

The challenge of managing the commercial harvesting of *Paracentrotus lividus*: are novel approaches required?

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Many fish species are overexploited, and many stocks have collapsed. This crisis, along with increasing concerns over flow-on effects on ecosystems, has caused a re-evaluation of fisheries management practices and the approach of ecosystem-based fisheries management. The aim of this work is to highlight the role of ecological key-factors in planning a sustainable harvesting of the functional species *Paracentrotus lividus* and preserve the marine coastal ecosystems. Recruitment and predation processes that mainly drive population dynamic of this species are strongly related with the environment. Sea urchin density and population structures of the Peninsula of Sinis (Western coast of Sardinia, Italy) were evaluated in relation environmental constrains in five different sectors identified for type of habitats and their spatial organization, average bottom current speed of water circulation and predatory fish abundance (inside/outside the local Marine Protected Area). Results show how sea urchins are more abundant in rocky habitat configured in high patch density. Negative correlations are found between densities of recruits with average bottom current speed as well as between densities of under-commercial size (middle-size sea urchins) with predatory fish abundance. The results of this work underlines the necessity to integrate ecological processes that regulate sea urchin population dynamic with standard management measures, providing the foundation for scientifically sound management that embeds spatio-temporal environmental process at the relevant scale for the assessment of the stock sustainability.

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Abstract

Many fish species are overexploited, and many stocks have collapsed. This crisis, along with increasing concerns over flow-on effects on ecosystems, has caused a re-evaluation of fisheries management practices and the approach of ecosystem-based fisheries management. The aim of this work is to highlight the role of ecological key-factors in planning a sustainable harvesting of the functional species *Paracentrotus lividus* and preserve the marine coastal ecosystems. Recruitment and predation processes that mainly drive population dynamic of this species are strongly related with the environment. Sea urchin density and population structures of the Peninsula of Sinis (Western coast of Sardinia, Italy) were evaluated in relation environmental constrains in five different sectors identified for type of habitats and their spatial organization, average bottom current speed of water circulation and predatory fish abundance (inside/outside the local Marine Protected Area). Results show how sea urchins are more abundant in rocky habitat configured in high patch density. Negative correlations are found between densities of recruits with average bottom current speed as well as between densities of under-commercial size (middle-size sea urchins) with predatory fish abundance. The results of this work underlines the necessity to integrate ecological processes that regulate sea urchin population dynamic with standard management measures, providing the foundation for scientifically sound management that embeds spatio-temporal environmental process at the relevant scale for the assessment of the stock sustainability.

Introduction

The continuous decline of fishery catches during the last decades pushed many fishermen to switch to new species at lower-trophic levels (Anderson et al., 2011). One of the clearest examples, reported for several temperate coastal ecosystems, is the overexploitation of target species involved in the typical tri-trophic interaction “fish-sea urchins-macroalgae”. In general, overfishing can seriously alter these trophic relationships and reducing populations of predatory fishes in many coastal areas. This can trigger an uncontrolled proliferation of sea urchins that can often lead to overgrazing of algal cover and, consequently, to the creation of ecosystem barrens (Steneck et al., 2002; Steneck, Vavrinec & Leland, 2004).

In addition, the intensive harvesting of sea urchins also increased (Andrew et al., 2002; James et al., 2016). Generally, sea urchin fisheries start as small activities that experience a phase of rapid expansion followed by a phase of full exploitation before the exhaustion of the resource (Andrew et al., 2002), following the short-term “boom-and-bust” pattern of many invertebrate fisheries. In fact, the systematic removal of hundreds of thousands of commercial-size individuals, which are the main reproducers, leads populations to the collapse (Tegner & Dayton, 1977; Pennington, 1985; Levitan, Sewell & Fu-Shiang Chia, 1992; Levitan & Sewell, 1998). Thus, the typical slow-growth of these organisms does not hold up the market demand.

From the ecological standpoint, in many cases, the drastic reduction of the sea urchin density determines a rapid development of large brown algae stands that leads to changes in the relative composition of fish and benthic community (e.g. Steneck et al., 2002). Among them, also the urchin predators increase and further weaken populations. This leads to a new steady state of the ecosystem structure that is generally unsustainable for the yield of the harvesting (Johnson and Wilson, 2012).

In light of these considerations, an integrated management strategy for social-ecological systems has been developed in many regions where this situation was verified, including Chile (the world’s largest fishery), Maine (U.S.), New Zealand, Canada, and Norway (James et al., 2016).

In the Mediterranean Sea, sea urchin fishery focuses on the functional species *Paracentrotus lividus* that is among one of the most important herbivores of benthic ecosystems (e.g. Hereu et al., 2005; Prado et al., 2012). *P. lividus* is generally observed to overgraze macrophyte communities, especially in the areas heavily exploited by fishery (Wallner-Hahn et al., 2015). The impact of overfishing through the impairment of predatory control on sea urchin

populations seems to be much more important than the overharvesting that takes place in few areas of the Mediterranean (McClanahan & Sala, 1997; Guidetti & Sala, 2007; Sala et al., 2012).

However, in other regions, including Sardinia (Western Mediterranean Sea), this species is intensively harvested for commercial purposes and populations suffered high human pressure since decades (Pais et al., 2007, 2012; Ceccherelli et al., 2011; Loi et al., 2017). The Peninsula of Sinis, in the central western coast of this region, is one of the largest high-pressure zone of the harvesting activity and it includes the Marine Protected Area “Penisola del Sinis, Isola di Mal di Ventre” (MPA). Accordingly, the rules governing the exploitation inside the MPA are more restrictive than outside, e.g. several no-take areas and only spearfishing.

Despite these restrictions have been in place from the early 2000s, individuals greater than 5 cm diameter (minimum commercial size or stock) are still uncommon in populations both inside and outside the MPA. From 2015 to 2017 scientific monitoring showed further decrease of both the total population of *P. lividus* and stock that in thirteen years has been reduced more than 80% (Coppa et al., 2018). The steep decline of sea urchin populations emphasizes the need to increase enforcement further the control actions and to evaluate even more restrictive management measures. However, such actions could be insufficient for long-term stock preserve unless they capture and effectively address the factors affecting the dynamics of sea urchin population in the area.

Thus, it appears evident that the management strategies should undergo a major transformation to avoid a fisheries collapse in this area (Ouréns, Naya & Freire, 2015). In this sense, there are a number of well managed and sustainable sea urchin fisheries around the world that tend to rely on a good overview of biology of the urchin species present in the area as well as sound knowledge of the dynamics of the sea urchin populations (James et al., 2016)

For example, in New Zealand, sea urchin fishery reached a very stable status thanks to the realization of a quota management system that has been integrated into the management system with measures such as the number of licences and the fishing limitations (season, commercial size classes, fishing gears etc.). The quota management system sets a total allowable catch and determines the individual fishing quota according to the assessment of the stock sustainability (Eddy et al., 2015).

In this regard, scientific monitoring can provide valuable information to estimate biological parameters and reference points useful for stock assessment. However, given the role of sea urchin as a functional species for coastal ecosystems, advanced approaches are required for proper management of its fisheries that can account for population and ecosystem dynamics, environmental interaction and spatial complexity (Andrew et al., 2002; James et al., 2016).

In the Mediterranean Sea, the sea urchin abundance vary widely from region to region and it is well known that it is primarily driven by variability in recruitment (Turon et al., 1995; López et al., 1998). Larval supply is strongly influenced by the oceanographic conditions (Fenaux, Cellario & Rassoulzadegan, 1988; Harmelin-Vivien et al., 2000; Prado et al., 2012; Farina et al., 2018), while other environmental constraints such as the substrate, type of habitat and predators influence the success of the settlement and post-settlement survival (Boudouresque & Verlaque, 2001; Tomas, Turon & Romero, 2004; Hereu et al., 2005; Oliva et al., 2016). Specifically, while settlement on the rocky substrata colonised by macroalgal assemblages appears to be coupled to larval supply, high post-settlement mortality limits the recruitment of sea urchin populations in the three-dimensional structure of seagrass meadows (Tomas, Turon & Romero, 2004; Farina et al., 2009).

Once in the benthos, structural complexity of the habitat is crucial for the population outcome as well as its spatial configuration that can strongly influence sea urchin distribution in relation of food availability and shelter (Pagès et al., 2012; Farina et al., 2014, 2016, 2017). In fact, fish predation is the prevalent mechanism of top-down control on sea urchin abundance and serves as a critical bottle-neck for urchin populations, representing a significant pressure until individuals reach the refuge size of ~ 5 cm (Fig.1; Guidetti et al., 2004; Hereu et al., 2005). The main sea urchin fish predators in the Mediterranean Sea are the labrid species *Coris julis* and the commercial sea breams *Diplodus spp.* and *Sparus aurata*, visual hunters of small and medium size classes respectively (Sala, 1997; Guidetti, Boero & Bussotti, 2005). In addition to these, there are also average bottom predators like some species of whelks (e.g. the muricidae gastropod *Hexaplex trunculus*) or the carnivore sea star *Marthasterias glacialis* that are well known to be consumers of sea urchins (Sala & Zabala, 1996) and whose effect on populations can be locally important (Bonaviri et al., 2009; Gianguzza et al., 2009; Farina et al., 2016).

Thus, recruitment and predation are ecological processes that strongly shape population structure acting on different spatial scales and influencing abundance and distribution of sea urchins (Harmelin-Vivien et al., 2000; Prado et al., 2012).

As one of the largest high-pressure zone of the harvesting in Sardinia, the coasts of Peninsula of Sinis has been widely monitored and the analysis of data gathered during the period 2004 to 2007 has provided relevant information about the sea urchin populations' structure. In fact, also due to a decade of intensive harvesting (Loi et al., 2017), this period precedes the most significant reduction of the sea urchin population which occurred from the 2007 (Pieraccini, Coppa & De Lucia, 2016) and that can be considered as a *pre-crisis era*. Therefore, the *pre-crisis era* represents a reference environmental status that could provides the identification of any

natural relationships among population structure, ecological processes influencing population dynamic and environmental constraints in terms of hydrodynamism, habitat and substrate, and pool of predators from the areas of total fishing prohibition up to the mildest restrictions and the outside fishing areas.

We are confident that results of the present work will be useful for future fishery management plans, incline to ecosystem preservation, will certainly profit from not negligible results that arise from this research.

Material & Methods

Study Area

The study was conducted along a stretch of coast of about 40 km on the West Coast of Sardinia, Italy (Sinis coastal area; Fig. 2, Fig. S1) between the Gulf of Oristano (39.8377° N, 8.4844° E) and Su Pallosu Bay (40.0379° N, 8.3938° E). The middle and southern parts of the study area are included in the Marine Protected Area of “Penisola del Sinis, Isola di Mal di Ventre”, which covers a surface of 250 Km² (Fig. 2). The surface area with full protection is relatively small (5 Km², Guala et al., 2008), while the remaining zones are intensively frequented by commercial and recreational fishermen (Pieraccini, Coppa & De Lucia, 2016).

In the *pre-crisis era*, sea urchin harvesting was allowed only to resident professional fishermen inside the MPA, from November to April, for a maximum catch quota of 1000 sea urchin (with diameter without spines >5 cm) per day per fisherman. The number of licensed fishermen varied from 125 in the 2001 up to over 270 in the 2004-2007 three-year period. Outside the MPA, sea urchin harvesting is managed by a regional decree (RAS, Regione

Autonoma della Sardegna decree no. 2524/DecA/102 of October 7, 2009 and subsequent amendments). Before 2007, along the whole coast of Sardinia, approximately 150 professional fishermen were authorized to collect sea urchins by scuba diving from November to April with each diver allowed to collect up to 2000 sea urchins per day.

The study area is limited to the bathymetry of 5 ± 1 m (mean depth at which the harvesters usually work) and it is subdivided in five sectors (Fig. S1). Study sector 1 is identified in the portion of coast located outside MPA from Su Pallosu Bay to the northern boundary of the MPA, including Cape Mannu (Fig.2). Sectors 2 and 3 enclose the stretch of coast inside the MPA exposed to the open sea, while sector 4 represents the MPA islands of Mal di Ventre and Catalano. Finally, sector 5 represents the Gulf of Oristano inside MPA at the southern limit.

On the study area seabed, the bedrock has three different natures: Palaeozoic granite basement, cropping out around Mal di Ventre Island; Pliocene basalt rock, in the Cape San Marco area and surrounding Catalano island (Fais, Klingele & Lecca, 1996; De Falco et al., 2003; Duncan et al., 2011; Conforti et al., 2016); the Miocene and Quaternary calcareous rocks located all along the study area coastline (Lecca & Carboni, 2007). The substrate morphologies influence the distribution of *Posidonia oceanica*; the meadow shows a patchy pattern where the matte is on the bedrock and continuous pattern where the matte lies on the unconsolidated sediments (Fig.2). The meadow is continuous on the eastern side of Mal di Ventre Island and inside the Gulf of Oristano, while in the rest of the study area *P. oceanica* shows a patchy meadows pattern.

Along the coastal area, the average bottom current speed (Fig.3) strongly influences the abundance of sea urchin recruits, (Farina et al., 2018). Average bottom current speed is mainly

generated by the action of the frequent and intense wind events, mostly from the North-West (Mistral wind) and, to a lesser degree, from the South-West (Libeccio wind), characterized by a yearly mean speed of 7m/s and a peak speed higher than 20 m/s (Zecchetto et al., 2016). Such two prevalent wind regimes may generate intense flows toward south, in the case of Mistral events, and weaker northward flows, in the case of Libeccio events. In both cases, within the Gulf of Oristano, recirculation cells develop in correspondence of the leeway side of the main two Gulf capes. We refer to Cucco et al. (2006, 2012) for a detailed description of sea current circulation in the study area.

Finally, field monitoring between 2004-2012 showed no clear patterns of fish abundance in time nor between protected and unprotected sites (Marra et al., 2016). However, during the *pre-crisis era* (before 2007), larger abundances of sea breams were found inside than outside (Marra et al., 2016; Table.1). Thus, although boundaries and management of the protection zones of the MPA have been changing over the years, study sectors falling inside the Marine Protected Area should be expected to present higher predatory fish activity respect to the outside zone and this should be evident on sea urchin population structures (Shears & Babcock, 2003; Guidetti & Sala, 2007).

Within sectors, on the base of the occurrence of different rocky substrates and type of *Posidonia oceanica* meadows, the environmental areas inhabited by sea urchins are defined as types of habitat (Abercrombie, Hickman & Johnson, 1966). Accordingly, sea urchin population structure in terms of size class ranges -recruits, under-commercial size (middle-size sea urchins) and commercial sea urchins- is compared in function of different types of habitat and sectors in the *pre-crisis era*. Moreover, a predictive model was run to predict spatial variability of the whole sea urchin density in relation with the spatial configuration of the types of habitat. Finally,

average bottom current speed measured through numerical model solutions (Farina et al., 2018) and predatory fish density derived by Marra et al., (2016) are related to the study sectors and their relationships with the abundance of recruits and middle-size sea urchins are investigated respectively.

Environmental constrains

Geomorphology was described through habitat mapping (Fig. 2). Available data consist of morpho-bathymetric data, aerial image and several geo-datasets. To ease processing and data sharing among researchers, all available data were integrated and organized in a geodatabase implemented through a GIS and the software suite Geoinformation Enabling Toolkit StarterKit® (GET-IT), (Fugazza, Oggioni & Carrara; Pavesi et al., 2016; Lanucara et al., 2017; Brambilla et al., 2019) developed by researchers of the Italian National Research Council for RITMARE project.

The distribution and extent of habitats have been plotted to create a map with complete coverage of the seabed (MESH, 2008). Seafloor mapping has been made imposing discrete boundaries between different morphotypes (Fig. 2) to provide a representation of how are structured. Five of them are considered suitable habitats for sea urchin colonization and are calcareous rock substrata (CR), granite substrata (GR), basalt substrata (BA), *Posidonia oceanica* patchy meadow (PM) and *Posidonia oceanica* continuous meadow (CM). These types of habitat are alternate heterogeneously along the coast. A pool of variables describing the basic characteristic of habitat spatial configuration was estimated for each sector with the free software Fragstats 4.1 (McGarial & Marks, 1995). The variable estimated are Patch Density on the total landscape area (PD, patch/Km²), Perimeter-to-area ratio (P/A ratio, 1/m), Mean Patch Size

(MPS, Km²), the Largest Patch Index (LPI, %) as the percentage of landscape area occupied by the largest patch of a class and Interspersion/Juxtaposition Index (IJI, %) that measures the degree of aggregation or “clumpiness” of a map based on adjacency of patches (O’Neill et al., 1988).

The hydrodynamic features of the investigated area were inferred from meteo-marine numerical model application. Specifically, the results obtained by the application of a three-dimensional, finite element hydrodynamic and wind wave model, SHYFEM-WWM (Umgiesser et al., 2004), were used to describe the average of water circulation in the area. The model was already used to reproduce the wind-wave and the 3D water circulation along the Sinis coastal areas (Cucco et al., 2006, 2016; De Falco et al., 2008). In Farina et al., (2018), a simulation run was performed to reproduce the water circulation for the biennium 2009 and 2010. The model and simulation setup accounted for both oceanic and meteorological seasonal variability. In particular, the 2009-2010 biennium was selected for its meteorological conditions that were highly representative of the local climate (Farina et al., 2018). In this work the same simulation run was carried out to reproduce the water circulation in the first 10 meters of water depth during the same biennium. We refer to Farina et al, (2018) for details of the model and simulation setup. The results, consisting in hourly data of 3D current fields in the Sinis area, were averaged in time considering the first six months of the year only. The obtained dataset consisted in the average distribution of the average water speeds at the bottom between January and June that corresponds to the period of recruitment is active (Fig.3; (Prado et al., 2012; Farina et al., 2018).

From a multi-year series of fish biomass data recollection, we extrapolated abundance of sea urchin predatory fish for each sector from 2004 to 2007 with the exception of sector 5 (Marra et al., 2016). Data represents abundance of Sparidae (*Diplodus spp.* and *Sparus aurata*) and

Labridae (*Coris julis*), on the rocky bottoms of shallow waters (5 metres in depth) collected using Underwater Visual Census (Marra et al., 2016). In the *pre-crisis era*, the reserve effect of MPA on fish biomass was not evident and no differences between inside and outside zones was detected (Marra et al., 2016), except for the commercial sea bream which showed a higher abundance inside the MPA than outside.

Sea urchin population structure

Sea urchin population structure was estimated in each type of habitat in the study sectors from multi-year series of data from 2004 to 2007 (*pre-crisis era*). During this period, 79 samplings were carried out following a standard protocol at depths between 2 and 10 m (Guala et al., 2008). Specifically, for each site and type of habitat, sea urchin density was estimated as the number of individuals per square meter (ind/m²) as the mean of five plots of one square meter each, placed randomly for a total of three times. The sizes of the individuals (without spines) were measured with callipers to the closest mm.

We define as recruits the size-classes *a* and *b* composed with individuals with diameter \leq 2 cm that survived approximately until two years after their settlement (Ouréns et al., 2013). Middle-size sea urchins between 2 and 5 cm (class *c*, *d*, and *e*) are vulnerable to predatory fish (see above) and over the 3.5 cm, individuals become the main contributors to the reproductive capacity of population (Loi et al., 2017). Finally, large sizes of sea urchins, 5-6 cm (class *f*) and over 6 cm (class *g*), represent the commercial stock of the current years.

The whole sea urchin density and population structure in the *pre-crisis era* are estimated for each type of habitat and sector (Table S2). We carried out an analysis of variance for the whole sea urchin density in function of "sector" and "habitat" as fixed factors and to compare

density of recruits (classes *a* and *b*), middle-size sea urchins (*c*, *d*, *e*) and commercial sea urchins (classes *f* and *g*) among the different populations. Assumptions of normal distribution and homogeneity of response variables were tested using D'Agostino-Pearson and Cochran's tests. Total sea urchin density and middle-size sea urchin density following normal distribution with unbalanced replicates were analysed with Linear Model (Zuur et al., 2009). Whereas, given the non-normal distribution followed by density of recruits and commercial size sea urchins, the analysis of variance was performed with no-parametric Kruskal-wallis test (Kruskal & Wallis, 1952). Pairwise multicomparisons were conducted among factors. All the analysis were performed using R Studio (R Core Team, 2014).

Relationships among population structure and environmental conditions

Spearman's rank correlation coefficient as no-parametric measure of rank correlation was carried out between non-normal distributed recruit density and the average bottom current speed, while Pearson's rank correlation, as parametric linear regression test, was used to estimate statistical relationship between density of middle-size sea urchins and density of predatory fish.

Generalized Linear Model (GLM) with Poisson family distribution was performed to assess prediction of spatial configuration of habitats on the future stock (diameter < 5cm).

Given the lack of data of fish visual census in *Posidonia oceanica* and since recruits are considerably underestimated inside meadows (Oliva et al., 2016), the habitats Patchy Meadow and Continuous Meadow were excluded from these analysis. All the analysis were performed using R Studio (R Core Team, 2014).

Results

296

297 **Environmental constrains**

298 Study sector 1 is the largest sector with an area of 12.7 Km² (Fig.2). The average current
 299 speed was 0.05 ± 0.003 m/s (Fig.3) that is the slowest current measured in the period of
 300 recruitment (from January to June; see Table 1). Conversely, study sector 4 is the smaller sector
 301 with a total area of 3.8 Km² (Fig.3) and the highest predatory fish abundance of 84.6 ± 12.6 ind/
 302 125m² (Table 1). Sectors 2 and 3 are extended 5.1 Km² and 4.4 Km² respectively (Fig.2) with
 303 intermediate values of average bottom current speed and predatory fish abundance (see Table 1
 304 and Fig.3). Finally sector 5 covers a total area of 11.9 Km² with the same average bottom current
 305 speed of sector 3, while predatory fish abundance was not available.

306 In terms of habitat organization, calcareous rock substrate (CR) covers a surface of 4.5
 307 km² in the sector 1 with a mean patch density of 1 patch for Km² (CR-1; Table 2). While
 308 *Posidonia oceanica* patchy meadow is the most extend habitat of this sector with a surface of 7.2
 309 Km² (PM-1; Table 2). CR-2 is the most extent habitat and with the highest level of patch
 310 aggregation with respect to all the others habitats in all the sectors (98.9% IJI; see Table 2). PM-
 311 3 and CR-3 cover 2 and 1 Km² respectively (Table 2) with a Mean Patch Density of 0.32 Km² for
 312 both of habitats. BA-3 covers 0.1 km² of the sector 3 (Table 2). BA-4 and GR-4 cover 0.1 km²
 313 and 1.8 Km² respectively (Table 2). Finally *Posidonia oceanica* continuous meadow represents
 314 the total surface of sector 5 (CM-5) covering 11.1 Km² with the largest patch covering 42.6% of
 315 the total landscape (see Table 2). Continuous meadow is also present in sector 4 but it has never
 316 been sampled and a variable proportion of sand, unsuitable habitat for sea urchins, is present
 317 along all the sectors with the except ion of the sector 4 (Table 2).

318

319 Sea urchin population structure

320 The whole sea urchin density is significantly different among habitats and sectors (Table
321 3 and Fig. 4). Sector 1 outside MPA had the highest density of 9.9 ± 1.1 ind/m² with the lowest
322 proportion of commercial sea urchins ($15.1 \pm 2.3\%$; Table 1 and Table S2). Inside the MPA the
323 whole sea urchin density ranged from 2.5 ± 0.2 ind/m² in correspondence of the Sector 5 to $9.8 \pm$
324 1.2 ind/m² in the sector 4 (Table 1). In the sector 4 the lowest proportion of middle-size sea
325 urchins was found ($21.2 \pm 5.5\%$; Fig.4 and Table S2).

326 Among types of habitat, the highest significant density was found in CR-1 with a whole
327 density of 16.3 ± 1.4 ind/m² (Table S3). High values of whole sea urchin density were also found
328 in CR-2 and CR-3 (10.6 ± 1.3 and 10.1 ± 0.8 ind/m² respectively) and in GR-4 (11 ± 1.1 ind/m²;
329 Table S2). Otherwise, the lowest sea urchin density was estimated in correspondence of CM-5
330 with a mean density of 2.5 ± 0.2 ind/m² (Table 1).

331 Recruit and middle-size sea urchin densities were significantly different among
332 populations as the combination of habitats and sectors (Fig. 4; Table S4). Recruit density (size-
333 classes *a* and *b*) was higher in CR-1 (7.7 ± 1.3 ind/m²) than in CR-2, CR-3, GR-4 and BA-4 and it
334 was significantly higher than PM-2, PM-3 and BA-3 characterized by the low values of 0.3 ± 0.1 ,
335 0.3 ± 0.2 , 0.1 ± 0 ind/m² respectively (Table S4). Whilst recruit density was found zero in PM-1
336 and CM-5 (Fig.4).

337 Density of middle-size sea urchins was significantly higher in CR-1 (7.2 ± 0.8 ind/m²) and
338 higher in CR-2 and CR-3 (6.3 ± 0.9 and 5.4 ± 0.7 ind/m² respectively) than BA-3, BA-4 and GR-4
339 (3.1 ± 1.1 , 0.5 ± 0.2 and 3.3 ± 0.8 ind/m² respectively). In CM-5 density of middle-size sea urchins
340 was 1.9 ± 0.8 ind/m² (Table S2).

341

342 Relationships among population structure and environmental conditions

343 In rocky habitats CR, BA, GR recruit density does not follow a normal distribution due
 344 to the high number of sampled zeros and values are significantly correlated with the average
 345 bottom current speed (Spearman's rank correlation p-value = 0.02574; $\rho = -0.3184671$; Fig.5a).
 346 Whereas, density of middle-size sea urchins follows a normal distribution and it resulted
 347 significantly correlated with predatory fish density (Pearson's correlation p-value = 0.04268,
 348 *correlation coefficient* = -0.5118654; Fig. 5b). Finally General Linear Model highlights high
 349 significant influence of Patch Density (PD; p-value<0.01) and significant influence of the Mean
 350 Patch Size (MPS; p-value=0.01) on density distribution of on the future stock (diameter < 5cm;
 351 see Table 4 and Fig. S5).

352

353 Discussion

354

355 During the *pre-crisis era* (samplings realized during the period 2004 to 2007)
 356 conspicuous differences in sea urchin density were found across study sectors and type of
 357 habitats. Calcareous rock, basalt and granite support larger populations of sea urchins than
 358 *Posidonia oceanica*. However, differences in whole density were found also into the types of
 359 habitat: for example density in CR-1 was 1.5 and 1.6 times higher than in CR-2 and CR-3
 360 respectively. The highest density of recruits was found in CR-1 and was approximately 3 times
 361 higher than in CR of the other sectors; 1.5 times higher than in GR and even more than 5 times
 362 higher than in BA. Conversely, density of recruits found in *Posidonia oceanica* was most of the

times around zero. Density of middle-size sea urchins was still significantly higher in CR: for example, it was 4 times higher than in BA-4 and GR-4.

Considering results obtained from the analysis on the habitat configuration, high values of Patch Density and Mean Patch Size seem to further increase sea urchin population even if they have practically continuous distribution over the surface of the habitats. Surprisingly, although sector 1 (outside the MPA) had the lowest proportion of commercial stock and considering the large extensions of CR-1 characterize by a high Patch Density (one for square kilometre), the whole sea urchin density in CR-1 was approximately two times higher than in the sectors 2 and 3 (inside the MPA).

Population structures that we analysed are consistent with the high variability of the environmental constrains found along the Peninsula. From January, the spawning period, to June, when recruitment process generally ended, average bottom current speed was slowest in sector 1. It was almost half speed than in sectors 2 and 4 and a third less than speed in sectors 3 and 5. Recruit densities resulted negatively correlated with average bottom current speed. Specifically, to low values of average bottom current speed (< 0.1 m/s) correspond recruit densities above 3.5 ind/m^2 . It is interesting to notice that the average bottom current speed in CR-1 is under this critical threshold. In effect, this condition seems to support the existence of local standing circulation structures that determine a higher regime of natural recruitment (Farina et al., 2018).

Predation is the process regulating sea urchin population structure at local scale (Guidetti, 2004; Hereu, Zabala & Sala, 2008; Boada et al., 2015). During the *pre-crisis era*, density of middle-size sea urchins in rocky habitats resulted negatively correlated with density of predatory fish. In the sector 4 (the two Islands inside MPA), density of sea breams was found 1.2 higher

than in sector 1 (outside the MPA; Marra et al. 2016). The low abundance of sea breams in sector 1 is most likely due to the strong pressure by recreational spear fishermen (Marra et al., 2016), while the considerable distance from the coast could have made the islands of sector 4 less accessible to spear fishermen, protecting the local predatory fish community (Stallings, 2009). Consistently with this, in correspondence of the sector 4 was found the lowest density of middle-size sea urchins that suggests a high predation activity in this area. Conversely, the highest density was found in the sector 1.

Our results confirm how certain environmental constraints driving sea urchin population dynamic and are not quite as homogenous as it might seem in the Peninsula of Sinis. Thus, a management plan for sustainable harvesting should start from the assumption that sea urchin population in this region could be composed of multiple smaller populations with their own population dynamic.

However, the planktonic early life-stage could make sea urchin populations demographically open (López et al., 1998; Morgan et al., 2000; Prado et al., 2012; Trembl et al., 2012) and could have a degree of identifiable demographic influence from surrounding populations, which could be connected via process of larval dispersion (Knight & Landres, 2002). This concept emphasizes the importance of connectivity in generating a system of discrete local populations from inside to outside the MPA. In effect, the phenomenon where “source” populations supplement “sink” populations via dispersing individuals is a rescue effect that should be considered crucial for planning management actions and sustainable fisheries especially for the conservation requirements of an MPA (Paterno et al., 2017).

After all, a system of local sea urchin populations could be connected also by the spread of predators from the MPA that however, maintain a strong inter-habitat variability of predation pressure in all the surrounding area. In effect, a high proportions of middle-size sea urchins in the populations were generally found in patchy meadows (PM) in accordance with the efficient shelter effect that *Posidonia oceanica* provide versus predatory fish (Farina et al., 2009, 2014).

However, density of sea urchin population in the sector 5 in the Gulf of Oristano was the lowest then the whole study area. The high presence of whelks (bottom predators) in the continuous meadow is probably the potential cause of the scarcity of sea urchins in this habitat (authors pers. obs.). In effect, if for any reason the local pool of predators is dominated by bottom predators, the three-dimensional structure of a large seagrass meadow convert in a ‘death trap’ for sea urchins more than a protective habitat (Farina et al., 2014, 2016; Schmidt & Kuijper, 2015).

Fisheries management that aim to provide long-term sustainable exploitation of the resources should take in consideration not only the monitoring but also population dynamic, its ecological drivers and what they depend on (Hilborn & Walters, 1992). Accordingly, a clear understanding about the processes regulating realistic population dynamics at relevant spatial and temporal scale is a prerequisite of any management strategy and the results obtained in this study shed new light that might help management plans for sea urchin in this area.

Thus, there is increasing attention to identify and explicitly consider the key aspects regulating population dynamics in formal stock assessment and management (Skern-Mauritzen et al., 2016), including consideration of the spatial structure (Kerr et al., 2016; Cadrin et al., 2019) and food web interactions (Fulton et al., 2004).

Fisheries models can be strategic management tools for assessing and testing hypotheses about direct and indirect human impacts on the environment. Simulations obtained by fisheries models with ecosystem approach can allow to test alternative management strategies such as, for example, inclusion of total allowable catches, reduction of fishing effort and changes in gear (e.g. Spedicato et al., 2010). These measures should allow modulating fishing effort on specific components of the populations (for example, to reduce harvesting on the most productive age classes or areas). These tools, however, rely strongly on the basic understanding about population dynamics, its spatial structure, and the interaction with other elements of the ecosystem, including other species and environmental variables.

The Sinis Area offers a peculiar case study, where ecological and economic information and data is building up, and the involved stakeholders, including small-scale fisheries organisations, MPA and local administration are demanding a science-based management system. There is currently momentum toward implementation of a long-term vision entailing a data collection strategy aiming to provide management strategy plans toward a sustainable management of the sea urchin fishery, sharing the objectives of conservation of ecological features and of traditional and socio-economics values. Moreover, to be able to achieve values of sustainable fishing in the two main resources, as sea urchins and sea breams, that are compatible with preserving well-structured macrophyte communities, permit to provide in the sustainable way the ecosystem services needed for a high environmental quality.

Conclusion

Although the rates of recruitment and mortality from predation have not yet been studied in depth in this area, this study suggests how these mechanisms are of crucial importance to ensure long-term sustainable exploitation of the resource. Strong natural relationships have been demonstrated to exist between sea urchin population structures and the variability of certain environmental constraints and interactions with other species in this region. In this system, the continuous and inexorable decrease of the natural resource from 2007 is chased by frantic adjustments of the management measures. Hence, testing alternative management strategies through the development of a local fisheries model with an ecosystem approach would foster a systemic territorial planning addressed both to support environmental protection actions and to promote the sustainable use of the fishing resources.

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Figure 1

Figure 1. Diagram describing sea urchin population dynamic.

Letters represent different life stage of populations: a) commercial stock and main reproducers of sea urchin populations, b) larval supply for populations, c) settlement in suitable habitats, d) interactions with habitat structure for food and shelter, e) predator-prey interactions with local predator community, f) fishing pressure both on fish and sea urchins.

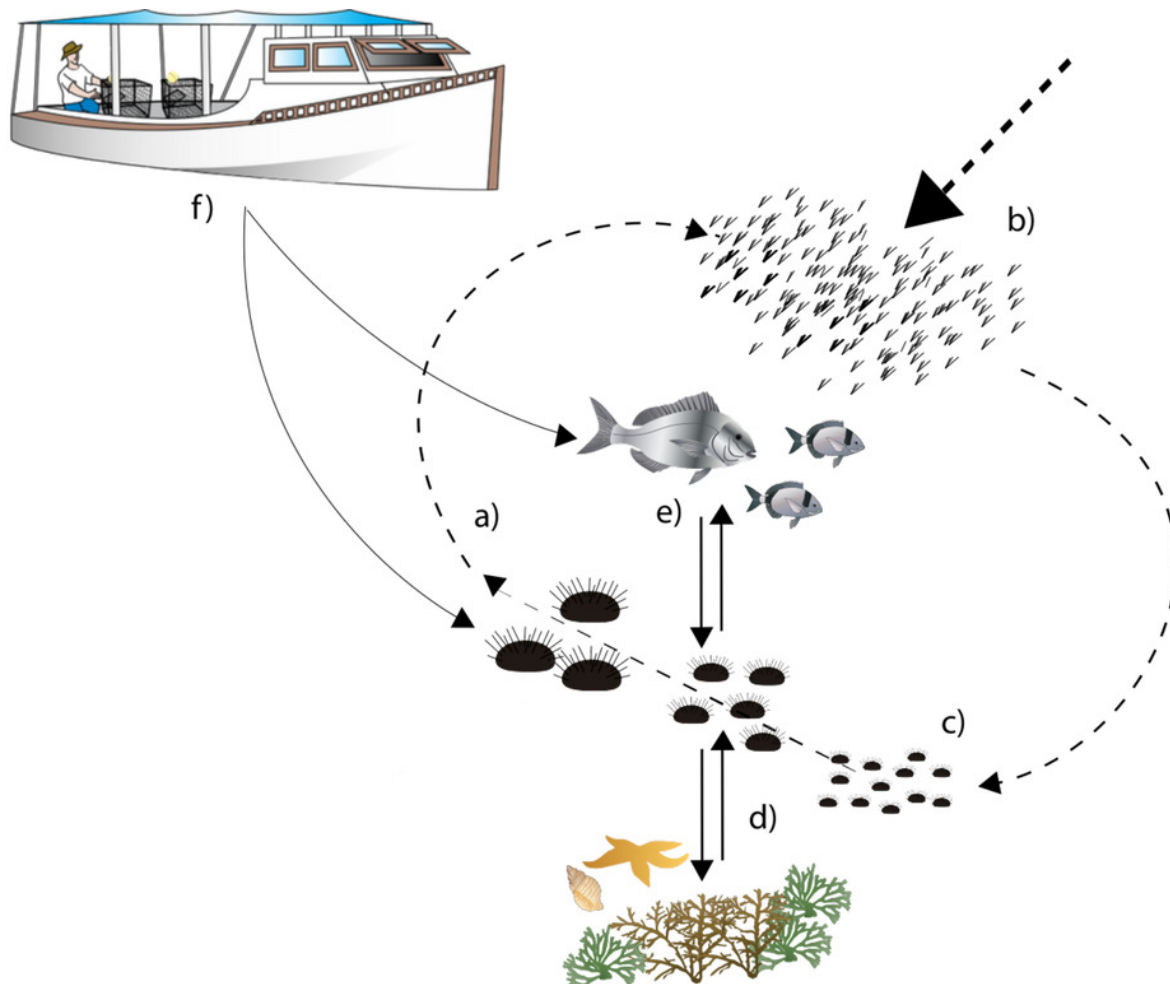


Figure 2

Figure 2. Detailed digital mapping of geomorphology in the study area.

Colours indicated different sectors and type of habitats: calcareous rock (CR in grey), granite (GR in light blue), basalt (BA in red), *Posidonia oceanica* patchy meadow (PM in dark green), *Posidonia oceanica* continuous meadow (CM in light green) and sand (in yellow).

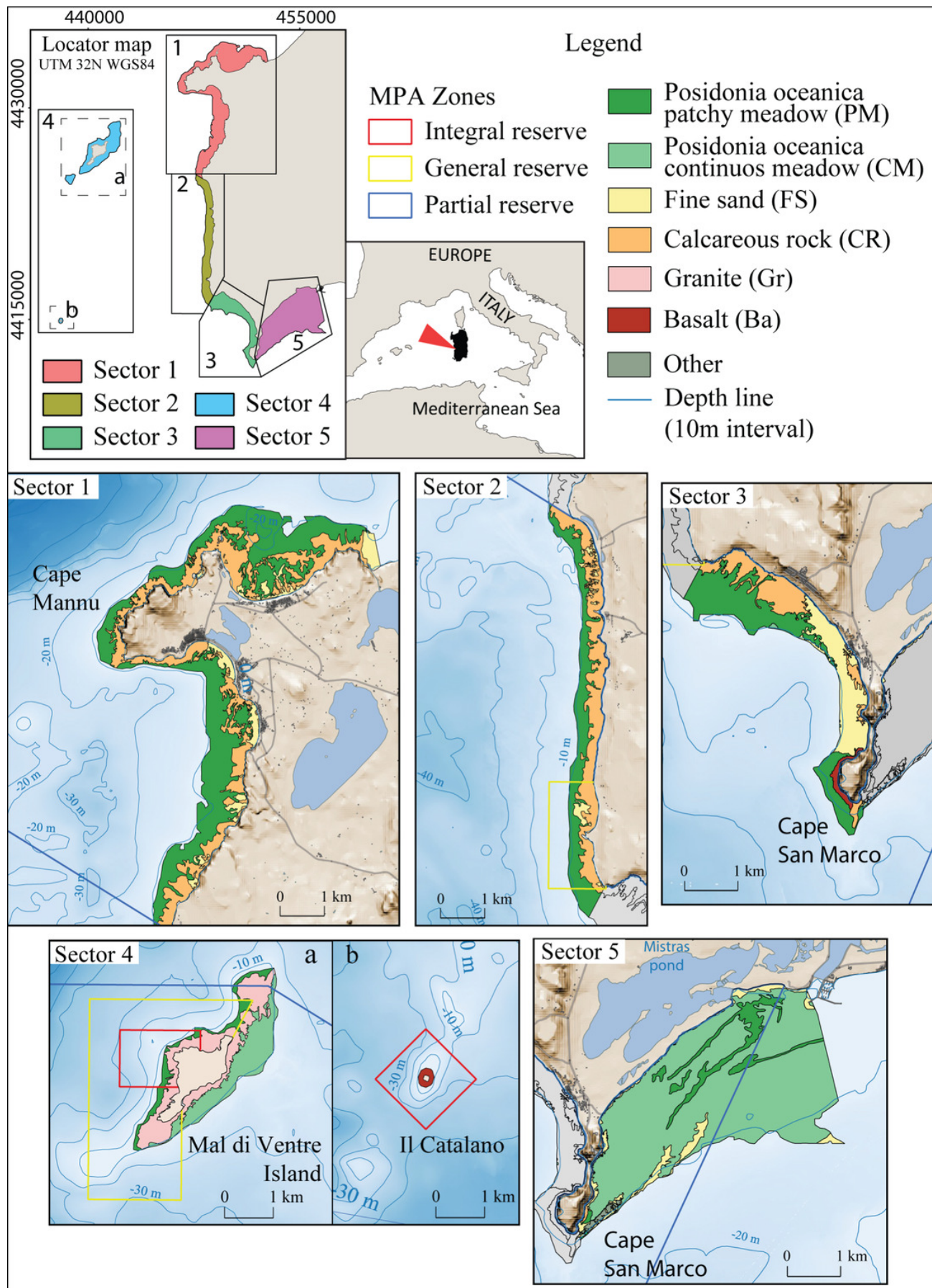


Figure 3

Figure 3. Detailed digital mapping of hydrodynamism in the study area.

Map representing average bottom current speed obtained by the oceanographic model in the area of interest during six months from spawning time to the period of settlement (January-June).

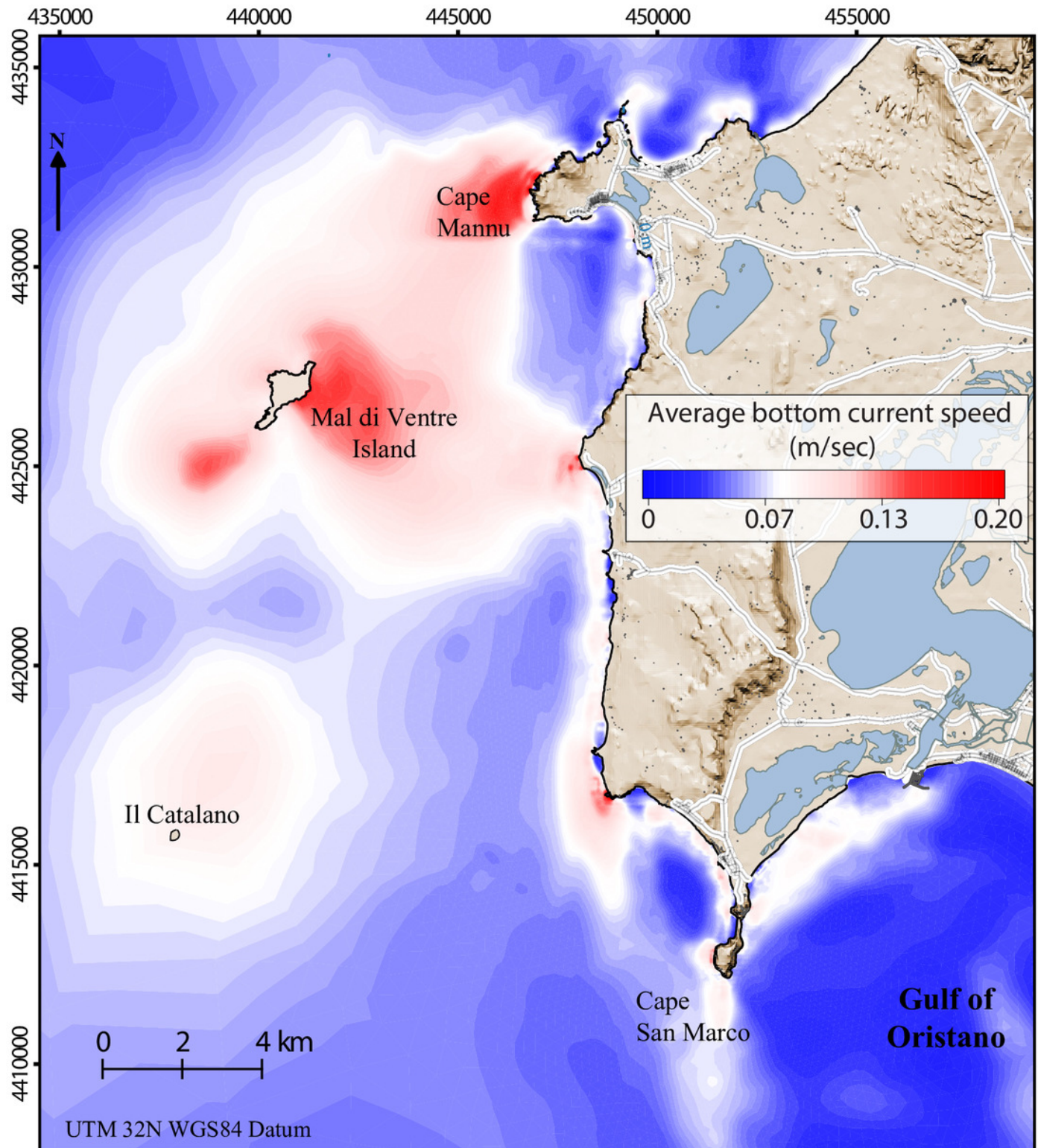


Figure 4

Figure 4. Graph representing different population structures.

Populations of each type of habitat in each sectors: calcareous rock of sector 1(CR-1), patchy meadow of sector 1 (PM-1), calcareous rock of sector 2 (CR-2), patchy meadow of sector 2 (PM-2), calcareous rock of sector 3 (CR-3), patchy meadow of sector 3 (PM-3), basalt of sector 3 (BA-3), granite of sector 4 (GR-4), basalt of sector 4 and continuous meadow of sector 5 (CM-5).

Population structures

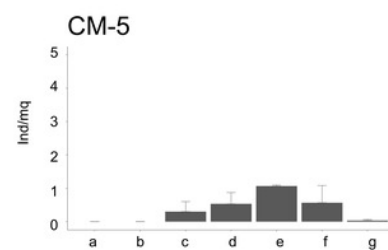
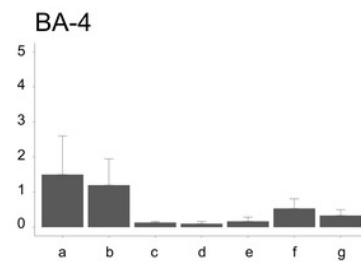
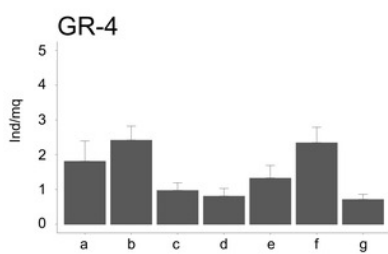
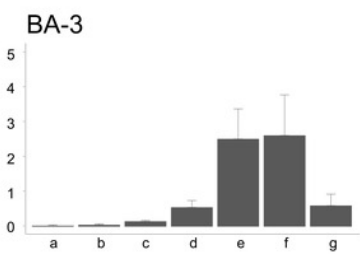
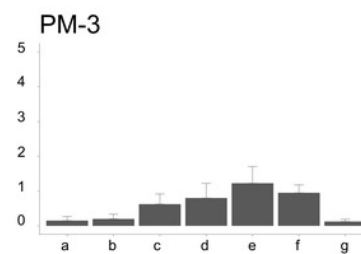
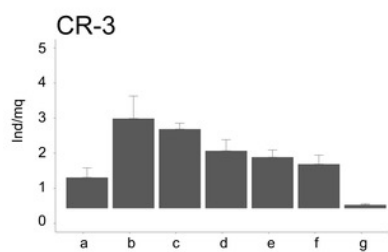
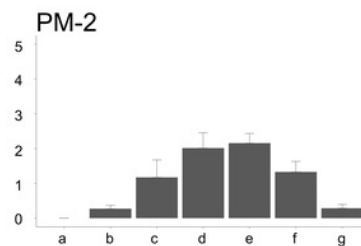
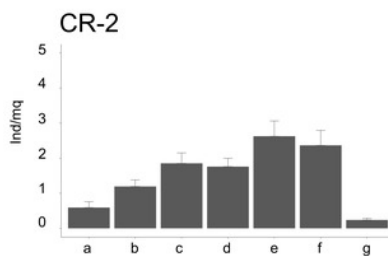
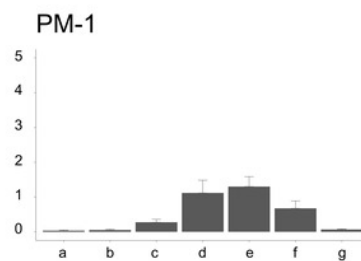
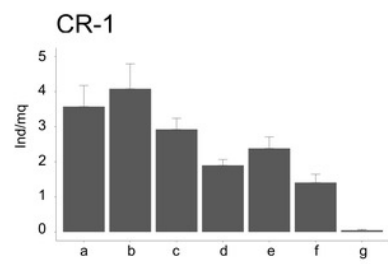


Figure 5

Figure 5. Graphs representing relationships between sea urchin densities and environmental constraints.

In rocky habitat a) density of recruits is correlated with the average bottom current speed (Spearman's rank correlation p-value = 0.02574; $\rho = -0.3184671$) and b) densities of middle-size classes with predatory fish densities (Pearson's correlation p-value = 0.04268, *correlation coefficient* = -0.5118654). Number of points used in the graph a corresponds to the sea urchin sampling stations while in the graph b to the stations of fish visual census.

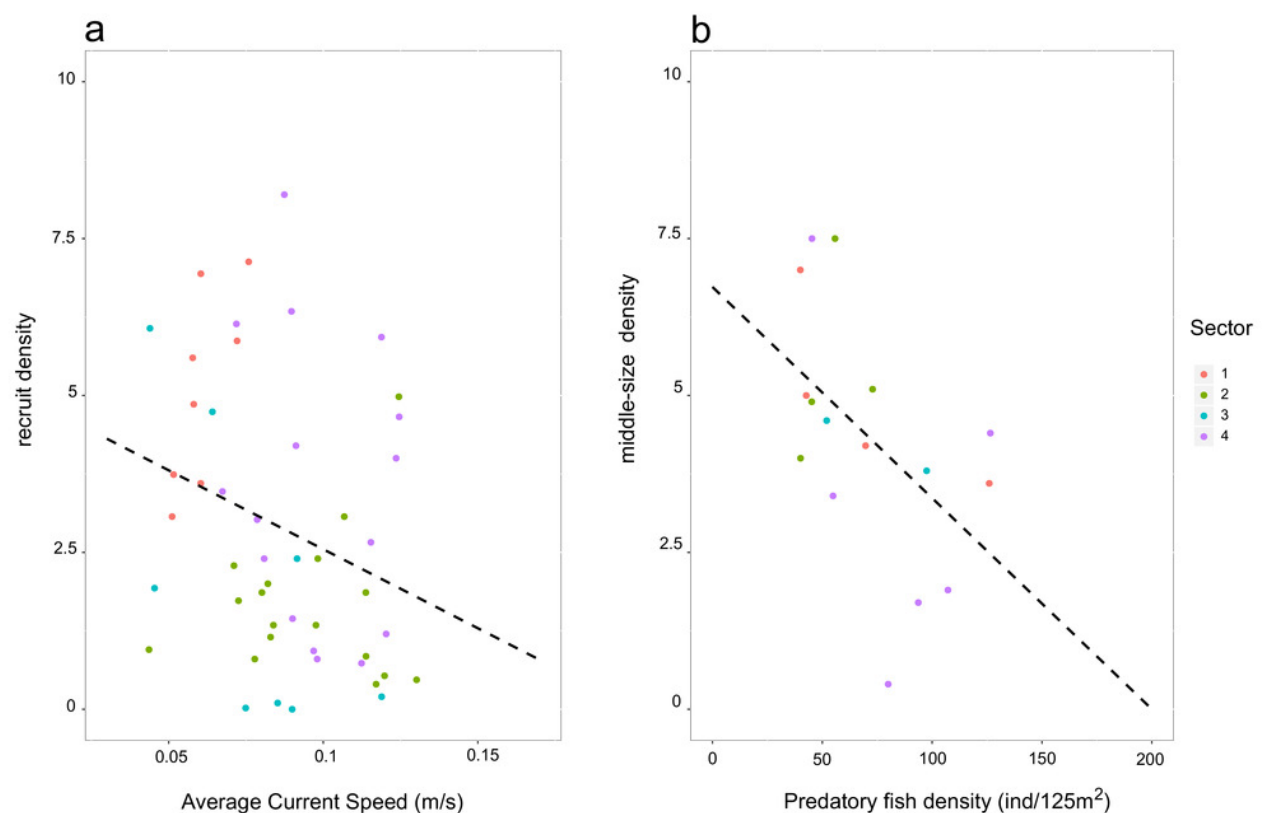


Table 1(on next page)

Table 1. Table showing differences among sectors of average bottom current speed and predatory fish density (in sector 5 only one observation was carried out).

1 **Table 1**

| Sector | Total area (Km²) | Average Current Speed (m/s) | Average predatory fish (ind/125m²) | Total sea urchin density | Stock proportion (%) |
|---------------|------------------------------------|------------------------------------|--|---------------------------------|-----------------------------|
| 1 | 12.7 | 0.05 ±0.003 | 69.6 ± 20 | 9.9 ±1.6 | 15.1 ±2.3 |
| 2 | 5.1 | 0.09 ±0.004 | 53.5 ± 7.2 | 9.5 ±1.0 | 23.3 ±2.2 |
| 3 | 4.3 | 0.07 ±0.007 | 74.8 ± 22.8 | 7.1 ±1.1 | 28.7 ±4.7 |
| 4 | 3.8 | 0.10 ±0.004 | 84.6 ± 12.6 | 9.8 ±1.2 | 27.8 ±3.6 |
| 5 | 11.9 | 0.07 ±0.003 | - | 2.5 ±0.2 | 20.0 ±1.8 |

2

Table 2(on next page)

Table 2. Spatial configuration of sampled habitats for each study sector. Dash means no samplings were realized.

1 **Table 2**

| Sector | Habitat | code | N° of samplings | Area (Km²) | PD (n/Km²) | P/A ratio (1/m) | MPS (Km²) | LPI (%) | IJI (%) |
|---------------|-----------------|-------------|------------------------|------------------------------|------------------------------|------------------------|-----------------------------|----------------|----------------|
| 1 | Calcareous Rock | CR-1 | 12 | 4.5 | 1.01 | 21.1 | 0.07 | 3 | 68.6 |
| | Patchy Meadow | PM-1 | 12 | 7.2 | 0.16 | 11.0 | 0.72 | 5.3 | 55.3 |
| | Sand | | - | 1.0 | - | - | - | - | - |
| 2 | Calcareous Rock | CR-2 | 15 | 2.5 | 0.62 | 15.2 | 0.31 | 17 | 98.9 |
| | Patchy Meadow | PM-2 | 7 | 2.3 | 0.08 | 13.2 | 2.28 | 17.8 | 46.3 |
| | Sand | | - | 0.3 | - | - | - | - | - |
| 3 | Calcareous Rock | CR-3 | 5 | 1.0 | 0.32 | 16.2 | 0.17 | 4.5 | 44.6 |
| | Patchy Meadow | PM-3 | 4 | 2.0 | 0.32 | 10.4 | 0.33 | 8.2 | 61.7 |
| | Basalt | BA-3 | 4 | 0.1 | 3.5 | 0.3 | 0.11 | 0.6 | 33.9 |
| | Sand | | - | 1.2 | - | - | - | - | - |
| 4 | Granite | GR-4 | 14 | 1.8 | 0.02 | 16.4 | 1.85 | 2.9 | 62.7 |
| | Basalt | BA-4 | 3 | 0.1 | 0.02 | 21.4 | 0.08 | 0.1 | 0 |
| | Patchy Meadow | | - | 0.5 | - | - | - | - | - |
| | Cont. Meadow | | - | 1.4 | - | - | - | - | - |
| 5 | Cont. Meadow | CM-5 | 3 | 11.1 | 2.6 | 2.1 | 3.7 | 42.6 | 5.5 |
| | Other | | - | 0.1 | - | - | - | - | - |
| | Sand | | - | 0.7 | - | - | - | - | - |

2

Table 3 (on next page)

Table 3. Analysis of variance table of lm model for sea urchin total density in function of Sector and Habitat as fixed factors.

Results of one-way Anova of rank for recruits (Kruskal-Wallis test), middle-size sea urchins (lm) and stock (Kruskal-Wallis test) in function of populations. Degree of freedom (df), F-value (F) and significance level (p-value) are provided for fixed effects. Significant effects are given in bold. Multiple comparison post hoc test was carried out (see Appendix A4 and A5).

1 **Table 3**

| Analysis of variance | | | | |
|--------------------------|---------------|-----------|---------------------------------|-----------------------------|
| <i>Response variable</i> | <i>Source</i> | <i>df</i> | <i>F-value</i> | <i>p-value</i> |
| Total density | Sector | 4 | 2.8474 | 0.02992 |
| | Habitat | 3 | 17.8476 | 9.23e⁻⁰⁹ |
| | residuals | 72 | | |
| <i>Response variable</i> | <i>Source</i> | <i>df</i> | <i>Chi-squared (or F-value)</i> | <i>p-value</i> |
| Recruit density | Population | 9 | 63.711 | 2.569e⁻¹⁰ |
| Middle-size density | | | 5.6147 | 8.522e⁻⁰⁶ |
| Stock density | | | 27.359 | 0.00122 |

2

Table 4(on next page)

Table 4. Generalized linear model (GLM).

The upper section shows the significant effects of the assessed explanatory variables (determinants) on density of commercial under-sized classes (TD<5cm). Coefficient estimates (Estimate), standard errors (SE), z-values, and significance level (p-value) for variables retained in the best model are provided for fixed effects (explanatory variables). Significant effects are given in bold.

1 **Table 4**

| General Linear Model analysis | | | | | |
|--------------------------------------|---------------|-----------------|-----------|----------------|----------------------------|
| Response variable | Effect | Estimate | SE | z-value | P-value |
| Sea urchin density | intercept | 1.301309 | 0.288039 | 4.518 | 6.25e ⁻⁰⁶ |
| | MPS | 0.310135 | 0.120982 | 2.563 | 0.0104 |
| | PD | 1.073995 | 0.201901 | 5.319 | 1.04e⁻⁰⁷ |
| | IJI | 0.001116 | 0.004847 | 0.230 | 0.8179 |
| | LPI | -0.011801 | 0.019027 | -0.620 | 0.5351 |
| | P/A ratio | 0.007291 | 0.015867 | 0.460 | 0.6459 |

2