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

Nicole Ruberti[1], Gianni Brundu[2], Giulia Ceccherelli[3], Daniele Grech[2], Ivan Guala[2], Barbara Loi[2], Simone Farina[4,5]

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

[2] IMC - 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

40
41
42
43
44 **Abstract**
45

46 The harvest of the edible sea urchin *Paracentrotus lividus* is intensively practiced in some regions
47 of the Western Mediterranean Sea. The removal of the largest individuals can determine an overall
48 reduction in population size and a size class truncation that can lead to a drastic drop the self-
49 sustenance. The aim of this study is to evaluate the variability of the population reproductive
50 potential across five years in one of the main harvest hotspots of Sardinia (Western Mediterranean
51 Sea). The breeding stock consists of commercial and under-commercial size individuals which
52 were sampled on a monthly basis to estimate their GonadoSomatic Index (GSI) and the Individual
53 Gamete Output IGO). In addition, the reproductive potential of the population - Total Gamete
54 Output (TGO) - was calculated across the five-year period in relation with the variation of the
55 density of the breeding stock. During the last year, the reproductive potential was also estimated
56 in a well-conserved population of a nearby Marine Protected Area. No significant variability in
57 GSI and IGO was found over the five years nor when compared with the ones of protected
58 population in the last year. However, the intensive harvest drastically rescaled the population body-
59 size: although density of the commercial size class remained low, density of the under-commercial
60 size-class halved from the beginning to the end of the study. Accordingly, the proportional
61 decrease of their gamete output contribution led to a 40% loss of the reproductive potential of the
62 whole population in the five-year period. Interestingly, despite the loss of reproductive potential
63 due to the decrease of the breeding stock density, the average values of IGO slightly increased
64 across the years leading to the highest Annual Gamete Output during the fourth year of sampling.
65 This positive pattern could suggest a mechanism of reproductive investments of the survivors in
66 terms of gonad production rate or increase in spawning intensity. This work provides evidence of
67 the direct effect of size-selective harvesting on the rapid loss of population self-sustenance.
68 Furthermore, it lays new prospective for future research of the indirect effects of the rescaling
69 population body-size in functional traits of the sea urchin *P. lividus* and that could become
70 important for both, sustainable exploitation and ecosystem conservation management.

71
72
73
74
75
76
77
78
79
80
81
82
83

84
85
86
87
88
89
90
91
92
93
94

95   **1. Introduction**

96

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

98   it is size-selective by definition (Longhurst, 2006). Worldwide well-managed fisheries are based

99   on removing individuals above a minimum legal size (Jackson et al., 2001) and in theory juveniles

100   can grow large enough to reproduce at least once before being harvested, guaranteeing a

101   sustainable harvest (Law, 2000). However, nowadays fishing is so intense (Baum et al., 2003;

102   Myers & Worm, 2003; Pauly et al., 1998) that affects many aspects of the biology of a target

103   species, such as demography, life history and ecology (Fenberg & Roy, 2008).

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

105   structure of the population. Specifically, the continuous removal of the largest individuals can

106   determine an overall reduction in population abundance and body-size structure (Fenberg & Roy,

107   2008). Thus, under heavy size-selective harvest, an age-size truncation of the populations occurs,

108   leading to a multitude of consequences (Festa-Bianchet, 2003; Heino & Godo, 2002). Firstly, this

109   phenomenon is critical for the self-sustainability of populations and involves the loss of the main

110   breeding stock and a serious decline of population density (Enberg, Jørgensen & Mangel, 2010).

111   Effectively, it is widely demonstrated that large individuals give the greatest contribution to the

112   successful offspring and the larval size and quality of some exploited marine fish have been shown

113   to be positively correlated to maternal length and age (Berkeley, Chapman & Sogard, 2004;

114 Trippel, 1995; Vallin & Nissling, 2000). Thus, the removal of largest and oldest individuals

115 generally decreases the population ability to replenish itself.

116   The animal body-size is central to ecology, from the organismal physiology to the

117 functioning of communities and ecosystems (Peters, 1983). The intensive size-selective harvest

118 can cause alterations in the growth rate and in the timing of maturation of youngest specimens

119 (Hamilton et al., 2007). The decrease in mean size and abundance of the target fishes can also

120 generate negative effects on non-target species through the food web interactions (Audzijonyte et

121 al., 2013), for example reducing the predator-prey interactions and causing the proliferation of

122 preys (e.g. Pinnegar et al., 2000). This mechanism is widely demonstrated in temperate reefs tri-

123 trophic interactions between fish, sea urchins and macrophytes. Overfishing depletes populations

124 of predatory fish and the substantial loss of large predators that exert a top-down control

125 mechanism, causing an unregulated increase in sea urchin population densities (Guidetti, Boero &

126 Bussotti, 2005; McClanahan & Shafir, 1990; Micheli et al., 2005; Sala et al., 2012; Sala,

127 Boudouresque & Harmelin-Vivien, 1998; Shears & Babcock, 2003).

128   The indirect impact of the size-selective harvesting on the ecosystems largely depends on

129 the functional role and competitive dominance of the target species (Kaiser & Jennings, 2001). For

130 example, heavy size-selective harvest of sea urchin top-predators generates cascading effects

131 pushing the system beyond the resilience tipping points (Ling et al. 2015), in extreme cases

132 facilitating the shift from vegetated coastal marine ecosystems to bare rocky areas - barrens -

133 hosting low biodiversity (e.g., Bianchelli & Danovaro 2020).

134   In the last decades the lower-trophic-level fisheries intensified the exploitation on

135 remaining commercial species, including invertebrates (e.g., Anderson et al., 2011), among which

136 sea urchins represent a relevant economic resource (Andrew et al., 2002). Sea urchin fisheries

137 further worsen the functioning of the ecological system: in fact, in addition to the effects due to

138 low density and biomass of top-predators due to overfishing, the intensive sea urchin harvest leads

139 to their abrupt decline and, ultimately, determining the collapse of their populations (e.g., Johnson

140 et al. 2012).

141   Since the gonad size is proportional to the sea urchin size, being more mature and

142 developed in the largest individuals (Mita et al., 2007), the size-selective harvest of the largest sea

143 urchins can gradually compromise the population fertility (Brewin et al., 2000; Byrne, 1990;

144 Guettaf, San Martin & Francour, 2000). Populations under heavy harvest pressure are often

145 destinated to collapse unless they receive enough larval supply from the outside (Dubois et al.,

146 2016), determining important changes in the community structure (Steneck et al., 2002; Vadas &

147 Steneck, 1995; Villouta, 2000).

148   The edible sea urchin *Paracentrotus lividus* (Lamarck 1816) is the most exploited species

149 in the Mediterranean Sea but, at the same time, it is an indispensable functional herbivore in

150 controlling macroalgal communities through their grazing activity (Boada et al., 2017; Guarnieri

151 et al., 2014; McClanahan & Sala, 1997; Prado et al., 2007). In some regions of the Western

152 Mediterranean Sea, the intensive harvest of *P. lividus* locally re-scaled population body-size

153 determining an evident cut-off of their population structure above the commercial size-class of 50

154 mm (test diameter without spines; TD) and with the depletion of the breeding stock (Couvray et

155 al., 2015; Gianguzza et al., 2006; Guidetti, Boero & Bussotti, 2004).

156   In Sardinia (Italy, Western Mediterranean Sea), *P. lividus* is extensively harvested since

157 the early 2000s which has dramatically reduced the sea urchin density in extensive coastal areas

158 (Ceccherelli et al., 2011; Pais et al., 2012, 2007; Pieraccini, Coppa & De Lucia, 2016; Ceccherelli

159 et al., 2021). In the worst cases, the loss of the largest and oldest individuals shifted the

160 reproductive potential of the population to the smaller fertile individuals (Loi et al., 2017).

161   Estimating through time the gamete production of the exploited sea urchin populations can

162 be crucial to manage the local fishery sustainability and to prevent the population collapse. The

163 spatial and temporal variation of the gamete production can be assessed through the analysis of

164 the annual reproductive cycle (Brewin et al., 2000). The reproductive cycle is generally evaluated

165 through the estimation of the GonadoSomatic Index (GSI), as fluctuations in gonad size and

166 spawning periods (Gianguzza et al., 2013; Shpigel et al., 2004; Spirlet, Grosjean & Jangoux, 1998),

167 and from which the reproductive potential of a population (the total gamete output) depends on

168 (Brewin et al., 2000). The variation of GSI is strictly associated to environmental changes, such as

169 sea surface temperature (Beddingfield & McClintock, 1998; Levitan, 1991; Levitan, Sewell &

170 Chia, 1992; Spirlet, Grosjean & Jangoux, 2000; Spirlet, Grosjean & Jangoux, 1998), wave height

171 and food quality (Brady & Scheibling, 2006; Byrne, 1990; Gianguzza et al., 2013; Lozano et al.,

172 1995; Minor & Scheibling, 1997; O'Hara & Thórarinsdóttir, 2021; Sellem & Guillou, 2007).

173   Overall, the largest adults represent the major breeding stock of the population but at the

174 same time are the target commercial size-class (TD $\geq$ 50 mm), whilst the smaller fertile individuals

175 at under-commercial size-class ($40 \leq TD < 50$ mm), are important contributors for the self-

176 sustenance of the population (e.g. Loi et al., 2017) and represent the future fishing stock. The

177 breeding stock can produce one or more cohort of mature gametes in a single breeding season

178 (Mita et al., 2007), being their reproductive cycle characterized by one or more seasonal peaks

179 (Boudouresque & Verlaque, 2001; Ouréns, Fernández & Freire, 2011).

180   The aim of this study is to determine the variability across five years of the reproductive

181 potential in one of the most harvested sea urchin populations of Sardinia. The reproductive

182   potential was evaluated by the estimation of GSI and IGO in relation to the population density.

183   During the last year of the study, a comparison of the reproductive potential of an unexploited

184   population (in the nearby Marine Protected Area) was also done.

185   The reproductive potential corresponds to the gamete output produced by the whole

186   population in relation with the portion of the breeding stock (large and small fertile individuals).

187   In the study area the annual trend of the Gonadosomatic Index and the consequently gamete output

188   were expected not to change over the years, with the exception of the occurrence of sea surface

189   temperature or wave height anomalies. Conversely, the intense size-selective harvest that

190   systematically removes the largest breeder contributors, would be the cause of an important

191   decrease in the reproductive potential of the population. Accordingly, a drastic decline of the

192   reproductive potential due to the rescaling population body-size is supposed.

193

194   **2.   Material and Methods**

195
196   *2.1.   Study site*
197

198   This study was conducted at Su Pallosu Bay (40.0489° N, 8.4161° E), located in the north

199   of the Peninsula of Sinis (central western Sardinia), a high natural density area of sea urchins that

200   has been overexploited by fishermen for many years (e.g. Coppa et al. 2021; Fois et al., 2020;

201   Farina et al., 2020).

202   The favorable environmental conditions, such as the shallow calcareous plateau with

203   *Posidonia oceanica* patches (De Falco et al., 2008) support a high sea urchin density in this area.

204   The low current speed determining recirculation cells of water surface at Su Pallosu Bay promotes

205   the recruitment success of the population respect to the nearby Marine Protected Area (Farina et

206   al., 2018). The low abundance of top-predators (Marra et al., 2016), typical of the fishing areas,

207   reduces the natural mortality of juveniles and medium size-classes (Oliva et al., 2016; Farina et al.

208   2020).

209   Accordingly, Su Pallosu Bay is considered one of the most important sea urchin harvest

210   hotspots in Sardinia (Fig.1). In this area, as well as in the whole island, the professional sea urchin

211   harvest is officially open from November to April and it is allowed with scuba diving. Since 2009,

212   189 professional licenses have been released and the limit of the daily catch amount has been fixed

213   to 1500 per fisherman or 3000 per boat, while the minimum urchin catch size (test dimeter with

214   no spines) is 5cm (RAS, Autonomous Region of Sardinia, decree no. 2524/DecA/102 of 7 October

215   2009).

216   In the nearby Marine Protected Area ("Penisola del Sinis - Isola di Mal di Ventre",

217   established in 1997; Fig.1) the sea urchin harvest was intensively practiced before 2009 (Coppa et

218   al. 2021). Since 2009 this activity progressively decreased and, nowadays, it is restricted in terms

219   of fishing licenses (55 licenses are allowed only for residents in this area), of catch quota per day

220   which amounts to 500 individuals, while recreational fishing has been banned (Farina et al. 2020;

221   Ceccherelli et al., 2022). Inside the MPA, the reproductive potential of the unexploited sea urchin

222   population of Cape Seu (39.8980° N, 8.4010° E) was sampled during the last year of study.

223   The harvest and protected localities have homogeneous macroalgal communities (Guala et

224   al. 2006; Anedda et al. 2016) and are far from urbanizations, harbours, aquaculture activities and

225   rivers. Accordingly, there was no anthropogenic influence on the dissolved nutrient concentration

226   on macroalgal composition and abundance over the years (Loi et al., 2017). Moreover, dispite the

227   low abundance of top predators, no barren grounds are present in this area.

228   The annual average of the Sea Surface Temperature (SST) in the area ranged between 17.5

229   and 19 °C, with colder open waters and warmer coastal waters (Cucco et al., 2006). The wind-

230 waves are generated on a wide fetch by the prevailing winds that, in the form of severe winter

231 storms, can produce intense Sea Wave Height (SWH) of up to 5m (Simeone et al., 2016). Data of

232 the daily SST were extrapolated from NOAA dataset and free downloaded from "Asia-Pacific

233 Data Research Centre" webpage (http://apdrc.soest.hawaii.edu/las/v6/dataset?catitem=1233).

234 Data of the hourly SWH (m) were free downloaded from Copernicus Marine Environmental

235 Monitoring   Service

236 (https://resources.marine.copernicus.eu/?option=com_csw&task=results&pk_vid=20be7e57367a

237 57a51616599440425bbc). The monthly mean SST and SWH were calculated choosing an

238 intermediate point between the two sampling sites, representing the trend of SST and SWH in each

239 locality during the sampling period.

240
241   *2.2.   GonadoSomatic Index and Annual Gamete Output*
242
243   Sea urchins were monthly sampled across five years from 2013 to 2019 at the harvest

244 locality and in 2018-19 at the protected locality. However, due to adverse marine weather

245 conditions persisting over time, samplings could not be done in a few months (Fig.2, Fig.S3).

246   The sea urchins were collected by scuba diving at two sites few hundred meters apart and

247 over a rocky bottom at the bathymetry of $5 \pm 1m$, corresponding to the mean depth at which the

248 harvesters usually work. During monitorings, 12 to 20 individuals were collected for each site,

249 both for the commercial (CS, test diameter TD $\geq$ 50 mm) and the under-commercial size-class

250 (US, $40 \leq$ TD < 50 mm).

251   In accordance with maturity rating proposed by Byrne et al. (1990), sea urchins were in

252 recovery stage mainly during summer and autumn, from June to October. Gametogenesis began

253 at the end of autumn and lasted until early spring, fully mature stage was found from January to

254 April and spawning events occurred mostly in winter-spring (Ghisaura et al., 2016; Siliani et al.,

255 2016). In general, there are no significant asynchronisms in the reproductive cycle between males

256 and females of *P. lividus* (Crapp & Willis, 1975) and 1:1 sex ratio was generally observed in this

257 specific populations (e.g., Loi 2018). Finally, population fecundity in this area can be considered

258 suitable accordingly to the analysis conducted by Loi et al. (2017) and the eggs fertilization rate

259 obtained in Brundu et al. (2016, 2017).

260   The gonadosomatic index (GSI) represents the gonad mass as a proportion of the total body

261 mass of the animals (Lawrence et al. 1965). Accordingly, size (cm of test diameter without spine)

262 and wet weight (g) were recorded in each sea urchin, gonads collected and weighted (g), and the

263 GSI of each sampled individual calculated as:

264

265   *([gonad wet weight / total wet weight] x 100) %*   (Lawrence et al., 1965)

266   Accordingly, the individual GSI were pooled together by month to determine monthly

267 mean GSI by size classes by locality (monthly mean GSI; Brewin et al. 2000). The complete annual

268 reproductive cycle, described by GSI calculated from May of one year to June of the following

269 year, represents a sampling period. Thus, GSI of both commercial and under-commercial, size-

270 classes were monthly calculated for five sampling periods (P1-P5) at the harvest locality and for

271 the last sampling period (P5) at the protected locality.

272   The GSI annual pattern was estimated for the whole population as the average of the

273 monthly mean GSI values for each sampling period in each locality. The highest and the lowest

274 peaks of the monthly mean GSI recorded over a sampling period correspond to the time before the

275 beginning (pre-spawning) and after the end (post-spawning) of a spawning event.

276   The mean individual gamete output (IGO) was then calculated as:

277

278   *(pre spawning GSI- post spawning GSI)/ 100* $g\ g^{-1}\ se^{-1}$ (Brewin et al., 2000)

279
280
281 which is the difference between the monthly mean pre-spawning GSI and the monthly mean post-

282 spawning GSI in units of gamete wet weight per sea urchin per spawning event ($g\ g^{-1}\ se^{-1}$; Brewin

283 et al. 2000). The sum of the all-year-round differences (IGOs) represents the Annual Gamete

284 Output (AGO), which is the reproductive contribution per year of each fertile size-class and it is

285 measured in units of gonad wet weight per sea urchin wet weight per year ($g\ g^{-1}\ yr^{-1}$; Brewin et

286 al. 2000).

287
288   *2.3.*   *Population density and reproductive potential*
289
290   Sea urchin population structure was estimated during P1 (2013-14) and P5 (2018-19)

291 sampling periods at the harvest locality, and during P5 (2018-19) at the protected locality as well.

292 Density and size frequency distribution of sea urchins of both localities were evaluated in the same

293 two sites where GSI was estimated by independent underwater counts (Guala et al. 2006). The

294 counts were carried out in three replicates of $5m^2$ (20 contiguous 50x50cm quadrats) each, the

295 minimum optimal surface to detect aggregative distribution of sea urchins, as consequence of the

296 habitat heterogeneity.

297   All the animals found in the sampling quadrats were counted and measured with a calliper.

298 The abundance was then estimated as density (ind m^{-2}) and individuals were grouped in size-

299 classes of 10 mm of test diameter to build the population structure (e.g., Farina et al., 2020, 2022).

300   Finally, the population reproductive potential was estimated as the Total Gamete Output

301 (TGO) for each fertile size-class and for the whole population per m^2 per year (popTGO) and

302 defined as the sum of the AGO of each fertile size-class multiplied for the sea urchin density (g

303 $g^{-1}\ m^{-2}\ yr^{-1}$; Loi et al., 2017).

304

305   *2.4.   Data analysis*

306

307   Variability of the monthly mean SST at the harvest locality was evaluated among the

308   sampling periods P1-P5 (from 2013 to 2019) throughout the non-parametric analysis of variance

309   Kruskal-Wallis test (Kruskal & Wallis, 1952). Moreover, the monthly mean SST during P5 was

310   compared with the SST at the protected locality (Mann-Whitney test; Mann & Whitney, 1947).

311   Similarly, difference in the monthly mean SWH was estimated among the sampling periods with

312   a parametric analysis of variance (Anova 1-way, Underwood, 1997). Since the SST and SWH

313   strongly influence the annual trend of GSI (see the introduction), in order to exclude their statistical

314   effects, they were successively set as further predictors with random distribution and independent

315   from the response variables in the following analysis.

316   Exploration of GSI and AGO data was carried out to check that ANOVA assumptions (i.e.,

317   normal distribution and homogeneity of variance) were met (Zuur, Ieno & Elphick, 2010). Since

318   the GSI data were characterized by a different number of replicates collected during the years, and

319   non-normal distribution, General Linear Mixed Model (GLMM) with Poisson family was chosen

320   as the best tool to handle unbalanced data involving random factors (SST and SWH).

321   A General Mixed Model (GLMM) was performed to assess the variance of the monthly mean GSI

322   in the harvest locality setting "Period" (five levels) and "Size" (two levels) as fixed factors, "SST"

323   (twelve levels) and "SWH" (twelve levels) nested "Period" and "Site" (two levels) as random

324   factors in order to exclude their statistical effects on the response variable. A second GLMM was

325   run to evaluate differences in the monthly mean GSI between harvest and protected localities

326   during P5. This analysis was set with "Locality" (two levels) and "Size" (two levels) as fixed

327   factors and, "SST", "SWH" and "Site" as random factors. A Linear Mixed Model (LMM) was

328   also performed to investigate potential significant differences in AGO emitted by the harvested

329   population over the sampling periods. The model was set with AGO as response variable, "Period"

330   as fixed factor, and "Size" as random factor. Graphical validations of all the statistical models are

331   provided in the supplementary materials.

332   Finally, a statistical analysis to evaluate differences in the density of sea urchin population

333   structures was carried out between P1 and P5 in the harvest locality. LMMs were performed setting

334   density of recruits (TD <10 mm), juveniles and middle size-classes (10≤ TD <40 mm), density of

335   US and CS size-classes as response variables and "Period" and "Site" as fixed and random factors,

336   respectively.

337   All the described procedures and analyses were performed using the Nortest and lme4

338   packages in R software (Venerables & Smith, 2010).

339

340   **3. Results**

341

342   The monthly mean SST did not change significantly neither in the harvest locality through

343   time (Kruskal Wallis test: chi-squared = 0.43005, p-value = 0.98; Fig.2 and Table S1), nor between

344   the harvest and the protected localities during P5 (Mann-Whitney test: p-value = 0.7561; see Fig.2

345   and Table S1). Furthermore, the difference in the monthly mean SWH was not significant across

346   the five-year period (Anova one-way test: p-value=0.579; Table S2).

347

348   *3.1.   GonadoSomatic Index and Annual Gamete Output*

349

350   Overall, an annual average of 400 sea urchins of both fertile size-classes (CS and US) were

351   collected during the five-year period to estimate the monthly mean GSI trend in the harvest locality

352   (Fig.S1). The monthly mean GSI was significantly influenced by the "Size" (p-value<0.001), but

353   not by the "Period" (AIC=5903.2, R^2=0.39; see Fig. 2, Table 1a and Fig.S2). The monthly mean

354   GSI compared between localities (the harvest and the protected) during P5 was also significantly

355   influenced by the "Size" (p-value=0.0019), but not by the "Locality" (AIC=2199.4; R^2=0.54; see

356   Fig. 2, Table 1b and Fig. S3).

357   The main pre-spawning GSI was in March, except for the P3 that was in August, while smaller

358   spawning events were observed in Autumn (Fig. 2, Table 2 and Fig.S1). The main pre-spawning

359   GSI ranged between 5.5±0.71% during P2 and 7.07 ±0.43% during P5 for CS, while US ranged

360   between 4.05±0.52% and 5.48±0.42% during P3 and P5, respectively (Fig.2 and Table 2). In the

361   protected locality the main pre-spawning GSI was also found in March and was 6.3±0.5% and

362   5.41±0.61% for CS and US, respectively (Fig.2 and Table 2). Conversely, in the harvest locality,

363   the average IGO value increased over the years and the higher AGO was estimated during the last

364   periods, when values were 0.13 and 0.11 g g^{-1} yr^{-1}, respectively for P4 (p-value=0.008) and P5

365   (Fig.3 and Table 3). During P5 in the protected locality, the average IGO was 0.026 g g^{-1} se^{-1} and

366   the AGO was 0.11 g g^{-1} yr^{-1} (Table 2).

367

368   *3.2.   Population density and reproductive potential*
369
370   In the harvest locality the density of CS did not change significantly from P1 (0.6 ±0.2 ind

371   m^{-2}) to P5 (0.5 ±0.1 ind m^{-2}), while the US density decreased significantly from 2.7 ±0.3 to1.2 ±0.4

372   ind m^{-2} over the same years (Fig.4, Table 4, Fig.S4). Variations in density of recruits, juveniles and

373   middle size-class individuals were also non-significant between P1 and P5 (Fig.4, Table 4 and

374   Fig.S4).

375   Accordingly, in the harvest locality, the reproductive potential of CS was 0.03 during P1

376   and 0.04 g g^{-1} m^{-2} yr^{-1} during P5, whilst in the same periods was 0.12 and 0.05 g g^{-1} m^{-2} yr^{-1} for

377 US (Fig. 5 and Table 2). In the protected locality during P5, density of CS and US was 0.9 ±0.4

378 and 0.8 ±0.4 ind m^{-2}, respectively, and the population reproductive potential was 0.04 and 0.005 g

379 g^{-1} m^{-2} yr^{-1} for CS and US, respectively (Fig. 5, Table 2). Consistently with these results, the

380 reproductive potential (TGO) of the harvested population was 0.15 during P1 and 0.086 g g^{-1} m^{-2}

381 yr^{-1} during P5 (Fig.5, Table 2), whilst it was 0.09 g g^{-1} m^{-2} yr^{-1} for the protected population during

382 P5 (Table 2).

383

384 **Discussion**

385

386   The temporal pattern of the monthly mean GSI at the harvest locality was not significantly

387 different over the years, but it was significantly higher in the large individuals (CS) rather than in

388 the smaller ones (US), confirming the major role of commercial size urchins on the population

389 breeding stock. The main spawning events occurred generally in spring according with Spirlet,

390 Grosjean & Jangoux (1998), except for P3 when there was no evidence of abrupt spawning events.

391 Finally, during the last sampling period (P5), the monthly mean GSI of the population at the harvest

392 locality was not significantly different from the protected locality.

393   Due to the overexploitation, density of CS urchins in the harvest locality remained at low

394 values across the five-year period (less than one individual per square meter). Contrarily, US

395 density significantly decreased from more than two individuals to less than one individual per

396 square meter, leading to a proportional decrease of their gamete output and the loss of 40% of the

397 whole population reproductive potential.

398   In the North-Western Sardinia, the intensive size-selective sea urchin harvest strongly

399 affects the density of the largest (CS) individuals (Pais et al., 2007; Ceccherelli et al., 2021). Su

400 Pallosu Bay is one of the main hotspots along this coast, where the harvest of sea urchins

401   determines the persistence of truncated demographic population structure above the commercial

402   size-class over time (Loi et al. 2017). To date, the scarcity of the major population breeding stock

403   (CS) was buffered by the high natural density of younger animals (US) and supported by an

404   effective recruitment rate in the area (Farina et al. 2018).

405   Nevertheless, our results suggest that the intensive harvest in recent years has drastically

406   rescaled the population body size, often exceeding in the legal limit of commercial size and thus

407   affecting the youngest breeding stock, as demonstrated by the density of US individuals almost

408   halved in five years. Although no data are available to estimate larval connectivity among the

409   harvest population and outside populations, our results suggest that the sea urchin recruitment in

410   the future years will have to totally rely on larvae coming from other populations.

411   The density of the commercial size-class in the protected locality was estimated during the

412   last period of the study (P5) and corresponded to an intermediate value with respect to the density

413   recorded before (2010) and after (2012) the stock contraction caused by the intensive harvesting

414   practiced in the past (see Coppa et al., 2022). In effect, stricter sea urchin fishery regulations were

415   introduced in the MPA after the population contraction (Marra et al., 2016; Pieraccini, Coppa &

416   De Lucia, 2016). Accordingly, despite the GSI was no estimated during P1 for the protected

417   population, a slight recovery of the commercial size-class after the collapse kept stable the

418   reproductive potential of the population over the 5-year monitoring period. Conversely, the

419   continuous and inexorable deterioration of the reproductive potential of the harvest population

420   could be a direct consequence of the harvesting activity aiming to market the gonads of individuals

421   under commercial legal size (Furesi et al., 2016).

422   However, indirect effects can be manifested also at community level (Kaiser & Jennings,

423   2001), since the key role of the functional herbivore *P. lividus* in the ecosystems (Boudouresque

424   & Verlaque, 2001). For example, the intensive harvesting of *P. lividus* can encourage the

425   proliferation of the habitat competitor *Arbacia Lixula,* a sea urchin species harvested by humans

426   and weakly preyed in nature (Guidetti, 2004).

427   Moreover, the rescaling population body-size can also impair the fertility, in terms of

428   gamete quality, egg size (Moran & McAlister, 2009), larval development and survival (Berkeley,

429   Chapman & Sogard, 2004), and it pushes the smallest fertile sea urchins to increase their

430   reproductive investment (Fenberg & Roy, 2008). Consistently with these mechanisms, our results

431   seem to suggest a growing trend of the IGO across the years, indicating the increase over time of

432   the amount of gamete per urchin per spawning event. Accordingly, the AGO was high in the last

433   two years, especially during P4.

434   Nevertheless, the reproductive investment is a well-documented compensatory response

435   that induces physiological and behavioural changes in the survivors, such as alterations in the

436   timing of maturation, metabolism and growth rate (Ali, Nicieza & Wootton, 2003; Enberg et al.,

437   2012). Although a long time series of data need to confirm this trend, it would wonder whether the

438   persistence of the harvesting pressure could induce survivors to improve their reproductive

439   investment in gonad production rate or spawning intensity to deal with the chronic lack of the

440   major breeding stock (largest commercial size-class urchins).

441

442   **Conclusions**

443

444   The intensive size-selective harvest has deeply changed the demographic structure of the

445   sea urchin population and has determined a drastic decrease of its reproductive potential, by

446   affecting the portion of the youngest part of the breeding stock. An in-depth analysis of the results

447   also highlights an interesting growing trend of the amount of gamete emitted by the survivors.

448   Due to such evidence, mitigating the ecological consequences of size-selective sea urchin

449   exploitation in this area probably requires a shift in management strategies designed to modulate

450   yields on the natural variability in size-classes characterizing the sea urchin population structure.

451   Ideally, it would be useful to address local harvest activities towards a size-balanced population

452   fishing, avoiding the complete depletion of the largest classes (e.g., Law & Plank, 2018). Such

453   approach should necessarily go through a shared vision with the stakeholders that includes the rise

454   of awareness of fishermen and much more effective control of illegal practices. Actually, in the

455   context of the small-scale fisheries, the engagement of local fisheries and other stakeholders to

456   establishing a co-management mechanism of the resources would improve achieving an effective

457   fishery governance (e.g., Mahon et al. 2003; Sousa et al. 2020). Whatever, the effects of the

458   rescaling sea urchin population body-size identified in this study can contribute to the development

459   of an ecosystem-based-management fishing plan to ensure the sustainable exploitation of the

460   resource and the conservation of the ecosystem.

461

462

463   *Acknowledgement*
464   The authors would like to thank the administration of the Marine Protected Area "Penisola del
465   Sinis-Isola di Mal di Ventre" for providing the boat for the monthly sampling and all the students
466   who helped in the field and in the laboratory during these years.

467

468

469

470

471

472

473

474   **References**

475

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

478 Anderson, S.C., Mills Flemming, J., Watson, R., Lotze, H.K., 2011. Rapid Global Expansion of
479   Invertebrate Fisheries: Trends, Drivers, and Ecosystem Effects. PLoS One 6, e14735.
480   https://doi.org/10.1371/journal.pone.0014735
481 Andrew, N.L., Agatsuma, Y., Ballesteros, E., Bazhin, A.G., Creaser, E.P., Barnes, D.K.A.,
482   Botsford, L.W., Bradbury, A., Campbell, A., Dixon, J.D., Einarsson, S., Gerring, P.K.,
483   Hebert, K., Hunter, M., Hur, S.B., Johnson, C.R., Juinio-Menez, M.A., Kalvass, P., Miller,
484   R.J., Moreno, C.A., Palleiro, J.S., Rivas, D., Robinson, S.M.L., Schroeter, S.C., Steneck,
485   R.S., Vadas, R.L., Woodby, D.A., Xiaoqi, Z., 2002. Status and management of world sea
486   urchin fisheries, in: Oceanogr. Mar. Biol. an Annual Review. Taylor & Francis LTD, 11
487   New Fetter Lane, London ec4p 4ee, England, pp. 343–425.
488 Anedda, R., Siliani, S., Melis, R., Loi, B., Baroli, M., 2021. Lipid metabolism of sea
489   urchin Paracentrotus lividus in two contrasting natural habitats. Sci Rep 11, 14174.
490   https://doi.org/10.1038/s41598-021-93669-9
491 Audzijonyte, A., Kuparinen, A., Gorton, R., Fulton, E.A., 2013. Ecological consequences of
492   body size decline in harvested fish species: Positive feedback loops in trophic interactions
493   amplify human impact. Biol. Lett. 9. https://doi.org/10.1098/rsbl.2012.1103
494 Baum, J., Myers, R., Kehler, D., Worm, B., Harley, S., Dohert, P., 2003. Collapse and
495   Conservation of Shark Populations in the Northwest Atlantic. Science 299 (5605), 389–392.
496   https://doi.org/10.1126/science.1079777
497 Beddingfield, S.D., McClintock, J.B., 1998. Differential survivorship, reproduction, growth and
498   nutrient allocation in the regular echinoid *Lytechinus variegatus* (Lamarck) fed natural
499   diets. J. Exp. Mar. Bio. Ecol. 226, 195–215. https://doi.org/10.1016/S0022-0981(97)00247-
500   5
501 Berkeley, S., Chapman, C., Sogard, S., 2004. Maternal age as a determinant of larval growth and
502   survival in a marine fish, Sebastes melanops. Ecology 85, 1258–1264.
503   https://doi.org/10.1890/03-0706
504 Bianchelli, S., Danovaro, R., 2020. Impairment of microbial and meiofaunal ecosystem functions
505   linked to algal forest loss. Sci. Rep. 10, 1–12. https://doi.org/10.1038/s41598-020-76817-5
506 Boada, J., Arthur, R., Alonso, D., Pagès, J.F., Pessarrodona, A., Oliva, S., Ceccherelli, G., Piazzi,
507   L., Romero, J., Alcoverro, T., 2017. Immanent conditions determine imminent collapses:
508   nutrient regimes define the resilience of macroalgal communities. Proc. Royal Soc. B. 284,
509   20162814. https://doi.org/10.1098/rspb.2016.2814
510 Boudouresque, C.F., Verlaque, M., 2001. Ecology of *Paracentrotus lividus*, in: Miller, J. (Ed.),
511   Edible Sea Urchins: Biology and Ecology. Elsevier Science, pp. 177–216.
512 Brady, S.M., Scheibling, R.E., 2006. Changes in growth and reproduction of green sea urchins,
513   *Strongylocentrotus droebachiensis* (Müller), during repopulation of the shallow subtidal
514   zone after mass mortality. J. Exp. Mar. Bio. Ecol. 335, 277–291.
515   https://doi.org/10.1016/j.jembe.2006.03.016
516 Brewin, P.E., Lamare, M.D., Keogh, J.A., Mladenov, P.V., 2000. Reproductive variability over a
517   four-year period in the sea urchin *Evechinus chloroticus* (Echinoidea: Echinodermata) from
518   differing habitats in New Zealand. Mar. Biol. 137, 543–557.
519   https://doi.org/10.1007/s002270000366
520 Brundu, G., Vallainc, D., Baroli, M., Figus, A.M., Pinna, A., Carboni, S., 2017. Effects of on-
521   demand feeding on sea urchin larvae (*Paracentrotus lividus*; Lamarck, 1816), development,
522   survival and microalgae utilization. Aquac. Res. 48, 1550–1560.
523   https://doi.org/10.1111/are.12990

524 Brundu, G., Vian Monleón, L., Vallainc, D., Carboni, S., 2016. Effects of larval diet and
525   metamorphosis cue on survival and growth of sea urchin post-larvae (*Paracentrotus lividus*;
526   Lamarck, 1816). Aquaculture 465, 265–270.
527   https://doi.org/10.1016/j.aquaculture.2016.09.014
528 Byrne, M., 1990. Annual reproductive cycles of the commercial sea urchin *Paracentrotus lividus*
529   from an exposed intertidal and a sheltered subtidal habitat on the west coast of Ireland. Mar.
530   Biol. 104, 275–289. https://doi.org/10.1007/BF01313269
531 Ceccherelli, G., Addis, P., Atzori, F., Cadoni, N., Casu, M., Coppa, S., De Luca, M., de Lucia,
532   G.A., Farina, S., Fois, N., Frau, F., Gazale, V., Grech, D., Guala, I., Mariani, M., Marras,.
533   M.S.G., Navone, A.G., Pansini, A., Panzalis, P., Pinna, F., Ruiu, A., Scarpa, F., Piazzi, L.,
534   2022. Sea urchin harvest inside marineprotected areas: an opportunity to investigate the
535   effects of exploitation where trophic upgrading is achieved. PeerJ 10:e12971
536   http://doi.org/10.7717/peerj.12971
537 Ceccherelli, G., Pais, A., Pinna, S., Sechi, N., Chessa, L.A., 2011. Human impact on
538   *Paracentrotus lividus*: the result of harvest restrictions and accessibility of locations. Mar.
539   Biol. 158, 845–852. https://doi.org/10.1007/s00227-010-1611-5
540 Coppa, S., Pronti, A., Massaro, G., Brundu, R., Camedda, A., Palazzo, L., Nobile, G., Pagliarino,
541   E., de Lucia, G.A., 2021. Fishery management in a marine protected area with compliance
542   gaps: socio-economic and biological insights as a first step on the path of sustainability. J.
543   Environ. Manage. 280 (2021): 111754.
544 Couvray, S., Miard, T., Bunet, R., Martin,Y., Grillasca J.P., Bonnefont J.L., Coupé S., 2015.
545   Experimental release of *Paracentrotus lividus* sea urchin juveniles in exploited sites along
546   the french mediterranean coast. J. Shellfish Res. 34, 1–9.
547   https://doi.org/10.2983/035.034.0240
548 Crapp, G.B., Willis, M.E., 1975. Age determination in the sea urchin *Paracentrotus lividus*
549   (Lamarck), with notes on the reproductive cycle. J. Exp. Mar. Biol. Ecol. 20(2), pp.157-178.
550 Cucco, A., Perilli, A., De Falco, G., Ghezzo, M., Umgiesser, G., 2006. Water circulation and
551   transport timescales in the Gulf of Oristano. Chem. Ecol. 22, 307–331.
552   https://doi.org/http://doi.org/10.1080/02757540600670364
553 Cucco, A., Sinerchia, M., Ribotti, A., Olita, A., Fazioli, L., Perilli, A., Sorgente, B., Borghini,
554   M., Schroeder, K., Sorgente, R., 2012. A high-resolution real-time forecasting system for
555   predicting the fate of oil spills in the Strait of Bonifacio (western Mediterranean Sea). Mar.
556   Pollut. Bull. 64, 1186–1200. https://doi.org/https://doi.org/10.1016/j.marpolbul.2012.03.019
557 De Falco, G., Baroli, M., Cucco, A., Simeone, S., 2008. Intrabasinal conditions promoting the
558   development of a biogenic carbonate sedimentary facies associated with the seagrass
559   Posidonia oceanica. Cont. Shelf Res. 28, 797–812. https://doi.org/10.1016/j.csr.2007.12.014
560 Dubois, M., Rossi, V., Ser-Giacomi, E., Arnaud-Haond, S., López, C., Hernández-García, E.,
561   2016. Linking basin-scale connectivity, oceanography and population dynamics for the
562   conservation and management of marine ecosystems. Glob. Ecol. Biogeogr. 25, 503–515.
563   https://doi.org/10.1111/geb.12431
564 Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S.,
565   Heino, M., 2012. Fishing-induced evolution of growth: Concepts, mechanisms and the
566   empirical evidence. Mar. Ecol. 33, 1–25. https://doi.org/10.1111/j.1439-0485.2011.00460.x
567 Enberg, K., Jørgensen, C., Mangel, M., 2010. Fishing-induced evolution and changing
568   reproductive ecology of fish: The evolution of steepness. Can. J. Fish. Aquat. Sci. 67, 1708–
569   1719. https://doi.org/10.1139/F10-090

570 Farina, S., Ceccherelli, G., Piazzi, L., Grech, D., Panzalis, P., Navone, A.G., Guala, I., 2022.
571   Protection effectiveness and sea urchin predation risk: The role of roving predators beyond
572   the boundaries of a marine protected area in the Western Mediterranean Sea. Aquat.
573   Conserv. 32, 1101-1114. https://doi.org/10.1002/aqc.3819
574 Farina, S., Baroli, M., Brundu, R., Conforti, A., Cucco, A., De Falco, G., Guala, I., Guerzoni, S.,
575   Massaro, G., Quattrocchi, G., Romagnoni, G., Brambilla, W., 2020. The challenge of
576   managing the commercial harvesting of the sea urchin *Paracentrotus lividus* : advanced
577   approaches are required. PeerJ, 8, e10093. https://doi.org/10.7717/peerj.10093
578 Farina, S., Quattrocchi, G., Guala, I., Cucco, A., 2018. Hydrodynamic patterns favouring sea
579   urchin recruitment in coastal areas: A Mediterranean study case. Mar. Environ. Res.
580   https://doi.org/10.1016/j.marenvres.2018.05.013
581 Fenberg, P.B., Roy, K., 2008. Ecological and evolutionary consequences of size-selective
582   harvesting: How much do we know? Mol. Ecol. 17, 209–220.
583   https://doi.org/10.1111/j.1365-294X.2007.03522.x
584 Festa-Bianchet, M., 2003. Exploitative wildlife management as a selective pressure for life-
585   history evolution of large mammals, in: Festa-Bianchet, M., Apollonio, M. (Eds.), Animal
586   Behavior and Wildlife Conservation. Island Oress, Washington D.C., pp. 191–210.
587 Fois, N., Arrostuto, N., Serra, S., Trentadue, M., Guala, I., Farina, S., Ruberti, N., Brundu, G.,
588   Loi, B., Grech, D., Addis, P., Secci, M., Pierucci, A., (2020). Monitoraggio dello stock
589   commerciale di riccio di mare *(Paracentrotus lividus)* e stato della risorsa 2019/2020.
590   AGRIS Sardegna. Technical report
591 Furesi, R., Madau, F.A., Pulina, P., Sai, R., Pinna, M.G., Pais, A., 2016. Profitability and
592   sustainability of edible sea urchin fishery in Sardinia (Italy). J. Coast. Conserv., 20, pp.299-
593   306. https://doi.org/10.1007/s11852-016-0441-0
594 Ghisaura, S., Loi, B., Biosa, G., Baroli, M., Pagnozzi, D., Roggio, T., Uzzau, S., Anedda, R.,
595   Addis, M.F., 2016. Proteomic changes occurring along gonad maturation in the edible sea
596   urchin *Paracentrotus lividus*. J. Proteomics, 144, pp.63-72
597   https://doi.org/10.1016/j.jprot.2016.05.035
598 Gianguzza, P., Bonaviri, C., Prato, E., Fanelli, G., Chiantore, M., Privitera, D., Luzzu, F.,
599   Agnetta, D., 2013. Hydrodynamism and its in fluence on the reproductive condition of the
600   edible sea urchin *Paracentrotus lividus*. Mar. Environ. Res. 85, 29–33.
601   https://doi.org/10.1016/j.marenvres.2012.12.007
602 Gianguzza, P., Chiantore, M., Bonaviri, C., Cattaneo-Vietti, R., Vielmini, I., Riggio, S., 2006.
603   The effects of recreational *Paracentrotus lividus* fishing on distribution patterns of sea
604   urchins at Ustica Island MPA (Western Mediterranean, Italy). Fish. Res. 81, 37–44.
605   https://doi.org/10.1016/j.fishres.2006.06.002
606 Guala, I., de Lucia, G.A., De Falco, G., Domenici, P., Paliaga, B. 2006. Monitoraggio
607   dell'effetto riserva nell'Area Marina Protetta Penisola del Sinis–Isola di Mal di Ventre.
608   Technical report. Fondazione IMC, 35 pp.
609 Guarnieri, G., Bevilacqua, S., Vignes, F., Fraschetti, S., 2014. Grazer removal and nutrient
610   enrichment as recovery enhancers for overexploited rocky subtidal habitats. Oecologia 175,
611   959–970. https://doi.org/10.1007/s00442-014-2944-4
612 Guettaf, M., San Martin, G.A., Francour, P., 2000. Interpopulation variability of the reproductive
613   cycle of *Paracentrotus lividus* (Echinodermata: Echinoidea) in the south-western
614   Mediterranean. J. Mar. Biol. Assoc. UK 80, 899–
615   907.https://doi:10.1017/S0025315400002885

616 Guidetti, P., 2004. Consumers of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, in
617   shallow Mediterranean rocky reefs. Helgol. Mar. Res. 58, 110–116.
618   https://doi.org/10.1007/s10152-004-0176-4
619 Guidetti, P., Boero, F., Bussotti, S., 2005. Evaluating the effects of protection on fish predators
620   and sea urchins in shallow artificial rocky habitats: a case study in the northern Adriatic
621   Sea. Mar. Environ. Res. 59, 333–348. https://doi.org/10.1016/j.marenvres.2004.05.008
622 Guidetti, P., Terlizzi, A., Boero, F., 2004. Effects of the edible sea urchin, *Paracentrotus lividus*,
623   fishery along the Apulian rocky coast (SE Italy, Mediterranean Sea). Fish. Res. 66, 287–
624   297. https://doi.org/10.1016/S0165-7836(03)00206-6
625 Hamilton, S.L., Caselle, J.E., Standish, J.D., Schroeder, D.M., Love, M.S., Rosales-Casian, J.A.,
626   Sosa-Nishizaki, O., 2007. Size-selective harvesting alters life histories of a temperate sex-
627   changing fish. Ecol. Appl. 17, 2268–2280. https://doi.org/10.1890/06-1930.1
628 Heino, M., Godo, O., 2002. Fisheries-induced selection pressures in the context of sustainable
629   fisheries. Bull. Mar. Sci. 70, 639–656.
630 Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J.,
631   Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange,
632   C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner,
633   R.R., 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science
634   293 (5530), 629–637. https://doi.org/10.1126/science.1059199
635 James, P.J., 2006. The effects of wave and feeding disturbance on roe enhancement of the sea
636   urchin *Evechinus chloroticus* held in sea-cages. Aquaculture 252, 361–371.
637   https://doi.org/10.1016/j.aquaculture.2005.07.023
638 Johnson, T.R., Wilson, J.A., Cleaver, C. and Vadas, R.L., 2012. Social-ecological scale
639   mismatches and the collapse of the sea urchin fishery in Maine, USA. Ecol. and Soc., 17(2).
640   http://dx.doi.org/10.5751/ES-04767-170215
641 Kaiser, M., Jennings, S., 2001. An ecosystem perspective on conserving targeted and non-
642   targeted species, in: Reynolds, J., Mace, G., Redford, K., Robinson, J. (Eds.), Conservation
643   of Exploited Species. Cambridge University Press, London, pp. 343–369.
644 Kruskal, W.H., Wallis, W.A., 1952. Use of Ranks in One-Criterion Variance Analysis. J. Am.
645   Stat. Assoc. 47, 583–621. https://doi.org/10.1080/01621459.1952.10483441
646 Law, R., 2000. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57, 659–668.
647   https://doi.org/10.1006/jmsc.2000.0731
648 Law, R., Plank, M.J., 2018. Balanced harvesting could reduce fisheries-induced evolution. Fish
649   Fish, 19(6), pp.1078-1091. https://doi.org/10.1111/faf.12313
650 Levitan, D., 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in
651   response to food limitation. Mar. Biol. 111, 431–435. https://doi.org/10.1007/BF01319415
652 Levitan, D.R., Sewell, M.A., Chia, F.S., 1992. How distribution and abundance influence
653   fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecology. 73(1),
654   pp.248-254. https://doi.org/10.2307/1938736
655 Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon,
656   A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., 2015. Global
657   regime shift dynamics of catastrophic sea urchin overgrazing. Philos. Trans. R. Soc. Lond.,
658   B, Biol. Sci. 370(1659): 20130269. https://doi.org/10.1098/rstb.2013.0269
659 Loi, B., Guala, I., Pires, R., Brundu, G., Baroli, M., Farina, S., 2017. Hard time to be parents ?
660   Sea urchin fishery shifts potential reproductive contribution of population onto the
661   shoulders of the young adults. PeerJ, 5, p.e3067. https://doi.org/10.7717/peerj.3067

662 Loi, B., 2018. Changes in gonad conditions of the sea urchin *Paracentrotus lividus* in response to
663   anthropic, seasonal, environmental, physiological and dietary factors: suggestions for an
664   improvement of the actual harvesting practices and echinoculture production. PhD thesis,
665   Tuscia University of Viterbo, 190 pp.
666 Longhurst, A., 2006. The sustainability myth. Fish. Res. 81, 107–112.
667   https://doi.org/10.1016/j.fishres.2006.06.022
668 Lozano, J., Galera, J., Lopez, S., Turon, X., Palacin, C., Morera, G., 1995. Biological cycles and
669   recruitment of *Paracentrotus lividus* (Echinodermata: Echinoidea) in two contrasting
670   habitats. Mar. Ecol. Prog. Ser. 122, 179–192. http://doi.org/10.3354/meps122179
671 Mahon, R., Almerigi, S., McConney, P., Parker, C., Brewster, L., 2003. Participatory
672   methodology used for sea urchin co-management in Barbados. Ocean Coast Manag, 46(1-
673   2), 1-25. https://doi.org/10.1016/S0964-5691(02)00118-7
674 Mann, H.B., Whitney, D.R., 1947. On a Test of Whether one of Two Random Variables is
675   Stochastically Larger than the Other. Ann. Math. Stat. 18, 50–60.
676   https://doi.org/10.1214/aoms/1177730491
677 Marra, S., Coppa, S., Camedda, A., Mazzoldi, C., Wrachien, F., Massaro, G., de Lucia, G.A.,
678   2016. Recovery trends of commercial fish: The case of an underperforming mediterranean
679   marine protected area. PLoS One 11, 1–22. https://doi.org/10.1371/journal.pone.0146391
680 McClanahan, T.R., Sala, E., 1997. A Mediterranean rocky-bottom ecosystem fisheries model.
681   Ecol. Modell. 104, 145–164. https://doi.org/10.1016/S0304-3800(97)00121-X
682 McClanahan, T.R., Shafir, S.H., 1990. Causes and consequences of sea-urchin abundance and
683   diversity in kenyan coral-reef lagoons. Oecologia 83, 362–370.
684   https://doi.org/10.1007/BF00317561
685 Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, G.C., Romano,
686   F., 2005. Cascading human impacts, marine protected areas; and the structure of
687   Mediterranrean reef assemblages. Ecol. Monogr. 75, 81–102. https://doi.org/10.1890/03-
688   4058
689 Minor, M., Scheibling, R., 1997. Effects of food ration and feeding regime on growth and
690   reproduction of the sea urchin *Strongylocentrotus droebachiensis*. Mar. Biol. 129, 159–167.
691   https://doi.org/https://doi.org/10.1007/s002270050156
692 Mita, M., Sato, J., Hirosawa, Y., Nakamura, M., 2007. Gonadal maturation is dependent on body
693   size in the sea urchin, *Echinometra tsumajiroi* 50, 187–190.
694   https://doi.org/10.1080/07924259.2007.9652245
695 Moran, A.L., McAlister, J.S., 2009. Egg size as a life history character of marine invertebrates: is
696   it all it's cracked up to be? Biol. Bull. 216, 226–242. https://doi.org/10.2307/25548157
697 Moreno, C., 2001. Community patterns generated by human harvesting on Chilean shores: a
698   review. Aquat. Conserv. Mar. Freshw. Ecosyst. 11, 19–30. https://doi.org/10.1002/aqc.430
699 Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature
700   423, 280–283. https://doi.org/https://doi.org/10.1038/nature01610
701 O'Hara, T.E., Thórarinsdóttir, G.G., 2021. A depth-dependent assessment of annual variability in
702   gonad index, reproductive cycle (gametogenesis) and roe quality of the green sea urchin
703   (*Strongylocentrotus droebachiensis*) in Breidafjördur, west Iceland. Regional Studies in
704   Marine Science, 45, 101846.
705 Oliva, S., Farina, S., Pinna, S., Guala, I., Agnetta, D., Ariotti, P., Mura, F., Checcherelli, G.,
706   2016. Determinants of *Paracentrotus lividus* sea urchin recruitment under oligotrophic
707   conditions: implications for conservation management. Mar. Environ. Res. 117, 13–20.

708   https://doi.org/10.1016/j.marenvres.2016.02.013

709 Ouréns, R., Fernández, L., Freire, J., 2011. Geographic, population, and seasonal patterns in the
710   reproductive parameters of the sea urchin *Paracentrotus lividus*. Mar. Biol. 158, 793–804.
711   https://doi.org/10.1007/s00227-010-1607-1

712 Pais, A., Chessa, L. a., Serra, S., Ruiu, A., Meloni, G., Donno, Y., 2007. The impact of
713   commercial and recreational harvesting for *Paracentrotus lividus* on shallow rocky reef sea
714   urchin communities in North-western Sardinia, Italy. Estuar. Coast. Shelf Sci. 73, 589–597.
715   https://doi.org/10.1016/j.ecss.2007.02.011

716 Pais, A., Serra, S., Meloni, G., Saba, S., Ceccherelli, G., 2012. Harvesting effects on
717   *Paracentrotus lividus* population structure: a case study from northwestern Sardinia, Italy,
718   before and after the fishing season. J. Coast. Res. 28, 570–575.
719   https://doi.org/10.2112/JCOASTRES-D-10-00119.1

720 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food
721   webs. Science 279, 860–863. https://doi.org/10.1126/science.279.5352.860

722 Peters, R.H., 1983. The ecologcal implications of body size. Cambridge University Press,
723   Cambridge.

724 Pieraccini, M., Coppa, S., de Lucia, G.A., 2016. Beyond marine paper parks? Regulation theory
725   to assess and address environmental non-compliance. Aquat. Conserv. Mar. Freshw.
726   Ecosyst. https://doi.org/10.1002/aqc.2632

727 Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalament, F., Chemello, R., Harmelin-Vivien,
728   M.L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., Pipitone, C., 2000. Trophic cascades
729   in benthic marine ecosystems: lessons for fisheries and protected-area management.
730   Environ. Conserv. 27, 179–200. http://doi.org/10.1017/S0376892900000205

731 Prado, P., Tomas, F., Alcoverro, T., Romero, J., 2007. Extensive direct measurements of
732   *Posidonia oceanica* defoliation confirm the importance of herbivory in temperate seagrass
733   meadows. Mar. Ecol. Ser. 340, 63–71. https://doi.org/10.3354/meps340063

734 Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S.,
735   Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B.,
736   Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F.,
737   Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F., Zabala,
738   M., 2012. The Structure of Mediterranean Rocky Reef Ecosystems across Environmental
739   and Human Gradients, and Conservation Implications. PLoS One 7, e32742.
740   https://doi.org/10.1371/journal.pone.0032742

741 Sala, E., Boudouresque, C.F., Harmelin-Vivien, M., 1998. Fishing, trophic cascades, and the
742   structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82, 425–
743   439. https://doi.org/10.2307/3546364

744 Sellem, F., Guillou, M., 2007. Reproductive biology of *Paracentrotus lividus* (Echinodermata:
745   Echinoidea) in two contrasting habitats of northern Tunisia (south-east Mediterranean). J.
746   Mar. Biol. Assoc. UK. https://doi.org/10.1017/S002531540705521X

747 Shears, N.T., Babcock, R.C., 2003. Continuing trophic cascade effects after 25 years of no-take
748   marine reserve protection. Mar. Ecol. Prog. Ser. 246, 1–16.
749   https://doi.org/10.3354/meps246001

750 Shpigel, M., McBride, S.C., Marciano, S., Lupatsch, I., 2004. The effect of photoperiod and
751   temperature on the reproduction of the European sea urchin *Paracentrotus lividus*.
752   Aquaculture 232, 343–355. https://doi.org/10.1016/S0044-8486(03)00539-8

753 Siliani, S., Melis, R., Loi, B., Guala, I., Baroli, M., Sanna, R., Uzzau, S., Roggio, T., Addis,

754 M.F., Anedda, R., 2016. Influence of seasonal and environmental patterns on the lipid
755 content and fatty acid profiles in gonads of the edible sea urchin *Paracentrotus lividus* from
756 Sardinia. Mar. Environ. Res. 113, 124-133. https://doi.org/10.1016/j.marenvres.2015.12.001
757 Sousa, A., Jacinto, D., Penteado, N., Pereira, D., Silva, T., Castro, J.J., Leandro, S.M., Cruz, T.,
758 2020. Temporal variation of the fishers' perception about the stalked barnacle (Pollicipes
759 pollicipes) fishery at the Berlengas Nature Reserve (Portugal). Reg. Stud. Mar. Sci., 38,
760 p.101378. https://doi.org/10.1016/j.rsma.2020.101378
761 Spirlet, C., Grosjean, P., Jangoux, M., 2000. Optimization of gonad growth by manipulation of
762 temperature and photoperiod in cultivated sea urchins, *Paracentrotus lividus* (Lamarck)
763 (Echinodermata). Aquaculture 185, 85–99. https://doi.org/10.1016/S0044-8486(99)00340-3
764 Spirlet, C., Grosjean, P., Jangoux, M., 1998. Reproductive cycle of the echinoid *Paracentrotus
765 lividus*: analysis by means of the maturity index. Invertebr. Reprod. Dev. 34, 69–81.
766 https://doi.org/10.1080/07924259.1998.9652355
767 Steneck, R., Graham, M., Bourque, B., Corbett, D., Erlandson, J., Estes, J., Tegner, M., 2002.
768 Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ. Conserv. 29,
769 436–459. https://doi.org/10.1017/S0376892902000322
770 Trippel, E., 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45, 759–771.
771 https://doi.org/10.2307/1312628
772 Underwood, A.J., 1997. Experiments in ecology: their logical design and interpretation using
773 analysis of variance. Cambridge university press.
774 Vadas, R., Steneck, R., 1995. Overfishing and inferences in kelp-sea urchin interactions, in:
775 Skjoldal, H., Hopkins, K., Erikstad, K. (Eds.), Ecology of Fjords and Coastal Waters.
776 Elsevier Science, Amsterdam, pp. 509–524.
777 Vallin, L., Nissling, A., 2000. Maternal effects on egg size and egg buoyancy of Baltic cod,
778 Gadus morhua — implications for stock structure effects on recruitment. Fish. Res. 49, 21–
779 37. https://doi.org/10.1016/S0165-7836(00)00194-6
780 Venerables, W., Smith, D., 2010. R Development Core Team. 2010. An Introduction to R. Notes
781 on R: A Programming Environment for Data Analysis and Graphics Version 2.11. 1
782 Villouta, E., 2000. Potential ecological impacts of harvesting kina (*Evechinus chloroticus*) in
783 Fiordland. Conserv. Advis. Sci. Notes 286, 1–14.
784 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common
785 statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-
786 210X.2009.00001.x

Figure 1

Map of the study area

In the North of Sinis Peninsula, Su Pallosu Bay is one of the most important harvest hot-spot in West coast of Sardinia (harvest locality), while Cape Seu is a locality within the nearby Marine Protected Area (area in light blue) and monitored during the last period (protected locality). Sea urchin sampling sites are represented by the black dots.

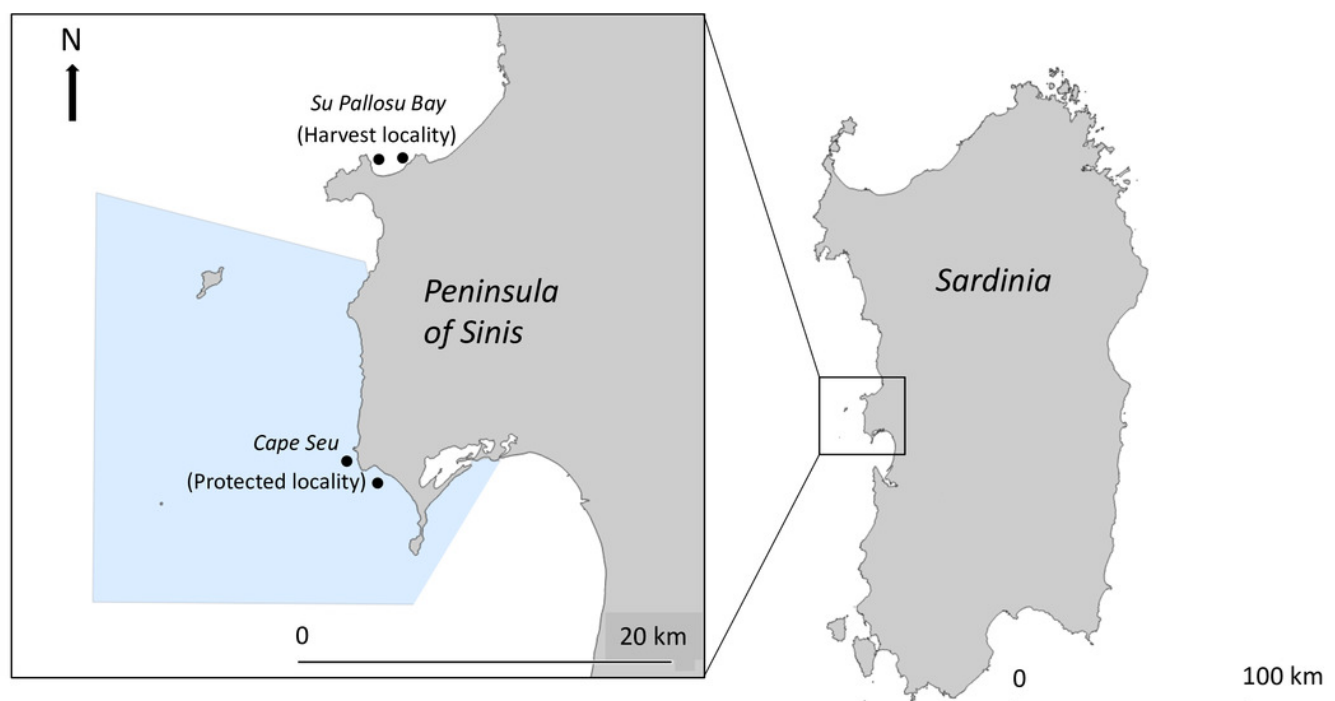



Figure 2

Graphs of GSI over the sampling periods

Average annual trend of the GonadoSomatic Index in the harvest locality and in the protected locality during the last sampling period (P5). GSI is represented as mean ±standard deviation for CS size-class (black line) and US size-class (gray line). Mean SST was also plotted (thinner gray line).

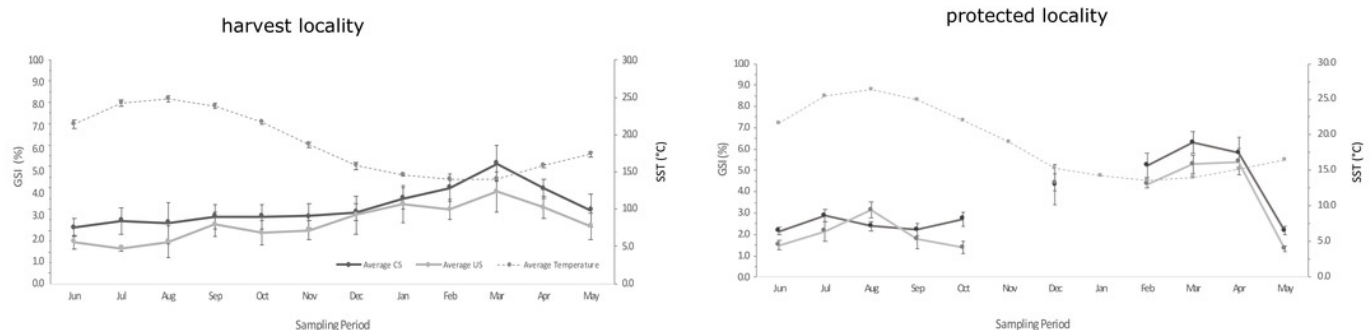



Figure 3

Graphs of the Individual Gamete Output and Annual Gamete Output over the sampling periods.

The inter-annual trend of Individual Gamete Output (IGO, g g-1 se^{-1}) and Annual Gamete

Output (AGO, g g^{-1} yr^{-1}) in the harvest population over the sampling periods.

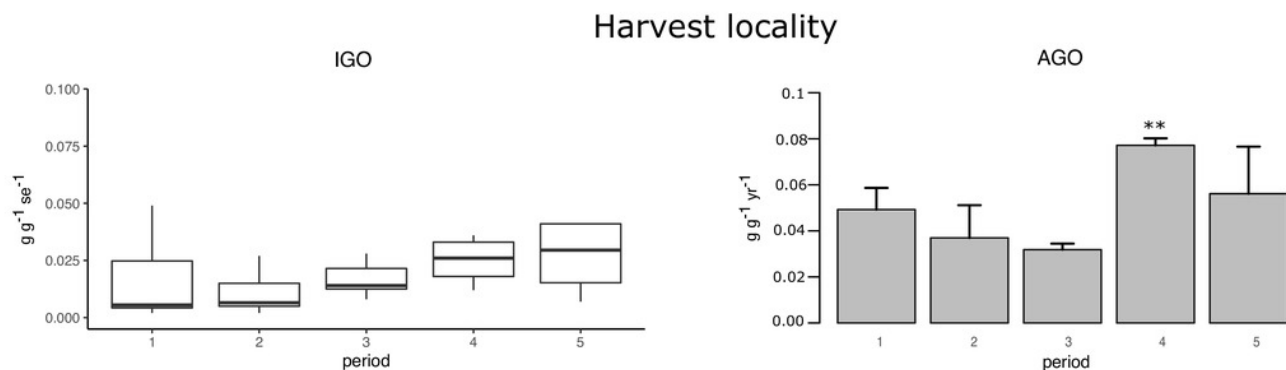



Figure 4

Sea urchin population structure

Size-density and size frequency distributions of the sea urchin population in the harvest locality during P1and P5. The range of the size classes is 10 mm of test diameter without spines (TD). Size-classes are grouped by stage in relation with the main ecological and anthropogenic processes influencing them (recruitment, predation and human harvesting).

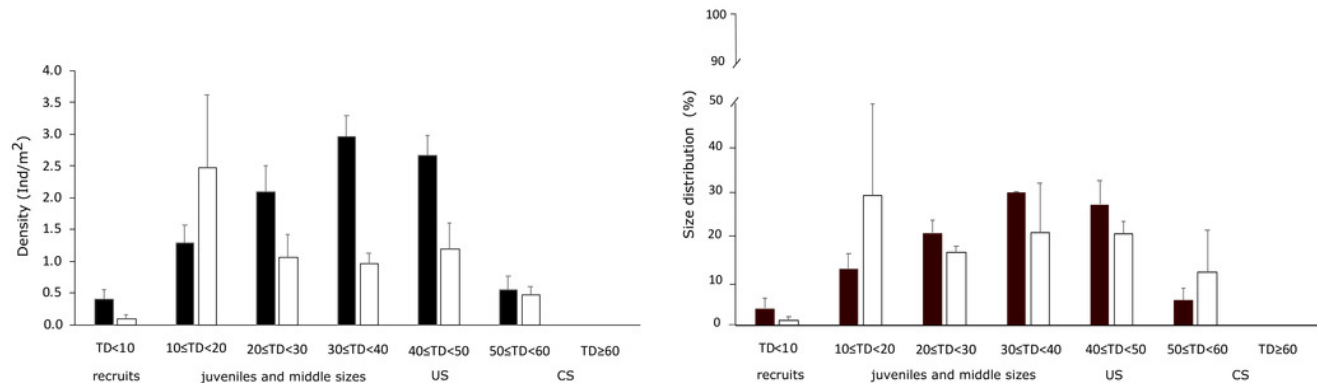
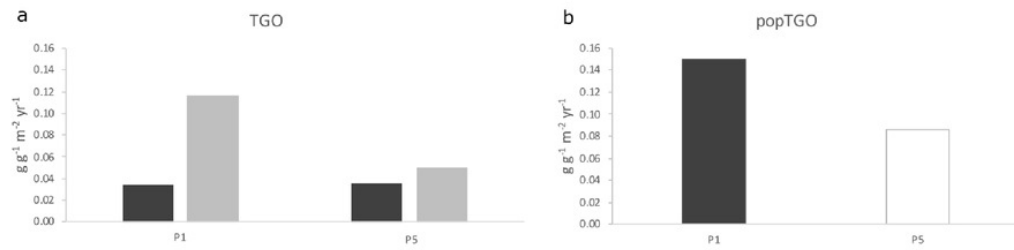



Figure 5

Population reproductive potential

Total Gamete Output (TGO, g g^{-1} m^{-2} yr^{-1}) of the CS and US size-classes and the reproductive potential of the whole population (popTGO) of the harvest locality during P1 and P5.

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 "SST", "SWH" 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	-0.25406	0.03251	-7.815	**$5.5e^{-15}$**
	Random effect	**Variance**	**Std.Dev**		
	Site	$4.517e^{-03}$	0.067211		
	Period:SST	$1.259e^{-01}$	0.354813		
	Period:SWH	$1.225e^{-09}$	0.000035		
AIC=5903.2; R^2=0.39					
b	Fixed effects	Estimate coeff	Std. error	z-value	p-value
GSI	Intercept	3.4725	0.4812	7.217	$5.42e^{-06}$
	Locality	-0.8230	0.4084	-2.015	0.0695
	Size	-0.4714	0.1196	-3.943	**$9.03e^{-05}$**
	Random effect	**Variance**	**Std.Dev**		
	Site	0.01395	0.1181		
	SST	0.76585	0.8751		
	SWH	1.23354	1.1106		
AIC= 2199.4; R^2= 0.54					

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

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

Period	Size-class	GSI (%) pre-spawning	GSI (%) post-spawning	IGO (g g⁻¹ se⁻¹)	AGO (g g⁻¹ yr⁻¹)	Urchin density (ind m⁻²)	TGO (g g⁻¹ m⁻² yr⁻¹)
1	CS	2.39±0.13	2.17±0.15	0.002	0.06	0.6±0.2	0.03
	CS	2.95±0.26	2.52±0.16	0.004			
	CS	6.55±0.29	1.61±0.11	0.049			
	US	1.76±0.14	1.14±0.14	0.006	0.04	2.7±0.3	0.12
	US	2.61±0.32	2.07±0.19	0.005			
	US	4.43±0.39	1.33±0.21	0.031			
	Pop			0.016	0.11	3.3±0.5	0.15
2	CS	2.72±0.50	2.20±0.19	0.005	0.03	-	-
	CS	2.44±0.23	2.25±0.28	0.002			
	CS	3.67±0.34	3.11±0.31	0.006			
	CS	5.45±0.61	4.03±0.57	0.014			
	US	1.83±0.27	1.33±0.88	0.005	0.05	-	-
	US	2.99±0.18	1.53±0.90	0.015			
	US	5.47±0.64	2.73±0.53	0.027			
	Pop			0.010	0.08	-	-
3	CS	5.33±0.62	3.96±0.40	0.014	0.03	-	-
	CS	4.09±0.33	2.46±0.37	0.016			
	US	4.05±0.52	3.26±0.51	0.008	0.03	-	-
	US	3.96±0.47	2.72±0.69	0.012			
	US	1.97±0.33	0.63±0.07	0.013			
	Pop			0.012	0.06	-	-
4	CS	4.27±1.34	1.52±0.37	0.027	0.08	-	-
	CS	3.25±0.40	2.04±0.26	0.012			
	CS	5.34±0.58	1.73±0.47	0.036			
	US	4.23±0.98	2.24±0.56	0.020	0.05	-	-
	US	4.59±0.32	1.40±0.19	0.032			
	Pop			0.025	0.13	-	-
5	CS	2.72±0.34	0.89±0.13	0.018	0.07	0.5±0.1	0.04
	CS	1.65±0.22	1.38±0.26	0.003			
	CS	7.07±0.43	2.11±0.30	0.050			
	US	1.40±0.19	0.98±0.18	0.004	0.04	1.2±0.4	0.05
	US	5.48±0.42	1.73±0.21	0.038			
	Pop			0.022	0.11	1.7±0.5	0.09
5P	CS	2.88±0.29	2.22±0.29	0.007	0.05	0.9±0.4	0.04
	CS	6.30±0.50	2.17±0.20	0.041			
	US	3.14±0.38	1.39±0.28	0.018	0.06	0.8±0.4	0.05
	US	5.41±0.61	1.35±0.13	0.041			
	Pop			0.026	0.11	1.7±0.8	0.09

LMM result for Annual Gamete Output (AGO) in function of "Period".

The "Size", was set as random effect. 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
AGO	Intercept	0.049250	0.006017	8.185	9.63e-06
	Period 2	-0.012300	0.008510	-1.445	0.17894
	Period 3	-0.017400	0.008510	-2.045	0.06811
	Period 4	0.027900	0.008510	3.279	**0.00831**
	Period 5	0.006900	0.008510	0.811	0.43633
	Random effect	**Variance**	**Std.Dev**		
	Size	7.241e-05	0.00851		
LogLink=33.5; R^2=0.79					

LMM result of changes in population demographic structure in the harvest locality between P1 and P5.

"Period" is set as fixed effect and "Site" is set as random effects. Estimate coefficient, Standard Error, t-value and significance level (p-value) are provided for fixed effect.

a.	Fixed effects	Estimate coeff	Std. error	t-value	p-value
US density	Intercept Period	2.7500 -1.4167	0.6080 0.5765	4.523 -2.457	0.0409 **0.0436**
	Random effect	**Variance**	**Std.Dev**		
	Site	0.3405	0.5835		
AIC=33.21; R²=0.52					
b.	Fixed effects	Estimate coeff	Std. error	t-value	p-value
CS density	Intercept Period	0.20621 -0.02516	0.09052 0.11687	2.278 -0.215	0.0352 0.8320
	Random effect	**Variance**	**Std.Dev**		
	Site	0	0		
AIC=23.3; R²=0.01					
c.	Fixed effects	Estimate coeff	Std. error	t-value	p-value
Mid size density	Intercept Period	1.0919 -0.3490	0.1951 0.1733	5.597 -2.013	0.0326 0.0541
	Random effect	**Variance**	**Std.Dev**		
	Site	0.02326	0.4823		
AIC=51.29; R²=0.24					
d.	Fixed effects	Estimate coeff	Std. error	t-value	p-value
Recruits	Intercept Period	0.29574 -0.20927	0.09478 0.12236	3.12 -1.71	0.0142 0.1256
	Random effect	**Variance**	**Std.Dev**		
	Site	0	0		
AIC=7.27; R²=0.01					