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

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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.

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44 **Abstract**

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46 The harvest of the edible sea urchin *Paracentrotus lividus* is intensively practiced in some
47 regions of the Western Mediterranean Sea. The removal of the largest individuals can determine
48 an overall reduction in population size and a size class truncation that can lead to a drastic drop
49 the self-sustenance. The aim of this study is to evaluate the reproductive cycle and reproductive
50 potential across five years of a population in one the main harvest hotspots of Sardinia (Italy).
51 The breeding stock consists of commercial and under-commercial size individuals and for this
52 reason they were sampled on a monthly basis to estimate their GonadoSomatic Index. The
53 reproductive potential of the population - Total Gamete Output - was calculated across the five-
54 year period in relation with the variation of the density of the major breeding stock. Moreover,
55 during the last year, the reproductive cycle and reproductive potential were also estimated in a
56 well-conserved population of the nearby Marine Protected Area, as a reference control. No
57 variation in GonadoSomatic Index and Individual Gamete Output was found over the five years
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59 harvesting drastically rescaled the population body-size: although density of the commercial size
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62 output contribution led to loss 40% of the reproductive potential of the whole population in the
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66 breeding stock, the inter-annual trends of GonadoSomatic Index and Annual Gamete Output
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96   **1. Introduction**

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98   Fishing is the most widespread human exploitative activity in the marine environment,

99   and it is size-selective by definition (Longhurst, 2006). Worldwide fishery is based on removing

100   individuals above a minimum legal size (Jackson et al., 2001) and in theory, juveniles can grow

101   large enough to reproduce at least once before being harvested, guaranteeing their own

102   replacement (Law, 2000). However, nowadays fishing is so intense (Baum et al., 2003; Myers &

103   Worm, 2003; Pauly et al., 1998) that affects many aspects of the biology of a target species, such

104   as demography, life history and ecology (Fenberg & Roy, 2008).

105   One of the main effects of the size-selective harvest is the deep change in demographic

106   structure of the population. Specifically, the continuous removal of the largest individuals rather

107   than the smallest ones can determine an overall reduction in population abundance and body-size

108   (Fenberg & Roy, 2008). Thus, under heavy size-selective harvest, an age-size truncation of the

109   populations occurs, leading to a multitude of consequences (Festa-Bianchet, 2003; Heino &

110   Godo, 2002). This phenomenon is critical for the self-sustenance of populations that need relying

111   totally on the youngest specimens and that eventually results in a serious decline of the

112   population growth rate (Enberg, Jørgensen & Mangel, 2010). Effectively, it is widely

113   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 destinated 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

2. Material and Methods

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210   *2.1.   Study site*

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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

244 57a51616599440425bbc). 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*

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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 $5 \pm 1m$ (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   *[gonad wet weight / total wet weight] x 100*   (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 (g g^{-1} 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 (g g^{-1} yr^{-1}).

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276   *2.3.*   *Population reproductive potential*
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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 $5m^2$ (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/m^2) 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 m^2 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   & Wnderwood, 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

3. Results

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

3.1. GonadoSomatic Index and Annual Gamete Output

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

In general, the main pre-spawning GSI was in March, except for the P3 that was in August, while smaller spawning events were also observed in Autumn (Fig. 2). The main pre-spawning GSI ranged between 5.5±0.71% in P2 and 7.07 ±0.43% in P5 for the CS urchins, while for the US urchins it ranged between 4.27±1.34% and 4.59±0.32% in P3 and P4, respectively. At the C locality the main pre-spawning GSI was also found in March and it was 6.30±0.50% and 5.41±0.61% in the CS and US urchins, respectively (Fig.2; Table S2). The annual mean GSI 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±0.66% in P5. In the same period (P5) at the C locality the

350 annual mean GSI was 6.71±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 g g^{-1} 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 g g^{-1} 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 g g^{-1} yr^{-1} and 0.11 g g^{-1}

357 yr^{-1} during P3 and P5, respectively, while the lowest AGO was 0.08 g g^{-1} yr^{-1} during P2. Finally,

358 the population AGO calculated during P5 in urchins of the C locality was 0.11 g g^{-1} 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 ±0.2 ind/m^2 and 0.5 ±0.1 ind/m^2 in P1

364 and P5 respectively, while the US density was 2.7 ±0.3 and 1.2 ±0.4 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 g g^{-1} m^{-2} yr^{-1} in P5, whilst in the same periods for the US urchins it was

367 0.116 and 0.05 g g^{-1} m^{-2} yr^{-1} (Fig. 5 and Table 3). Accordingly, the population reproductive

368 potential (TGO) at the H locality was estimated to be 0.15 g g^{-1} m^{-2} yr^{-1} in P1 and 0.086 g g^{-1} m^{-2}

369 yr^{-1} in P5.

370   Finally, at the C locality, urchin density of CS and US classes was 0.9 ±0.4 ind/m^2 and

371 0.8 ±0.4 ind/m^2, respectively, and the population reproductive potential (TGO) during P5 was

372 0.09 g g^{-1} m^{-2} yr^{-1} (Fig. 5, Table 3, Table S3).

373

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 threated 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.

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464
465
466

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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.

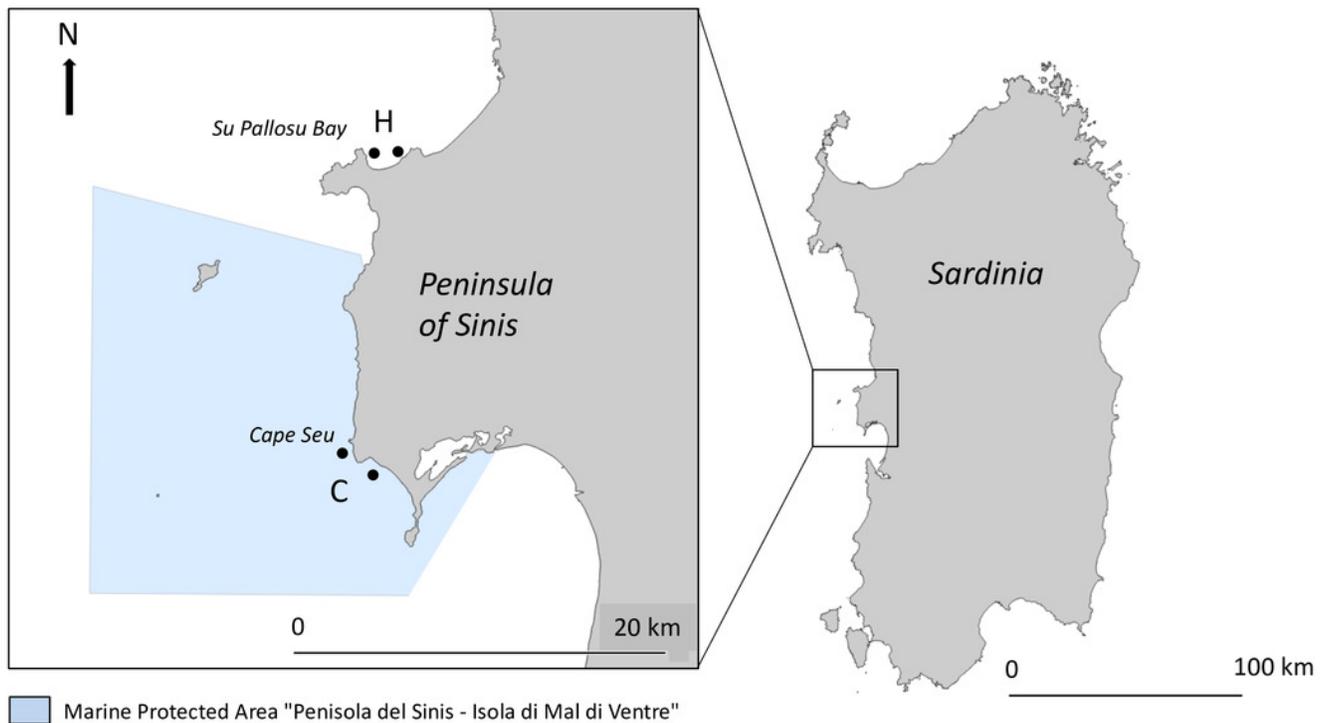



Figure 2

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 ±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).

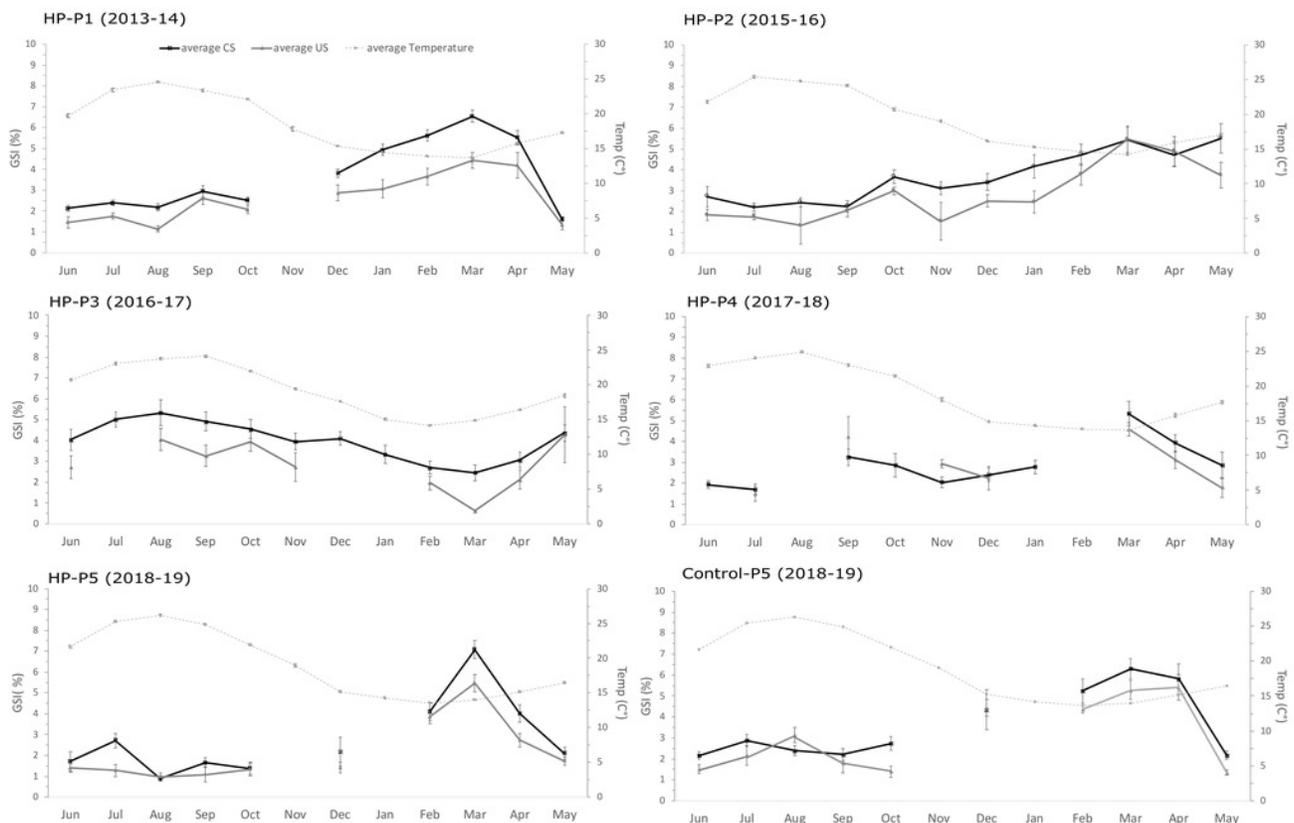



Figure 3

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.

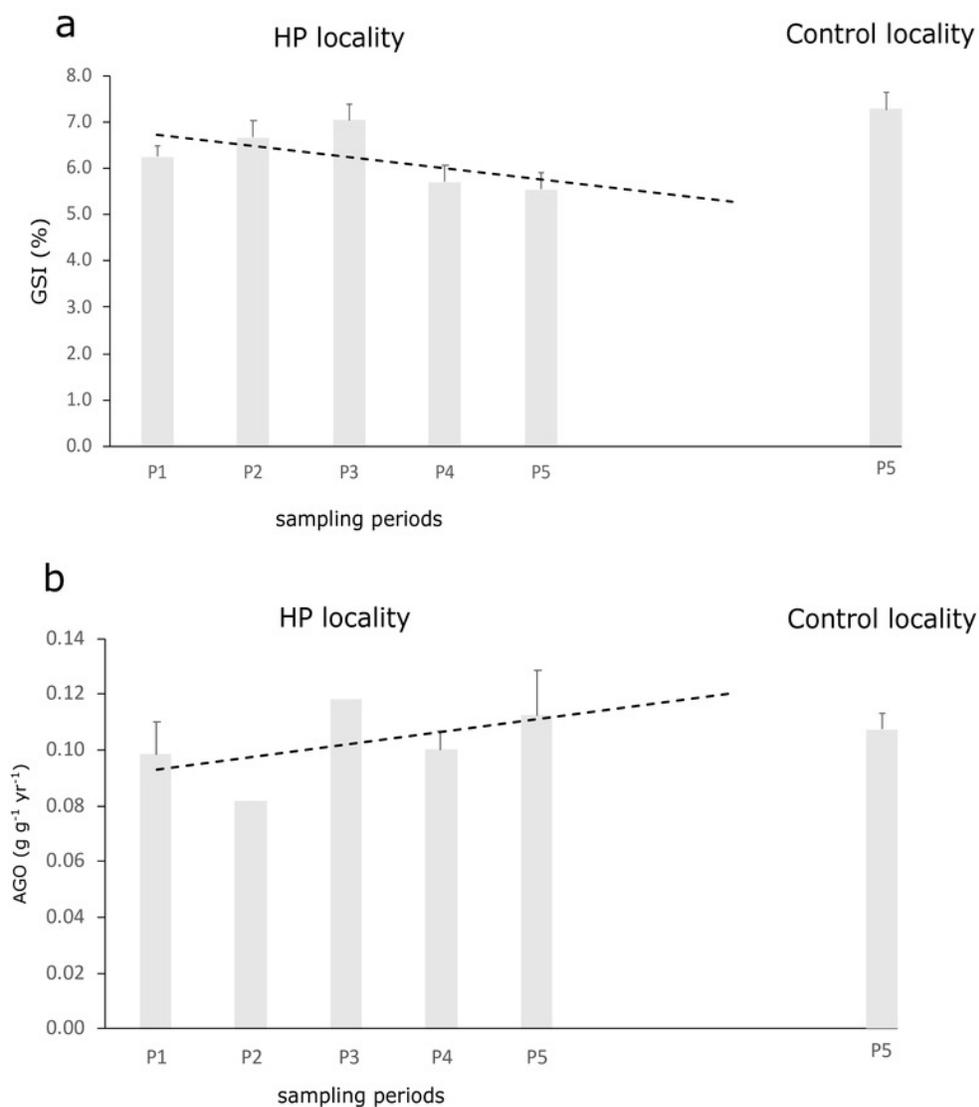



Figure 4

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.

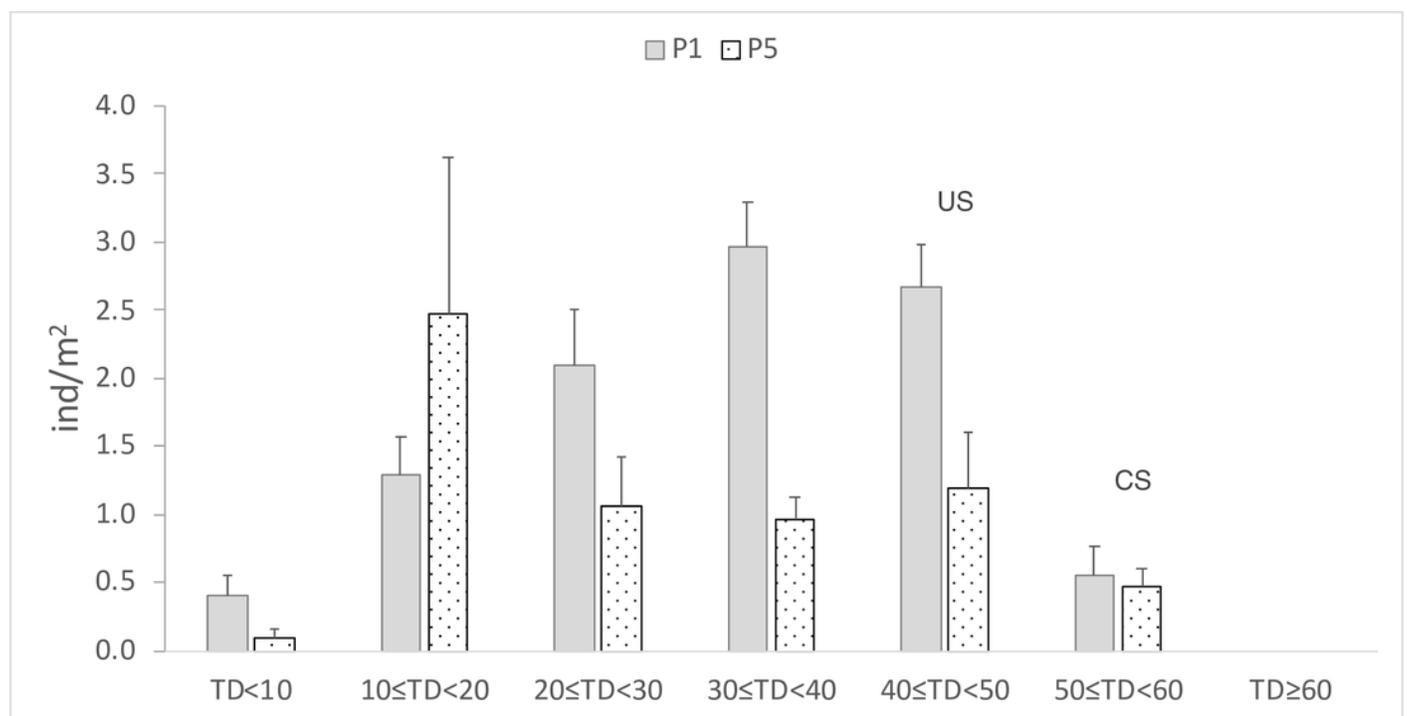
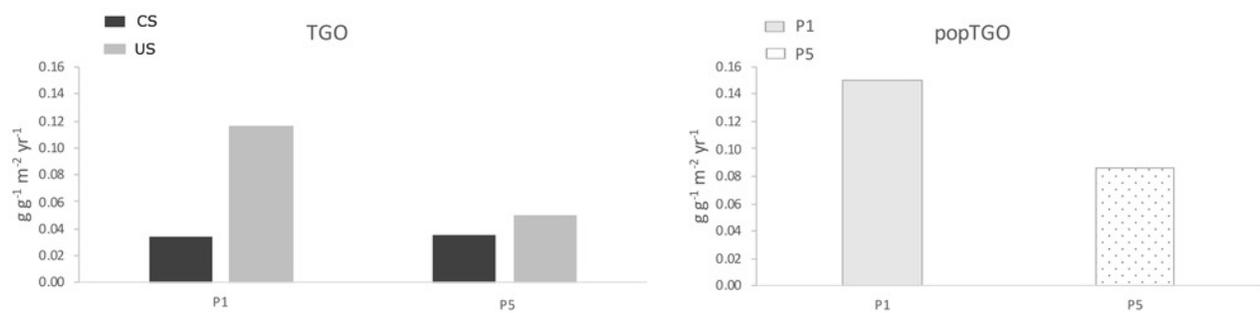



Figure 5

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.

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.

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					

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					

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