independent underwater counts (Guala et al. 2018). The counts were
282 carried out in three replicates of 5m² (20 contiguous 50x50cm quadrats) each, the minimum
283 optimal surface to detect aggregative distribution of sea urchins, as consequence of the habitat
284 heterogeneity.

285 All the sea urchins found in the sampling quadrats were counted and measured with
286 callipers. The sea urchin abundance was then estimated as density (ind/m²) and the individuals
287 were grouped in size-classes of 10 mm of test diameter to build the population structure (e.g.
288 Farina et al., 2020, 2022).

289 Finally, the population reproductive potential was estimated as the Total Gamete Output
290 (TGO) of the whole population per m² per year that is defined as the sum of the AGO of each
291 fertile size-class multiplied for the sea urchin density (g g⁻¹ m⁻² yr⁻¹).

292

293 2.4. *Data analysis*

294

295 Variability of the monthly mean SST at the H locality was evaluated among the sampling
296 periods P1-P5 (from 2013 to 2019) throughout the non-parametric analysis of variance Kruskal-
297 Wallis test (Kruskal & Wallis, 1952). Moreover, the monthly mean SST of the last sampling
298 period P5 was compared with the temperature of the C locality (Mann-Whitney test; Mann &
299 Whitney, 1947). Similarly, difference in the monthly mean SWH was estimated among the
300 sampling periods with parametric Analysis of variance (Anova 1-way, Underwood, Underwood
301 & Underwood, 1997). In order to exclude the statistical effects induced by the sea water

302 temperature and wave height, because non-significantly different among the sampling periods,
303 these variables were successively set as further predictors with random distribution and
304 independent from the response variables in the following analysis.

305 Exploration of the GSI and IGO data was carried out to test the data assumption (i.e.,
306 normal distribution and homogeneity of the variance) before the analysis of variance (Zuur, Ieno
307 & Elphick, 2010). Since the GSI data were characterized by a different number of replicates
308 collected during the years, and non-normal distribution, General Linear Mixed Model (GLMM)
309 with Poisson family was chosen as the best tool for analysis of variance of unbalanced data
310 involving random factors (temperature and waves).

311 A GLMM was performed to assess the variance of the monthly mean GSI of the H
312 locality with “period” (five levels) and “size-class” (two levels) as fixed factors, “temperature”
313 (twelve levels) and “wave height” (twelve levels) nested “period” and “site” (two levels) as
314 random factors in order to exclude their statistical effects on the response variable. A second
315 GLMM was carried out to evaluate differences in the monthly mean GSI between the localities
316 (H locality versus C locality) during the sampling period P5. This analysis was set with
317 “locality” (two levels) and “size-class” (two levels) as fixed factors and, “temperature”, “wave
318 height” and “site” as random factors. Finally, a LMM was achieved with log transformed IGO as
319 variable response, “period” and “size” as fixed factors, “temperature” and “wave height”
320 (referenced to the months average when spawning occurred) as random factors.

321 Graphical validations of all the models are provided in the supplementary materials. All
322 the described procedures and analyses were performed using the Nortest and lme4 packages in R
323 software (Venerables & Smith, 2010).

324

325 3. Results

326

327 The monthly mean SST did not change significantly in the H locality over the sampling
328 periods (Kruskal Wallis test: chi-squared = 0.43005, p-value = 0.9799) neither between the H
329 and the C localities during P5 (Mann-Whitney test: p-value = 0.7561; see Fig.2 and Table S1 of
330 Supplementary Material). Difference in the monthly mean SWH was also not significant across
331 the five-year periods (Anova one-way test: p-value=0.579; Table S2 of Supplementary Material).

332

333 3.1. *GonadoSomatic Index and Annual Gamete Output*

334

335 Overall, an annual average of 400 sea urchins of both fertile size-classes (CS and US)
336 were collected during the five-year period to estimate the monthly mean GSI trend of the
337 population in the H locality. The monthly mean GSI was significantly influenced by the Size but
338 not by the Period of sampling (AIC=5903.2, $R^2=0.39$; Table 1a, Fig. S1). Also, Locality resulted
339 no significant when the monthly mean GSI was compared between the H and C locality during
340 P5 (AIC=2171; $R^2=0.45$; Table 1b, Fig. S2). In both GLMM analyses, a high estimate coefficient
341 was assigned to the random effect of the monthly mean SST and SWH (Table 1).

342 In general, the main pre-spawning GSI was in March, except for the P3 that was in
343 August, while smaller spawning events were also observed in Autumn (Fig. 2). The main pre-
344 spawning GSI ranged between $5.5\pm 0.71\%$ in P2 and $7.07\pm 0.43\%$ in P5 for the CS urchins, while
345 for the US urchins it ranged between $4.27\pm 1.34\%$ and $4.59\pm 0.32\%$ in P3 and P4, respectively. At
346 the C locality the main pre-spawning GSI was also found in March and it was $6.30\pm 0.50\%$ and
347 $5.41\pm 0.61\%$ in the CS and US urchins, respectively (Fig.2; Table S2). The annual mean GSI
348 estimated for the whole population at H locality decreased over the year ($R^2=0.36$; Fig.3a) and it

349 reached the lowest values of $4.91 \pm 0.66\%$ in P5. In the same period (P5) at the C locality the
350 annual mean GSI was $6.71 \pm 0.78\%$ (Fig.3a, Table 3).

351 The annual mean IGO was not significantly different among the sampling periods and
352 between the size-classes (see Table 2 and Fig. S3). The highest IGO was recorded in P5 and it
353 was 4.96 and $3.75 \text{ g g}^{-1} \text{ se}^{-1}$ for CS and US urchins, respectively (Table S3). At the C locality, the
354 annual mean IGO calculated during P5 was 4.13 and $4.06 \text{ g g}^{-1} \text{ se}^{-1}$ for CS and US, respectively
355 (Table S3). However, the pattern of the AGO at the H locality tends to increase over the year
356 even if not significantly ($R^2=0.27$, Fig.3b). The highest AGO was $0.12 \text{ g g}^{-1} \text{ yr}^{-1}$ and 0.11 g g^{-1}
357 yr^{-1} during P3 and P5, respectively, while the lowest AGO was $0.08 \text{ g g}^{-1} \text{ yr}^{-1}$ during P2. Finally,
358 the population AGO calculated during P5 in urchins of the C locality was $0.11 \text{ g g}^{-1} \text{ yr}^{-1}$ (Table
359 3, Fig3b).

360

361 3.2. *Population reproductive potential*

362

363 At the H locality the density of CS urchins was $0.6 \pm 0.2 \text{ ind/m}^2$ and $0.5 \pm 0.1 \text{ ind/m}^2$ in P1
364 and P5 respectively, while the US density was 2.7 ± 0.3 and $1.2 \pm 0.4 \text{ ind/m}^2$ in the same periods
365 (Fig.4, Table 3, Table S4). Accordingly, the reproductive potential of CS urchins was calculated
366 as 0.034 in P1 and $0.036 \text{ g g}^{-1} \text{ m}^2 \text{ yr}^{-1}$ in P5, whilst in the same periods for the US urchins it was
367 0.116 and $0.05 \text{ g g}^{-1} \text{ m}^2 \text{ yr}^{-1}$ (Fig. 5 and Table 3). Accordingly, the population reproductive
368 potential (TGO) at the H locality was estimated to be $0.15 \text{ g g}^{-1} \text{ m}^2 \text{ yr}^{-1}$ in P1 and $0.086 \text{ g g}^{-1} \text{ m}^2$
369 yr^{-1} in P5.

370 Finally, at the C locality, urchin density of CS and US classes was $0.9 \pm 0.4 \text{ ind/m}^2$ and
371 $0.8 \pm 0.4 \text{ ind/m}^2$, respectively, and the population reproductive potential (TGO) during P5 was
372 $0.09 \text{ g g}^{-1} \text{ m}^2 \text{ yr}^{-1}$ (Fig. 5, Table 3, Table S3).

373

374 **Discussion**

375

376 The temporal pattern of the monthly mean GSI at the H locality was not significantly
377 different over the years but, it was significantly higher in the large individuals (CS) rather than in
378 the smaller (US), confirming the role of major population breeding stock of the commercial size
379 urchins. The main spawning events occurred generally in spring according with Spirlet, Grosjean
380 & Jangoux (1998), except for P3 when there was no evidence of abrupt spawning events. Finally,
381 during the last sampling period (P5), the monthly mean GSI of the population at H locality was
382 not significantly different from the C locality one.

383 Due to the overexploitation in the H locality, the low density of CS urchins remained
384 essentially stable on minimum values across the five-year period (less than one individual for
385 square meter). However, density of US urchins strongly decreased from more than two
386 individuals to less than one individual for square meter and the proportional decrease of their
387 gamete output contribution led to the loss of 40% of the reproductive potential of the whole
388 population. In general, in the North-Western Sardinia, the intensive size-selective harvesting
389 strongly affects the density of the largest CS sea urchins (Pais et al., 2007; Ceccherelli et al.,
390 2021) and in the harvest hotspot of Su Pallosu Bay have been at their minimum amount for many
391 decades (Loi et al. 2017). The systematic removal of the largest sea urchins at the H locality has
392 determined a truncated demographic structure of the population above the commercial size-class.
393 However so far, the scarcity of the major population breeding stock was buffered by a high
394 natural density of youngest fertile sea urchins (US) that would correspond to the future stock and
395 that suggests the population sustainability could be partially supported by their offspring
396 production (Farina etl a. 2018; Loi et al., 2017). Nevertheless, our results also highlight that the

397 intensive harvesting is drastically rescaling the population body-size breaking down the legal
398 limit of the commercial size, affecting the portion of the youngest part of the breeding stock. The
399 natural density of the US urchins was almost halved in five years. Thus, in accordance with the
400 mortality increase of fertile individuals, a drastic drop of the reproductive potential of the H
401 population has occurred and its self-sustenance could be seriously threatened in a decade. No data
402 are available to estimate the genetic flow of the H population with outside populations, but our
403 results indicate that if harvest pressure will not attenuate urchin recruitment has to rely totally on
404 settlers coming from other populations.

405 Overall, the condition of continuous and inexorable deterioration of the population
406 reproductive potential at the H locality seems to be a direct consequence of the **illegal harvesting**
407 **activity aiming to market the gonads of the individuals under the commercial size legal limit**
408 (Furesi et al. 2016). In fact, density of CS and US urchins at the C locality was also low during
409 the last sampling year (P5), but, although the protection from illegal harvesting is evidently not
410 still totally achieved in this MPA (Marra et al., 2016; Pieraccini, Coppa & De Lucia, 2016), the
411 population structure is much more balanced in all its size-classes. Thus, on this population there
412 is no evidence of a truncated demographic structure and the low density can depend on the low
413 natural recruitment in this area or high post-settlement predation typical inside a Marine
414 Protected Area (Guala et al. 2018; e.g., Farina et al. 2022).

415 Since the key role that *P. lividus* plays in the ecosystems (Boudouresque & Verlaque,
416 2001), sea urchin harvesting can have indirect effects also at community scale (Kaiser &
417 Jennings, 2001). In the Mediterranean Sea, the intensive harvesting of *P. lividus* encourages the
418 proliferation of the competitor species *A. lixula* that is non-harvested by human and weakly
419 preyed on in nature (Guidetti, 2004). However, the rescaling population body-size can also

420 impair the fertility in terms of gamete quality, size of the eggs (Moran & McAlister, 2009), larval
421 development and survival (Berkeley, Chapman & Sogard, 2004), and it pushes the smallest
422 fertile sea urchins to increase their reproductive investment (Fenberg & Roy, 2008). Consistently
423 with this hypothesis, the annual mean of GSI was estimated to decline, whilst the AGO slightly
424 increased over the five-year period of observations. Although a long time series of data needed to
425 confirm these patterns, a compensatory response as reproductive investment of the survivors in
426 gonad production rate or spawning intensity front to the lack of the largest sea urchins could
427 have occurred. Overall, the opposite trends of the annual mean GSI and AGO can suggest a more
428 frequent and constant gamete release. In effect, the reproductive investment is a well-
429 documented compensatory response that induces physiological and behavioural changes in the
430 survivors, such as alterations in the timing of maturation or growth and metabolism rates (Ali,
431 Nicieza & Wootton, 2003; Enberg et al., 2012). If this mechanism was confirmed, the systematic
432 removal of the major breeding stock of the population due to the human harvest could induce
433 negative indirect effects also at community scale. In effect, the truncated demographic structure
434 could lead to the exacerbation of the youngest sea urchin grazing on macroalgal community by
435 accelerating their metabolisms to produce gonads and by increasing their gamete emission in the
436 environment.

437

438 **Conclusions**

439

440 The intensive size-selective harvest has deeply changed the demographic structure of the
441 sea urchin population and determined a drastic decrease of its reproductive potential, as it is
442 affecting the portion of the youngest part of the breeding stock. However, an in-depth analysis of

443 the results also suggests possible stress effects on the youngest survivors that tend to increase
444 their gonad production and the gamete release.

445 Due to such evidence, mitigating the ecological consequences of size-selective
446 exploitation of commercial target species probably requires a shift in management strategies
447 designed to modulate yields on the natural variability of size-classes characterizing the sea
448 urchin population structure. However, to redefine the fishery history would be needed in order to
449 address a balanced harvest of individual sizes, avoiding the complete depletion of the largest
450 classes (e.g., Law & Plank 2018).

451 Such an approach should necessarily go through a shared vision with the stakeholders
452 that includes rise of awareness of fishermen and much more effective control of illegal practices.
453 Accordingly, a deeper understanding of the effects of the rescaling population body-size on the
454 functional herbivore *P. lividus* can contribute to developing an ecosystem-based-management,
455 ensuring the long-term persistence of the sustainable exploitation of the resource and the
456 ecosystems conservation.

457

458

459

460 **Acknowledgement**

461 The authors would like to thank the administration of the Marine Protected Area “Penisola del
462 Sinis-Isola di Mal di Ventre” for providing the boat for the monthly sampling and all the students
463 who help in the field and in the laboratory during these years.

464

465

466

467 **References**

468

469 Ali, M., Nicieza, A., Wootton, R.J., 2003. Compensatory growth in fishes: A response to growth
470 depression. *Fish Fish.* 4, 147–190. <https://doi.org/10.1046/j.1467-2979.2003.00120.x>

471 Anderson, S.C., Mills Flemming, J., Watson, R., Lotze, H.K., 2011. Rapid Global Expansion of
472 Invertebrate Fisheries: Trends, Drivers, and Ecosystem Effects. *PLoS One* 6, e14735.

- 473 <https://doi.org/10.1371/journal.pone.0014735>
- 474 Andrew, N.L., Agatsuma, Y., Ballesteros, E., Bazhin, A.G., Creaser, E.P., Barnes, D.K.A.,
475 Botsford, L.W., Bradbury, A., Campbell, A., Dixon, J.D., Einarsson, S., Gerring, P.K.,
476 Hebert, K., Hunter, M., Hur, S.B., Johnson, C.R., Juinio-Menez, M.A., Kalvass, P., Miller,
477 R.J., Moreno, C.A., Palleiro, J.S., Rivas, D., Robinson, S.M.L., Schroeter, S.C., Steneck,
478 R.S., Vadas, R.L., Woodby, D.A., Xiaoqi, Z., 2002. Status and management of world sea
479 urchin fisheries, in: *Oceanogr. Mar. Biol. an Annual Review*. Taylor & Francis LTD, 11
480 New Fetter Lane, London ec4p 4ee, England, pp. 343–425.
- 481 Audzijonyte, A., Kuparinen, A., Gorton, R., Fulton, E.A., 2013. Ecological consequences of
482 body size decline in harvested fish species: Positive feedback loops in trophic interactions
483 amplify human impact. *Biol. Lett.* 9. <https://doi.org/10.1098/rsbl.2012.1103>
- 484 Baum, J., Myers, R., Kehler, D., Worm, B., Harley, S., Dohert, P., 2003. Collapse and
485 Conservation of Shark Populations in the Northwest Atlantic. *Science* 299 (5605), 389–392.
486 <https://doi.org/10.1126/science.1079777>
- 487 Beddingfield, S.D., McClintock, J.B., 1998. Differential survivorship, reproduction, growth and
488 nutrient allocation in the regular echinoid *Lytechinus variegatus* (Lamarck) fed natural
489 diets. *J. Exp. Mar. Bio. Ecol.* 226, 195–215. [https://doi.org/10.1016/S0022-0981\(97\)00247-](https://doi.org/10.1016/S0022-0981(97)00247-5)
490 5
- 491 Berkeley, S., Chapman, C., Sogard, S., 2004. Maternal age as a determinant of larval growth and
492 survival in a marine fish, *Sebastes melanops*. *Ecology* 85, 1258–1264.
493 <https://doi.org/10.1890/03-0706>
- 494 Bianchelli, S., Danovaro, R., 2020. Impairment of microbial and meiofaunal ecosystem functions
495 linked to algal forest loss. *Sci. Rep.* 10, 1–12. <https://doi.org/10.1038/s41598-020-76817-5>
- 496 Boada, J., Arthur, R., Alonso, D., Pagès, J.F., Pessarrodona, A., Oliva, S., Ceccherelli, G., Piazzzi,
497 L., Romero, J., Alcoverro, T., 2017. Immanent conditions determine imminent collapses:
498 nutrient regimes define the resilience of macroalgal communities. *Proc. Royal Soc. B.* 284,
499 20162814. <https://doi.org/10.1098/rspb.2016.2814>
- 500 Boudouresque, C.F., Verlaque, M., 2001. Ecology of *Paracentrotus lividus*, in: Miller, J. (Ed.),
501 *Edible Sea Urchins: Biology and Ecology*. Elsevier Science, pp. 177–216.
- 502 Brady, S.M., Scheibling, R.E., 2006. Changes in growth and reproduction of green sea urchins,
503 *Strongylocentrotus droebachiensis* (Müller), during repopulation of the shallow subtidal
504 zone after mass mortality. *J. Exp. Mar. Bio. Ecol.* 335, 277–291.
505 <https://doi.org/10.1016/j.jembe.2006.03.016>
- 506 Brewin, P.E., Lamare, M.D., Keogh, J.A., Mladenov, P.V., 2000. Reproductive variability over a
507 four-year period in the sea urchin *Evechinus chloroticus* (Echinoidea: Echinodermata) from
508 differing habitats in New Zealand. *Mar. Biol.* 137, 543–557.
509 <https://doi.org/10.1007/s002270000366>
- 510 Byrne, M., 1990. Annual reproductive cycles of the commercial sea urchin *Paracentrotus lividus*
511 from an exposed intertidal and a sheltered subtidal habitat on the west coast of Ireland. *Mar.*
512 *Biol.* 104, 275–289. <https://doi.org/10.1007/BF01313269>
- 513 Ceccherelli, G., Addis, P., Atzori, F., Cadoni, N., Casu, M., Coppa, S., De Luca, M., De Lucia,
514 G.A., Farina, S., Fois, N., Frau, F., Gazale, V., Grech, D., Guala, I., Mariani, M., Marras,
515 M.S.G., Navone, A.G., Pansini, A., Panzalis, P., Pinna, F., Ruiu, A., Scarpa, F., Piazzzi, L.,
516 2022. Sea urchin harvest inside marineprotected areas: an opportunity to investigate the
517 effects of exploitation where trophic upgrading is achieved. *PeerJ* 10:e12971
518 <http://doi.org/10.7717/peerj.12971>

- 519 Ceccherelli, G., Pais, A., Pinna, S., Sechi, N., Chessa, L.A., 2011. Human impact on
520 *Paracentrotus lividus*: the result of harvest restrictions and accessibility of locations. Mar.
521 Biol. 158, 845–852. <https://doi.org/10.1007/s00227-010-1611-5>
- 522 Coppa, S., Camedda, A., Palazzo, L., Lucia, G.A., 2018. Monitoraggio della popolazione di
523 riccio di mare *Paracentrotus lividus*. Technical report, Cabras: Marine Protected Area
524 Penisola del Sinis-Isola di Mal di Ventre, 29.
- 525 Couvray, S., Miard, T., Bunet, R., Martin, Y., Grillasca J.P., Bonnefont J.L., Coupé S., 2015.
526 Experimental release of *Paracentrotus lividus* sea urchin juveniles in exploited sites along
527 the french mediterranean coast. J. Shellfish Res. 34, 1–9.
528 <https://doi.org/10.2983/035.034.0240>
- 529 Cucco, A., Perilli, A., De Falco, G., Ghezzi, M., Umgiesser, G., 2006. Water circulation and
530 transport timescales in the Gulf of Oristano. Chem. Ecol. 22, 307–331.
531 <https://doi.org/http://doi.org/10.1080/02757540600670364>
- 532 Cucco, A., Sinerchia, M., Ribotti, A., Olita, A., Fazioli, L., Perilli, A., Sorgente, B., Borghini,
533 M., Schroeder, K., Sorgente, R., 2012. A high-resolution real-time forecasting system for
534 predicting the fate of oil spills in the Strait of Bonifacio (western Mediterranean Sea). Mar.
535 Pollut. Bull. 64, 1186–1200. <https://doi.org/https://doi.org/10.1016/j.marpolbul.2012.03.019>
- 536 De Falco, G., Baroli, M., Cucco, A., Simeone, S., 2008. Intrabasinal conditions promoting the
537 development of a biogenic carbonate sedimentary facies associated with the seagrass
538 *Posidonia oceanica*. Cont. Shelf Res. 28, 797–812. <https://doi.org/10.1016/j.csr.2007.12.014>
- 539 Dubois, M., Rossi, V., Ser-Giacomi, E., Arnaud-Haond, S., López, C., Hernández-García, E.,
540 2016. Linking basin-scale connectivity, oceanography and population dynamics for the
541 conservation and management of marine ecosystems. Glob. Ecol. Biogeogr. 25, 503–515.
542 <https://doi.org/10.1111/geb.12431>
- 543 Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S.,
544 Heino, M., 2012. Fishing-induced evolution of growth: Concepts, mechanisms and the
545 empirical evidence. Mar. Ecol. 33, 1–25. <https://doi.org/10.1111/j.1439-0485.2011.00460.x>
- 546 Enberg, K., Jørgensen, C., Mangel, M., 2010. Fishing-induced evolution and changing
547 reproductive ecology of fish: The evolution of steepness. Can. J. Fish. Aquat. Sci. 67, 1708–
548 1719. <https://doi.org/10.1139/F10-090>
- 549 Farina, S., Ceccherelli, G., Piazzini, L., Grech, D., Panzalis, P., Navone, A.G. and Guala, I., 2022.
550 Protection effectiveness and sea urchin predation risk: The role of roving predators beyond
551 the boundaries of a marine protected area in the Western Mediterranean Sea. Aquat.
552 Conserv. 32, 1101-1114. <https://doi.org/10.1002/aqc.3819>
- 553 Farina, S., Baroli, M., Brundu, R., Conforti, A., Cucco, A., Falco, G. De, Guala, I., Guerzoni, S.,
554 Massaro, G., Quattrocchi, G., Romagnoni, G., Brambilla, W., 2020. The challenge of
555 managing the commercial harvesting of the sea urchin *Paracentrotus lividus* : advanced
556 approaches are required. PeerJ, 8, e10093. <https://doi.org/10.7717/peerj.10093>
- 557 Farina, S., Quattrocchi, G., Guala, I., Cucco, A., 2018. Hydrodynamic patterns favouring sea
558 urchin recruitment in coastal areas: A Mediterranean study case. Mar. Environ. Res.
559 <https://doi.org/10.1016/j.marenvres.2018.05.013>
- 560 Fenberg, P.B., Roy, K., 2008. Ecological and evolutionary consequences of size-selective
561 harvesting: How much do we know? Mol. Ecol. 17, 209–220.
562 <https://doi.org/10.1111/j.1365-294X.2007.03522.x>
- 563 Festa-Bianchet, M., 2003. Exploitative wildlife management as a selective pressure for life-
564 history evolution of large mammals, in: Festa-Bianchet, M., Apollonio, M. (Eds.), Animal

- 565 Behavior and Wildlife Conservation. Island Oress, Washington D.C., pp. 191–210.
- 566 Fois, N., Arrostituto, N., Serra, S., Trentadue, M., Chessa, F., Guala, I., et al. (2020).
- 567 Monitoraggio dello stock commerciale di riccio di mare (*Paracentrotus lividus*) e stato della
- 568 risorsa 2019/2020. AGRIS Sardegna. Technical report
- 569 Furesi, R., Madau, F.A., Pulina, P., Sai, R., Pinna, M.G., Pais, A., 2016. Profitability and
- 570 sustainability of edible sea urchin fishery in Sardinia (Italy). *J. Coast. Conserv.*, 20, pp.299-
- 571 306. <https://doi.org/10.1007/s11852-016-0441-0>
- 572 Gianguzza, P., Bonaviri, C., Prato, E., Fanelli, G., Chiantore, M., Privitera, D., Luzzu, F.,
- 573 Agnetta, D., 2013. Hydrodynamism and its influence on the reproductive condition of the
- 574 edible sea urchin *Paracentrotus lividus*. *Mar. Environ. Res.* 85, 29–33.
- 575 <https://doi.org/10.1016/j.marenvres.2012.12.007>
- 576 Gianguzza, P., Chiantore, M., Bonaviri, C., Cattaneo-Vietti, R., Vielmini, I., Riggio, S., 2006.
- 577 The effects of recreational *Paracentrotus lividus* fishing on distribution patterns of sea
- 578 urchins at Ustica Island MPA (Western Mediterranean, Italy). *Fish. Res.* 81, 37–44.
- 579 <https://doi.org/10.1016/j.fishres.2006.06.002>
- 580 Guala, I., Navarro-Pérez, M., Secci, G., Lukianova, I., Borrás Palomares, A.I., Andrades Carles,
- 581 L., Brambilla, W., Farina, S., 2018. Stima della variabilità spaziale dell'insediamento dei
- 582 settlers di *Paracentrotus lividus* nell'AMP Penisola del Sinis - Isola di Mal di Ventre.
- 583 Rapporto Tecnico Fondazione IMC – Centro Marino Internazionale ONLUS.
- 584 Guala, I., Simeone, S., Baroli, M., 2009. Abbondanza e struttura della popolazione di
- 585 *Paracentrotus lividus* nell'Area Marina Protetta Tavolara – Punta Coda Cavallo. Rapporto
- 586 Tecnico Fondazione IMC – Centro Marino Internazionale ONLUS.
- 587 Guarnieri, G., Bevilacqua, S., Vignes, F., Frascchetti, S., 2014. Grazer removal and nutrient
- 588 enrichment as recovery enhancers for overexploited rocky subtidal habitats. *Oecologia* 175,
- 589 959–970. <https://doi.org/10.1007/s00442-014-2944-4>
- 590 Guettaf, M., San Martin, G.A., Francour, P., 2000. Interpopulation variability of the reproductive
- 591 cycle of *Paracentrotus lividus* (Echinodermata: Echinoidea) in the south-western
- 592 Mediterranean. *J. Mar. Biol. Assoc. UK* 80, 899–
- 593 907. <https://doi.org/10.1017/S0025315400002885>
- 594 Guidetti, P., 2004. Consumers of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, in
- 595 shallow Mediterranean rocky reefs. *Helgol. Mar. Res.* 58, 110–116.
- 596 <https://doi.org/10.1007/s10152-004-0176-4>
- 597 Guidetti, P., Boero, F., Bussotti, S., 2005. Evaluating the effects of protection on fish predators
- 598 and sea urchins in shallow artificial rocky habitats: a case study in the northern Adriatic
- 599 Sea. *Mar. Environ. Res.* 59, 333–348. <https://doi.org/10.1016/j.marenvres.2004.05.008>
- 600 Guidetti, P., Terlizzi, A., Boero, F., 2004. Effects of the edible sea urchin, *Paracentrotus lividus*,
- 601 fishery along the Apulian rocky coast (SE Italy, Mediterranean Sea). *Fish. Res.* 66, 287–
- 602 297. [https://doi.org/10.1016/S0165-7836\(03\)00206-6](https://doi.org/10.1016/S0165-7836(03)00206-6)
- 603 Hamilton, S.L., Caselle, J.E., Standish, J.D., Schroeder, D.M., Love, M.S., Rosales-Casian, J.A.,
- 604 Sosa-Nishizaki, O., 2007. Size-selective harvesting alters life histories of a temperate sex-
- 605 changing fish. *Ecol. Appl.* 17, 2268–2280. <https://doi.org/10.1890/06-1930.1>
- 606 Heino, M., Godo, O., 2002. Fisheries-induced selection pressures in the context of sustainable
- 607 fisheries. *Bull. Mar. Sci.* 70, 639–656.
- 608 Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J.,
- 609 Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange,
- 610 C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner,

- 611 R.R., 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*
612 293 (5530), 629–637. <https://doi.org/10.1126/science.1059199>
- 613 James, P.J., 2006. The effects of wave and feeding disturbance on roe enhancement of the sea
614 urchin *Evechinus chloroticus* held in sea-cages. *Aquaculture* 252, 361–371.
615 <https://doi.org/10.1016/j.aquaculture.2005.07.023>
- 616 Johnson, T.R., Wilson, J.A., Cleaver, C. and Vadas, R.L., 2012. Social-ecological scale
617 mismatches and the collapse of the sea urchin fishery in Maine, USA. *Ecol. and Soc.*, 17(2).
618 <http://dx.doi.org/10.5751/ES-04767-170215>
- 619 Kaiser, M., Jennings, S., 2001. An ecosystem perspective on conserving targeted and non-
620 targeted species, in: Reynolds, J., Mace, G., Redford, K., Robinson, J. (Eds.), *Conservation*
621 *of Exploited Species*. Cambridge University Press, London, pp. 343–369.
- 622 Kruskal, W.H., Wallis, W.A., 1952. Use of Ranks in One-Criterion Variance Analysis. *J. Am.*
623 *Stat. Assoc.* 47, 583–621. <https://doi.org/10.1080/01621459.1952.10483441>
- 624 Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57, 659–668.
625 <https://doi.org/10.1006/jmsc.2000.0731>
- 626 Law, R., Plank, M.J., 2018. Balanced harvesting could reduce fisheries-induced evolution. *Fish*
627 *Fish*, 19(6), pp.1078-1091. <https://doi.org/10.1111/faf.12313>
- 628 Levitan, D., 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in
629 response to food limitation. *Mar. Biol.* 111, 431–435. <https://doi.org/10.1007/BF01319415>
- 630 Levitan, D., Sewell, M., 1998. Fertilization success in free-spawning marine invertebrates:
631 review of the evidence and fisheries implications. *Can. Spec. Publ. Fish. Aquat. Sci.* 159–
632 164.
- 633 Levitan, D.R., Sewell, M.A., Chia, F.S., 1992. How distribution and abundance influence
634 fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology*. 73(1),
635 pp.248-254. <https://doi.org/10.2307/1938736>
- 636 Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon,
637 A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., 2015. Global
638 regime shift dynamics of catastrophic sea urchin overgrazing. *Philos. Trans. R. Soc. Lond.,*
639 *B, Biol. Sci.* 370(1659): 20130269. <https://doi.org/10.1098/rstb.2013.0269>
- 640 Loi, B., Guala, I., Pires, R., Brundu, G., Baroli, M., Farina, S., 2017. Hard time to be parents ?
641 Sea urchin fishery shifts potential reproductive contribution of population onto the
642 shoulders of the young adults. *PeerJ*, 5, p.e3067. <https://doi.org/10.7717/peerj.3067>
- 643 Longhurst, A., 2006. The sustainability myth. *Fish. Res.* 81, 107–112.
644 <https://doi.org/10.1016/j.fishres.2006.06.022>
- 645 Lozano, J., Galera, J., Lopez, S., Turon, X., Palacin, C., Morera, G., 1995. Biological cycles and
646 recruitment of *Paracentrotus lividus* (Echinodermata: Echinoidea) in two contrasting
647 habitats. *Mar. Ecol. Prog. Ser.* 122, 179–192. <http://doi.org/10.3354/meps122179>
- 648 Mann, H.B., Whitney, D.R., 1947. On a Test of Whether one of Two Random Variables is
649 Stochastically Larger than the Other. *Ann. Math. Stat.* 18, 50–60.
650 <https://doi.org/10.1214/aoms/1177730491>
- 651 Marra, S., Coppa, S., Camedda, A., Mazzoldi, C., Wrachien, F., Massaro, G., De Lucia, G.A.,
652 2016. Recovery trends of commercial fish: The case of an underperforming mediterranean
653 marine protected area. *PLoS One* 11, 1–22. <https://doi.org/10.1371/journal.pone.0146391>
- 654 McClanahan, T.R., Sala, E., 1997. A Mediterranean rocky-bottom ecosystem fisheries model.
655 *Ecol. Modell.* 104, 145–164. [https://doi.org/10.1016/S0304-3800\(97\)00121-X](https://doi.org/10.1016/S0304-3800(97)00121-X)
- 656 McClanahan, T.R., Shafir, S.H., 1990. Causes and consequences of sea-urchin abundance and

- 657 diversity in kenyan coral-reef lagoons. *Oecologia* 83, 362–370.
658 <https://doi.org/10.1007/BF00317561>
- 659 Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, G.C., Romano,
660 F., 2005. Cascading human impacts, marine protected areas; and the structure of
661 Mediterranean reef assemblages. *Ecol. Monogr.* 75, 81–102. <https://doi.org/10.1890/03-4058>
- 662
- 663 Minor, M., Scheibling, R., 1997. Effects of food ration and feeding regime on growth and
664 reproduction of the sea urchin *Strongylocentrotus droebachiensis*. *Mar. Biol.* 129, 159–167.
665 <https://doi.org/https://doi.org/10.1007/s002270050156>
- 666 Mita, M., Sato, J., Hirose, Y., Nakamura, M., 2007. Gonadal maturation is dependent on body
667 size in the sea urchin, *Echinometra tsumajiroi* 50, 187–190.
668 <https://doi.org/10.1080/07924259.2007.9652245>
- 669 Moran, A.L., McAlister, J.S., 2009. Egg size as a life history character of marine invertebrates: is
670 it all it's cracked up to be? *Biol. Bull.* 216, 226–242. <https://doi.org/10.2307/25548157>
- 671 Moreno, C., 2001. Community patterns generated by human harvesting on Chilean shores: a
672 review. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 11, 19–30. <https://doi.org/10.1002/aqc.430>
- 673 Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature*
674 423, 280–283. <https://doi.org/https://doi.org/10.1038/nature01610>
- 675 Oliva, S., Farina, S., Pinna, S., Guala, I., Agnetta, D., Ariotti, P., Mura, F., Checcherelli, G.,
676 2016. Determinants of *Paracentrotus lividus* sea urchin recruitment under oligotrophic
677 conditions: implications for conservation management. *Mar. Environ. Res.* 117, 13–20.
678 <https://doi.org/10.1016/j.marenvres.2016.02.013>
- 679 Ouréns, R., Fernández, L., Fernández-Boán, M., Naya, I., Freire, J., 2013. Reproductive
680 dynamics of the sea urchin *Paracentrotus lividus* on the Galicia coast (NW Spain): Effects
681 of habitat and population density. *Mar. Biol.* 160, 2413–2423.
682 <https://doi.org/10.1007/s00227-013-2236-2>
- 683 Ouréns, R., Fernández, L., Freire, J., 2011. Geographic, population, and seasonal patterns in the
684 reproductive parameters of the sea urchin *Paracentrotus lividus*. *Mar. Biol.* 158, 793–804.
685 <https://doi.org/10.1007/s00227-010-1607-1>
- 686 Pais, A., Chessa, L. a., Serra, S., Ruiu, A., Meloni, G., Donno, Y., 2007. The impact of
687 commercial and recreational harvesting for *Paracentrotus lividus* on shallow rocky reef sea
688 urchin communities in North-western Sardinia, Italy. *Estuar. Coast. Shelf Sci.* 73, 589–597.
689 <https://doi.org/10.1016/j.ecss.2007.02.011>
- 690 Pais, A., Serra, S., Meloni, G., Saba, S., Ceccherelli, G., 2012. Harvesting effects on
691 *Paracentrotus lividus* population structure: a case study from northwestern Sardinia, Italy,
692 before and after the fishing season. *J. Coast. Res.* 28, 570–575.
693 <https://doi.org/10.2112/JCOASTRES-D-10-00119.1>
- 694 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food
695 webs. *Science* 279, 860–863. <https://doi.org/10.1126/science.279.5352.860>
- 696 Pennington, J.T., 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm
697 dilution, adult aggregation, and synchronous spawning. *Biol. Bull.* 169, 417–430.
698 <https://doi.org/10.2307/1541492>
- 699 Peters, R.H., 1983. *The ecological implications of body size*. Cambridge University Press,
700 Cambridge.
- 701 Pieraccini, M., Coppa, S., De Lucia, G.A., 2016. Beyond marine paper parks? Regulation theory
702 to assess and address environmental non-compliance. *Aquat. Conserv. Mar. Freshw.*

- 703 Ecosyst. <https://doi.org/10.1002/aqc.2632>
- 704 Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalament, F., Chemello, R., Harmelin-Vivien,
705 M.L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., Pipitone, C., 2000. Trophic cascades
706 in benthic marine ecosystems: lessons for fisheries and protected-area management.
707 Environ. Conserv. 27, 179–200. <http://doi.org/10.1017/S0376892900000205>
- 708 Prado, P., Tomas, F., Alcoverro, T., Romero, J., 2007. Extensive direct measurements of
709 *Posidonia oceanica* defoliation confirm the importance of herbivory in temperate seagrass
710 meadows. Mar. Ecol. Ser. 340, 63–71. <https://doi.org/10.3354/meps340063>
- 711 Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Frascchetti, S.,
712 Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B.,
713 Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F.,
714 Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F., Zabala,
715 M., 2012. The Structure of Mediterranean Rocky Reef Ecosystems across Environmental
716 and Human Gradients, and Conservation Implications. PLoS One 7, e32742.
717 <https://doi.org/10.1371/journal.pone.0032742>
- 718 Sala, E., Boudouresque, C.F., Harmelin-Vivien, M., 1998. Fishing, trophic cascades, and the
719 structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82, 425–
720 439. <https://doi.org/10.2307/3546364>
- 721 Sellem, F., Guillou, M., 2007. Reproductive biology of *Paracentrotus lividus* (Echinodermata:
722 Echinoidea) in two contrasting habitats of northern Tunisia (south-east Mediterranean). J.
723 Mar. Biol. Assoc. UK. <https://doi.org/10.1017/S002531540705521X>
- 724 Shears, N.T., Babcock, R.C., 2003. Continuing trophic cascade effects after 25 years of no-take
725 marine reserve protection. Mar. Ecol. Prog. Ser. 246, 1–16.
726 <https://doi.org/10.3354/meps246001>
- 727 Shpigel, M., McBride, S.C., Marciano, S., Lupatsch, I., 2004. The effect of photoperiod and
728 temperature on the reproduction of the European sea urchin *Paracentrotus lividus*.
729 Aquaculture 232, 343–355. [https://doi.org/10.1016/S0044-8486\(03\)00539-8](https://doi.org/10.1016/S0044-8486(03)00539-8)
- 730 Spirlet, C., Grosjean, P., Jangoux, M., 2000. Optimization of gonad growth by manipulation of
731 temperature and photoperiod in cultivated sea urchins, *Paracentrotus lividus* (Lamarck)
732 (Echinodermata). Aquaculture 185, 85–99. [https://doi.org/10.1016/S0044-8486\(99\)00340-3](https://doi.org/10.1016/S0044-8486(99)00340-3)
- 733 Spirlet, C., Grosjean, P., Jangoux, M., 1998. Reproductive cycle of the echinoid *Paracentrotus*
734 *lividus*: analysis by means of the maturity index. Invertebr. Reprod. Dev. 34, 69–81.
735 <https://doi.org/10.1080/07924259.1998.9652355>
- 736 Steneck, R., Graham, M., Bourque, B., Corbett, D., Erlandson, J., Estes, J., Tegner, M., 2002.
737 Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ. Conserv. 29,
738 436–459. <https://doi.org/10.1017/S0376892902000322>
- 739 Tegner, M., Dayton, P., 1977. Sea urchin recruitment patterns and implications of commercial
740 fishing. Science (80-). 196, 324–326. <https://doi.org/10.1126/science.847476>
- 741 Trippel, E., 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45, 759–771.
742 <https://doi.org/10.2307/1312628>
- 743 Underwood, A.J., Underwood, A.J. and Underwood, A.J., 1997. Experiments in ecology: their
744 logical design and interpretation using analysis of variance. Cambridge university press.
- 745 Vadas, R., Steneck, R., 1995. Overfishing and inferences in kelp-sea urchin interactions, in:
746 Skjoldal, H., Hopkins, K., Erikstad, K. (Eds.), Ecology of Fjords and Coastal Waters.
747 Elsevier Science, Amsterdam, pp. 509–524.
- 748 Vallin, L., Nissling, A., 2000. Maternal effects on egg size and egg buoyancy of Baltic cod,

749 Gadus morhua — implications for stock structure effects on recruitment. Fish. Res. 49, 21–
750 37. [https://doi.org/10.1016/S0165-7836\(00\)00194-6](https://doi.org/10.1016/S0165-7836(00)00194-6)
751 Venerables, W., Smith, D., 2010. R Development Core Team. 2010. An Introduction to R. Notes
752 on R: A Programming Environment for Data Analysis and Graphics Version 2.11. 1
753 Villouta, E., 2000. Potential ecological impacts of harvesting kina (*Evechinus chloroticus*) in
754 Fiordland. Conserv. Advis. Sci. Notes 286, 1–14.
755 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common
756 statistical problems. Methods Ecol. Evol. 1, 3–14. [https://doi.org/10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2009.00001.x)
757 [210X.2009.00001.x](https://doi.org/10.1111/j.2041-210X.2009.00001.x)
758
759
760
761
762

Figure 1

Map of the study area

Su Pallosu Bay, in the North of Sinis Peninsula, is a heavy harvesting pressure locality (H), while Cape Seu is the Control locality (C) within the nearby Marine Protected Area monitored during the last period. Sampling sites are represented by the black dots.

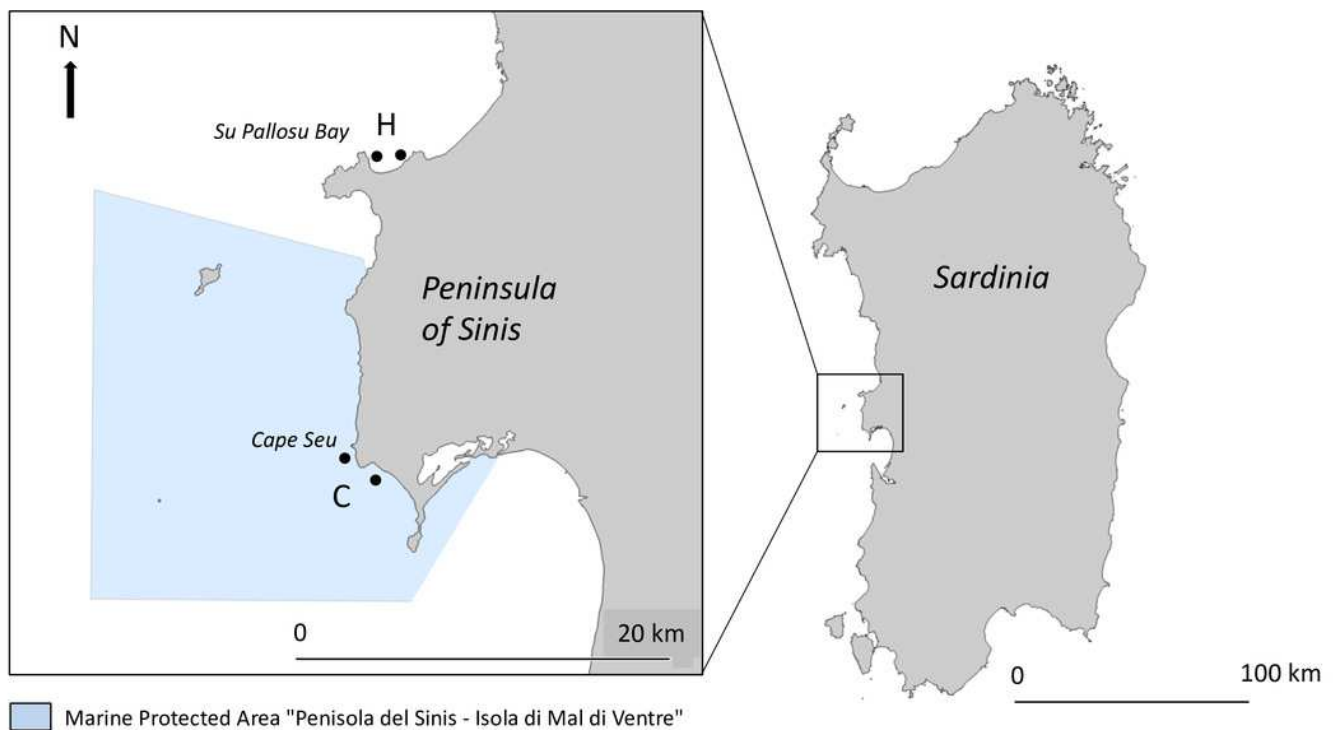


Figure 2

Graphs of GSI over the sampling periods

Annual trend of the GonadoSomatic Index during the sampling periods (P1-P5) in H locality and during the last sampling period (P5) in the C locality. GSI is represented as mean \pm standard error for CS size-class (black line) and US size-class (gray line). Due to adverse marine weather conditions, not all months were sampled. The reproductive cycle of 2014-15 was no estimated. Mean SST was also plotted (thinner gray line).

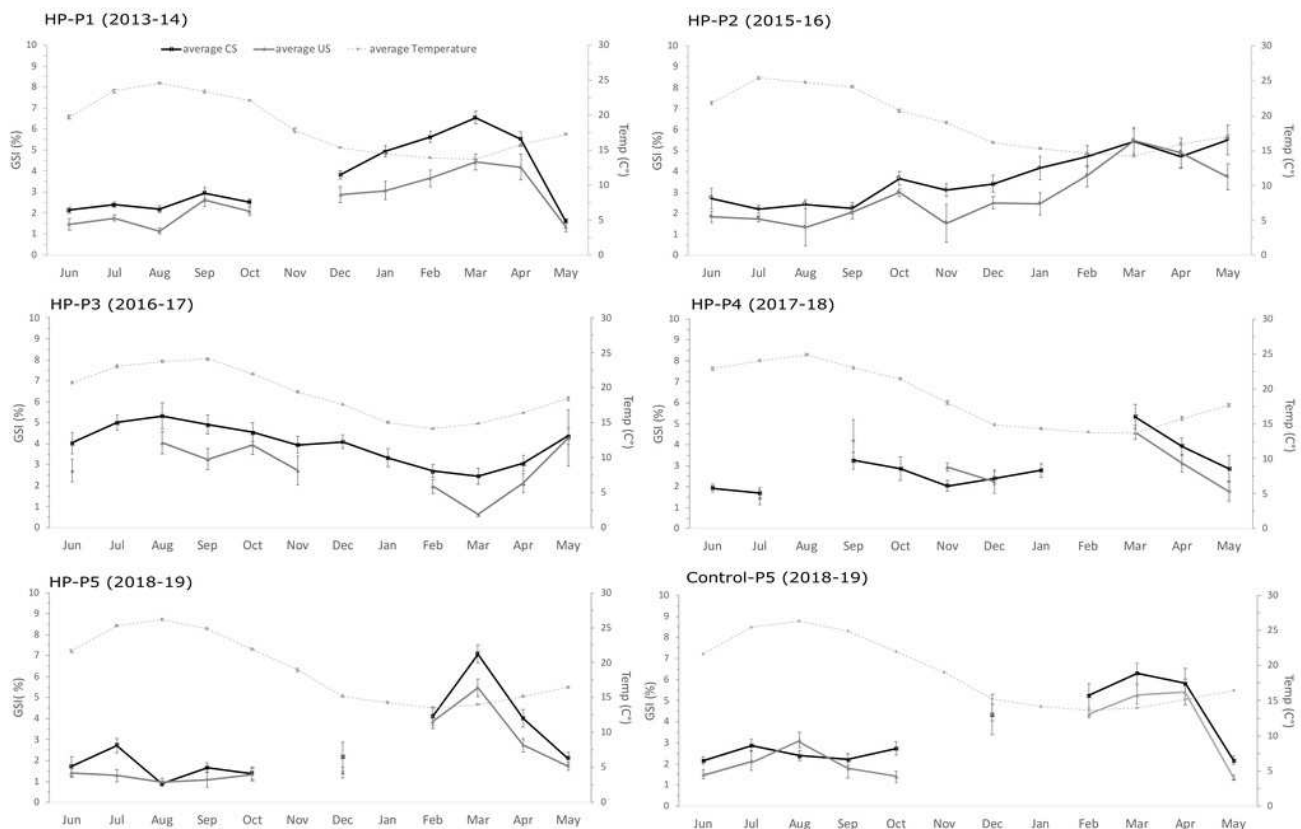


Figure 3

Graphs of annual GSI and AGO over the sampling periods

Trend across the five sampling periods of a) Annual mean GonadoSomatic Index ($R^2=0.36$)

and b) Annual Gamete Output ($R^2=0.27$) of the H population and of the C population in the

last sampling period.

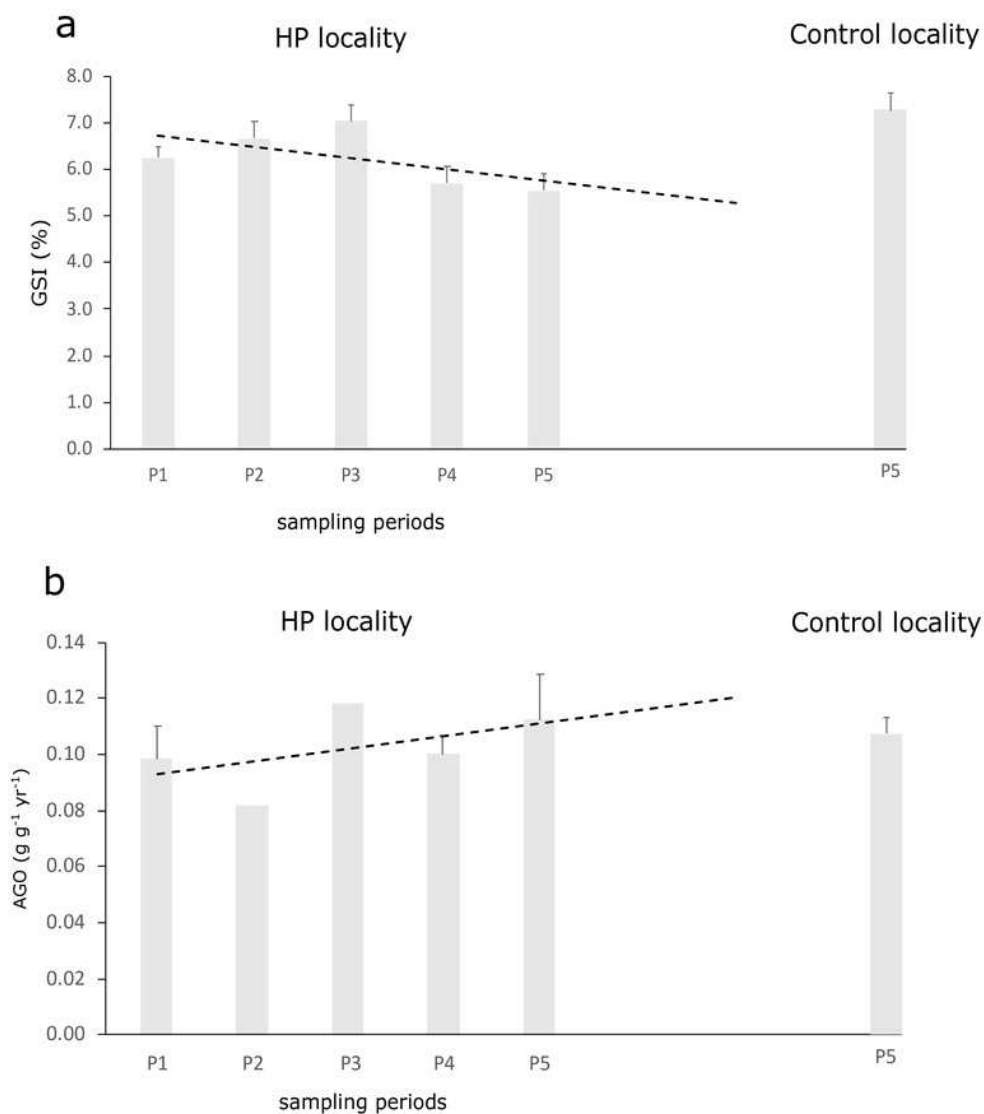


Figure 4

Sea urchin population structure

Size-density distribution of the sea urchin population at H locality in P1(full bars) and P5 (spotted bars) sampling periods. The range of the size classes is 10 mm of test diameter without spines (TD). Under Commercial (US) and Commercial size classes (CS) are indicated.

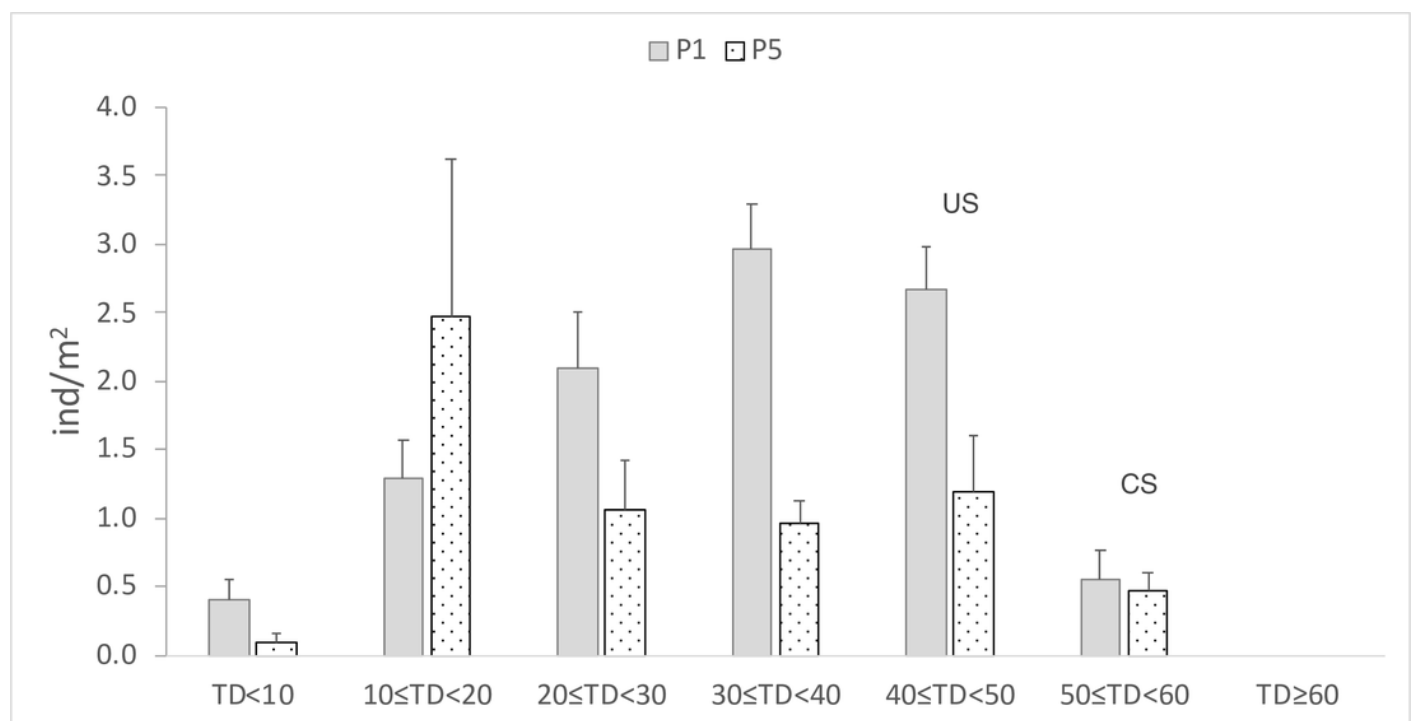


Figure 5

Population reproductive potential

Total Gamete Output (TGO) of the CS and US size-classes, and the reproductive potential of the whole population (popTGO) during P1 and P5 sampling periods.

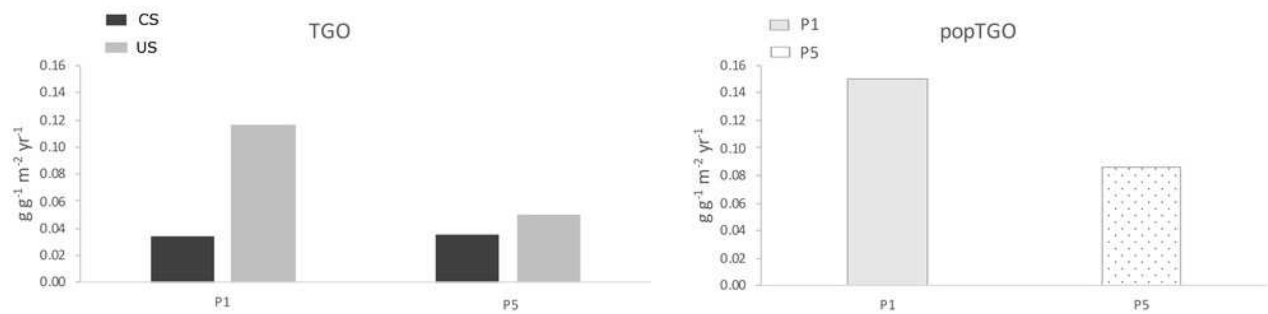


Table 1 (on next page)

GLMM results for GonadoSomatic Index in function of a) “period” and “size” across the five-year period and, b) “locality” and “size” during the last sampling period P5

The “temp”, “wave” and “site” are set as random effects. Estimate coefficient, Standard Error, z-value and significance level (p-value) are provided for fixed effects.

1

a	Fixed effects	Estimate coeff	Std. error	z-value	p-value
GSI	Intercept	1.14816	0.11983	9.582	$< 2e^{-16}$
	period 2	0.13448	0.15556	0.864	0.387
	period 3	0.23617	0.15456	1.528	0.127
	period 4	-0.12932	0.16203	-0.798	0.425
	period 5	-0.25762	0.16261	-1.584	0.113
	Size US	-0.25406	0.03251	-7.815	$5.5e^{-15}$
	Random effect	Variance	Std.Dev		
site	$4.517e^{-03}$	0.067211			
period:temp	$1.259e^{-01}$	0.354813			
period: wave	$1.225e^{-09}$	0.000035			
AIC=5903.2; $R^2=0.39$					
b	Fixed effects	Estimate coeff	Std. error	z-value	p-value
GSI	Intercept	1.16267	0.15917	7.305	$2.78e^{-13}$
	locality	-0.32646	0.15388	-2.122	0.03388
	size	-0.15012	0.04851	-3.095	0.00197
	Random effect	Variance	Std.Dev		
	site	0.001671	0.04088		
temp	0.102992	0.32092			
wave	0.111289	0.33360			
AIC=2171.6; $R^2=0.45$					

Table 2 (on next page)

LMM result for Individual Gamete Output in function of “period” and “size”

The “temp”, “wave” and “site” are set as random effects. Estimate coefficient, Standard Error, t-value and significance level (p-value) are provided for fixed effects.

	Fixed effects	Estimate coeff	Std. error	t-value	p-value
IGO	Intercept	-3.9411	0.4667	-8.445	5.5e-07
	period 2	-0.0676	0.5569	-0.121	0.9050
	period 3	0.4929	0.5709	0.863	0.4019
	period 4	0.9981	0.7259	1.375	0.1912
	period 5	0.9315	0.7259	1.283	0.2207
	Size US	0.3354	0.1678	1.998	0.0719
	Random effect	Variance	Std.Dev		
	period:temp	5.616e ⁻⁰¹	7.494e ⁻⁰¹		
	period: wave	5.208e ⁻¹⁶	2.282e ⁻⁰⁸		
	residual	1.413e ⁻⁰¹	3.759e ⁻⁰¹		
AIC=75.8; R ² =0.84					

1

Table 3 (on next page)

Summary table of GonadoSomatic Index, Individual Gamete Output and Annual Gamete Output

Table shows mean monthly GSI, IGO and AGO of H and C populations during the sampled periods (P1-P5). In the table are also reported the sea urchin density and the related reproductive potential of the H population in P1 and P5 and the C population in P5.

	Size-class	P1	P2	P3	P4	P5	Control (P5)
Avg. GSI (%)	CS	3.66±0.19	3.69±0.43	3.98±0.96	2.90±0.40	2.78±0.37	3.63±0.42
	US	2.60±0.32	2.86±0.49	2.86±0.55	2.91±0.47	2.13±0.29	3.08±0.35
	Pop	6.25±0.51	6.56±0.93	6.84±0.96	5.81±0.87	4.91±0.66	6.71±0.78
IGO (g g ⁻¹ se ⁻¹)	CS	0.002±0.1	0.005±0.3	0.014±0.2	0.012±0.1	0.018±0.2	0.007±0.0
		0.004±0.1	0.002±0.1	0.016±0.1	0.036±0.1	0.003±0.1	0.041±0.3
		0.050±0.2	0.006±0.0	0.027±0.1		0.050±0.0	-
		-	0.007±0.0	-	-	-	-
		-	0.014±0.2	-	-	-	-
	US	0.006±0.0	0.005±0.6	0.008±0.0	0.020±0.4	0.004±0.0	0.018±0.1
	0.005±0.1	0.015±0.6	0.012±0.2	0.032±0.1	0.038±0.2	0.041±0.5	
	0.031±0.2	0.027±0.1	0.013±0.9	-	-	-	
	-	-	0.028±1.0	-	-	-	
AGO (g g ⁻¹ yr ⁻¹)	CS	0.06	0.03	0.06	0.05	0.07	0.05
	US	0.04	0.05	0.06	0.05	0.04	0.06
	Pop	0.10	0.08	0.12	0.10	0.11	0.11
urchin density (ind/m ²)	CS	0.6±0.2				0.5±0.1	0.9±0.4
	US	2.7±0.3	NA	NA	NA	1.2±0.4	0.8±0.4
	tot fertile	3.3±0.5				1.7±0.5	1.7±0.8
TGO (g g ⁻¹ m ⁻² yr ⁻¹)	CS	0.034				0.036	0.043
	US	0.116	NA	NA	NA	0.050	0.047
	Pop	0.150				0.086	0.090