The challenge of managing the commercial harvesting of the sea urchin *Paracentrotus lividus*: advanced approaches are required

Simone Farina Corresp., 1 , **Maura Baroli** [1] , **Roberto Brundu** [2] , **Alessandro Conforti** [3] , **Andrea Cucco** [3] , **Giovanni De Falco** [3] , **Ivan Guala** [1] , **Stefano Guerzoni** [1] , **Giorgio Massaro** [3] , **Giovanni Quattrocchi** [3] , **Giovanni Romagnoni** [4, 5] , **Walter Brambilla** [3]

[1] IMC-International Marine Centre, Oristano, Italy

[2] Marine Protected Area "Penisola del Sinis-Isola di Mal di Ventre", Cabras, OR, Italy

[3] IAS -Institute of Anthropic Impacts and Sustainability in Marine Environment, CNR - National Research Council, Oristano, Italy

[4] COISPA Tecnologia & Ricerca, Bari, Italy

[5] Dept. of Biosciences, University of Oslo, Centre for Ecological and Evolutionary Synthesis (CEES), Oslo, Norway

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

In the Mediterranean Sea, both sea urchin predators (*Diplodus spp* and *Spaurus aurata*) and the sea urchin *Paracentrotus lividus* are target species for artisanal fisheries. Herbivorous sea urchins act as a keystone species and, as a consequence of the interactions between fish, sea urchins and macrophyte, fishing creates trophic disorders with a loss of biodiversity and nursery areas for commercially important fish. On this island of Sardinia (Western Mediterranean Sea), sea urchin harvesting is leading to ecosystem degradation. Regulations for sea urchin harvesting have been in place since the mid 90s. However, given the important ecological role of *P. lividus*, the single-species fishery management may fail to take into account important ecosystem interactions. Hence, the understanding of population dynamics, their dependence on environmental constraints and multispecies interactions help achieve long-term sustainable use of this resource. This work aims to highlight how differences among sea urchin population structure in relation to lenvironmental constraints and species interactions along different sectors of coast are crucial to differentiate the stocks available for fishing. The study area (Sinis Peninsula, West Sardinia, Italy) that includes a local Marine Reserve was divided into five sectors characterized by types of habitat (calcareous rock, granite, basalt, patchy and continuous meadows of *Posidonia oceanica)*, average bottom current speed and predatory fish abundance, as the most important environmental constraints influencing sea urchin population dynamics. Sectors have different fishing pressure depending on they are outside or inside the Marine Reserve. The abundance of sea urchin under commercial sized-class (< 5 cm diameter size) assessed during the period from 2004 to 2007, before that the whole population dramatically decreased, were compared for sectors and types of habitat. Correlations between recruits (0-1 cm diameter size) and bottom current speeds and between middle-sized sea urchins (2-5 cm diameter size) and predatory fish abundance were assessed. Parameters representing spatial configuration of the habitats (patch density, perimeter-to-area ratio, mean patch size, largest patch index, interspersion/juxtaposition index) were calculated and their influence on sea urchin density assessed. Density of under commercial sized-class was significantly higher in Calcareous rock and was significantly influenced by density and average size of rocky habitat patches. Recruits were significantly abundant in rocky habitats and significant negative correlated with average bottom current speed. Density of middle-sized sea urchins was lower in Basalt and Granite and negative correlated with predatory fish abundance. Our results highlight the importance of environmental constraints in influencing local sea urchin density and point out the need to account for these factors as important parameters in local fisheries management.

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Farina S.[1*], Baroli M.[1], Brundu R.[3], Conforti A.[2], Cucco A.[2], De Falco G.[2], Guala I.[1], Guerzoni S.[1], Massaro G.[2], Quattrocchi G.[2], Romagnoni G.[4,5], Brambilla W.[2]

[1]IMC- International Marine Centre, Loc. Sa Mardini, Torre Grande, 09170 Oristano, Italy

[2] CNR - National Research Council, IAS -Institute of Anthropic Impacts and Sustainability in Marine Environment, Loc. Sa Mardini, Torre Grande, 09170 Oristano, Italy.

[3]Marine Protected Area "Penisola del Sinis-Isola di Mal di Ventre", Cabras, Italy

[4]COISPA Tecnologia & Ricerca, Via dei Trulli 18/20, Bari, Italy

[5]Centre for Ecological and Evolutionary Synthesis (CEES), Dept. of Biosciences, University of Oslo, Norway

*corresponding author e-mail: simone.farina@snz.it; present address: IMC - Ischia Marine Centre, Stazione Zoologica Anton Dohrn, Punta San Pietro, 80077, Ischia, Naples, Italy

Abstract

In the Mediterranean Sea, both sea urchin predators (*Diplodus spp* and *Spaurus aurata*) and the sea urchin *Paracentrotus lividus* are highly valuable target species for artisanal fisheries. Herbivorous sea urchins act as a keystone species, regulating macrophyte forest density, which offers refuge for multiple species.

As a consequence of the interactions between fish, sea urchins and macrophyte, fishing creates trophic disorders with a loss of biodiversity and nursery areas for commercially important fish.

On this island of Sardinia (Western Mediterranean Sea), sea urchin harvesting is leading to ecosystem degradation. Regulations for sea urchin harvesting have been in place since the mid 90s. However, given the important ecological role of *P. lividus*, the single-species fishery management may fail to take into account important ecosystem interactions. Hence, a deeper understanding of population dynamics, their dependence on environmental constraints and multispecies interactions may help achieve long-term sustainable use of this resource.

This work aims to highlight how differences among sea urchin population structure in relation to local environmental constraints and species interactions along different sectors of coast are crucial in order to differentiate the stocks available for fishing.

The study area (Sinis Peninsula, West Sardinia, Italy) that includes a local Marine Reserve was divided into five sectors each characterized by specific types of habitat (calcareous rock, granite, basalt, patchy and continuous meadows of *Posidonia oceanica)*, average bottom current speed and predatory fish abundance, as the most important environmental constraints influencing sea urchin population dynamics. Also, the sectors have different levels of fishing pressure depending on the management measures in place outside and inside the Marine Reserve. An abundance of different size classes under commercial size (< 5 cm diameter size) assessed during the period from 2004 to 2007, before that the whole population dramatically decreased, were compared for sectors and types of habitat. Specific correlations between recruits (0-1 cm diameter size) and bottom current speeds and between middle-sized sea urchins (2-5 cm diameter size) and predatory fish abundance were assessed. Parameters representing spatial configuration of the habitats (patch density, perimeter-to-area ratio, mean patch size, largest patch index, interspersion/juxtaposition index) were calculated and their influence on sea urchin density assessed.

The density of sea urchins under commercial size was significantly higher in calcareous rock and was positively and significantly influenced by the density and average size of the rocky habitat patches. Recruits were significantly abundant in rocky habitats, especially in sector 1 and sector 4, while they were almost absent in Posidonia meadows. The density of middle-sized sea urchins was more abundant in calcareous rock than in basalt, granite or Posidonia. High densities of recruits resulted significantly correlated to low values of average bottom current speed, while a negative trend between the abundance of middle-sized sea urchins and predatory fish was found.

Our results highlight the importance of environmental constraints in influencing local sea urchin population structure through the ecological drivers of recruitment and predation. Consequently, we point out the need to account for these factors as important parameters in local fisheries management.

Introduction

The continuous decline of fishery catches during the last decades has 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’’(Jackson et al., 2001). The most common effect of overfishing on such target species is a critical reduction of fish predators that leads to an uncontrolled proliferation of sea urchins with the consequent creation of barrens (Steneck et al., 2002; Steneck, Vavrinec & Leland, 2004). However, the intensive harvesting of sea urchins is progressively increasing worldwide (Andrew et al., 2002; James et al., 2016) and the removal of hundreds of thousands of sea urchins has led sea urchin populations to collapse (Tegner & Dayton, 1977; Pennington, 1985; Levitan, Sewell & Fu-Shiang Chia, 1992; Levitan & Sewell, 1998). Moreover, in many areas of the world, sea urchin harvesting has been observed to have community-level effects, resulting in a rapid development of large, brown algae and changes in the relative composition of fish and benthic communities (e.g. Steneck et al., 2002). Clearly, the strong influence of urchins on subtidal communities needs to be considered for the development of sustainable urchin fisheries, and their potential impact on ecosystems (Tegner & Dayton, 2000).

Sea urchin fisheries generally follow the short-term “boom-and-bust” pattern of many invertebrate fisheries. It starts as a small-scale activity that undergoes a phase of rapid expansion followed by a phase of full exploitation before the exhaustion of the resource (Andrew et al., 2002). In light of these considerations, an integrated management strategy for social and -ecological systems has been developed in many regions where this situation has occurred. In Chile, for example, following the decline of populations and through a participatory forum with stakeholders, an effective management plan based on rotational fishing practices and the creation of new spawning reserves has been developed (Moreno et al., 2006). In Canada, the harvesting techniques and management measures (e.g., conditions of licence, open times, closed areas, etc.) are area specific and all the local fisheries are based on ecosystem approaches, such as managing the impact of fishing on benthic habitats, communities and species (Perry, Zhang & Harbo, 2002).

In the Mediterranean Sea, sea urchin fishery focuses on the edible species *Paracentrotus lividus* that is 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 when the areas are heavily exploited by fishing (Wallner-Hahn et al., 2015). The impact of overfishing through the impairment of predatory control on *P. lividus* determines a significant loss of macroalgal communities and biodiversity as a consequence (Micheli et al., 2005; Giakoumi et al., 2012; Sala et al., 2012). For this reason, it is widely accepted that sea urchin harvesting is a potentially effective method for mitigating the effects of severe overfishing (e.g. Piazzi & Ceccherelli, 2019).

However, there are regions of the Mediterranean Sea, where the commercial harvesting of *P. lividus* is practiced intensively by recreational and artisanal fisheries because it is considered a delicacy locally. In Sardinia (Italy, Western Mediterranean Sea) for example, populations have suffered unsustainable pressure since the early 2000s (Guidetti, Terlizzi & Boero, 2004; Pais et al., 2007, 2012; Ceccherelli et al., 2011). Sea urchin harvesting is managed by a regional decree (Department of Environmental Protection Decree No. 276 of March 3, 1994 and subsequent amendments). Before 2009, from November to April, 115 to 161 professional fishermen were authorized to collect up to 3000 sea urchins per day by scuba diving along the entire coast of Sardinia. Specific regulations are enforced in the marine protected areas and are generally more restrictive than outside these areas (e.g. several no-take areas and only spearfishing). The Peninsula of Sinis, in the central western coast of Sardinia, including the local Marine Protected Area "Penisola del Sinis, Isola di Mal di Ventre" (Marine Reserve from now on), is one of the main hotspots for harvesting activity. Inside the Marine Reserve, the rules governing exploitation are more restrictive than outside of it (e.g. several no-take areas and only free diving). Here, sea urchin harvesting was only allowed for resident, professional fishermen, from November to April, for a maximum catch quota of 1000 sea urchins per day per fisherman. The number of licensed fishermen varied from 125 in 2001 up to over 270 in the three-year period of 2004-2007 (counting free-diving fishermen and fishermen in boats).

After 2009, the number of regional licences increased to 189, but stricter regulations have been introduced for the harvesting, transportation, storage and processing of the sea urchins (RAS, Autonomous Region of Sardinia, decree no. 2524/DecA/102 of October 7, 2009). Daily catches per fisherman were reduced to 2000, the minimum catch size remained unchanged over the years (>5 cm diameter size). Inside the Marine Reserve, the number of licenced fishermen decreased progressively down to 54 in 2019, while the maximum daily catches per fisherman was reduced to 500 sea urchins and recreational fishing was banned.

Despite the tighter regulations in place since 2009, individuals larger than 5 cm diameter (minimum commercial size or stock) are still infrequent in populations both inside and outside the Marine Reserve. In fact, scientific monitoring in this area has shown a dramatic depletion both in commercial sizes (> 5 cm diameter size) and in the whole population which, in the last thirteen years have been reduced by 65% and 75% respectively (Coppa et al., 2018).

Accordingly, it appears evident that management strategies should undergo a major reshaping to prevent the collapse of fisheries in this area (e.g. 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 general knowledge of the biology of the urchin species present in the area as well as a sound understanding of the dynamics of sea urchin populations (James et al., 2016).

In New Zealand, for example, between 2002 and 2003, the sea urchin species *Evechinus chloroticus* was introduced into the quota management system of fishing thanks to the support of the highly detailed biological information provided by local research (Miller & Abraham, 2011). The quota management system is used to set the total allowed catch in twelve different fishing sectors according to the assessment of a set of biological criteria (Miller & Abraham, 2011). Sea urchin fishing in New Zealand relies on obtaining proper roe recovery rather than on an absolute size or weight of sea urchins (e.g. James, 2006). Accordingly, fishing areas are classified in relation to growth conditions of the gonads, spawning rate, larval diffusion and the connectivity of local populations (Kritzer & Sale, 2004; James, Heath & Unwin, 2007; James & Heath, 2008; James & Herbert, 2009; James et al., 2009; Wing, 2009).

In the Mediterranean Sea, sea urchin abundance varies widely from region to region and is primarily driven by recruitment (Turon et al., 1995; López et al., 1998). Within this process, larval supply is strongly influenced by coastal hydrodynamics (Fenaux, Cellario & Rassoulzadegan, 1988; Harmelin-Vivien et al., 2000; Prado et al., 2012; Farina et al., 2018), while the nature of the substrate, the type of habitat and the abundance of predatory fish strongly influence settlement success and post-settlement survival (Boudouresque & Verlaque, 2001; Tomas, Turon & Romero, 2004; Hereu et al., 2005; Oliva et al., 2016). Settlement on rocky habitats is generally higher than in seagrass *Posidonia oceanica,* where the abundance of cryptic predators determine a high mortality rate (Tomas, Turon & Romero, 2004).

Once in the benthos, predation becomes the most important ecological driver of sea urchin distribution (Hereu et al., 2005; Tomas, Romero & Turon, 2005). In the Mediterranean Sea, the main sea urchin fish predators are the labrid *Coris julis* and the commercial sea breams *Diplodus spp.* and *Sparus aurata*, that hunt recruits and middle-sized sea urchins respectively (Sala, 1997; Guidetti, Boero & Bussotti, 2005). The predation risk of sea urchins strongly depends on the availability of shelters provided by the structure of the habitats and their spatial configuration (Farina et al., 2009, 2017; Pagès et al., 2012) until the urchins reach the safety size of ~ 5 cm (Guidetti et al., 2004).

Recruitment and predation are therefore the main ecological processes driving sea urchin population dynamics and shaping population structure locally (Fig.1; Sala & Zabala, 1996; Goñi et al., 2000). Regular stock assessment of *P. lividus* has been proposed as a means of providing a scientific basis for management in Sardinia (Cau et al., 2007) based on ad-hoc data and on regular scientific monitoring of sea urchin density. However, given the key role played by *P. lividus* in coastal ecosystems, in order to provide long-term sustainable use, advanced approaches could be required. These would need to take into account the importance of environmental constraints in influencing local sea urchin population structure through the ecological drivers of recruitment and predation while promoting different amounts of potential stocks as a consequence (Miller & Abraham, 2011).

The first regional surveys of sea urchins in Sardinia were carried out in 2001, 2003 and again in 2007. As one of the largest high-pressure zones, the Peninsula of Sinis has been closely monitored since 2004. In the Marine Reserve, sea urchin stock suffered its first significant drop between 2004 and 2005, while the whole population has been dramatically decreasing since 2010 (Pieraccini, Coppa & De Lucia, 2016). This can be considered the onset of the deep crisis of the species in the area. We used data collected between 2004 (first sampling) and 2007 (before the population collapse) to provide relevant information on population structures (under the commercial size of 5 cm diameter) from when they were still undamaged (Pieraccini, Coppa & De Lucia, 2016).

The assumed pristine state of population structure in density and age of this period represents a precious reference for understanding natural relationships between local population dynamics and the environmental constraints in the study area. This highlights the importance of providing detailed biological information in order to develop scientifically sound, ecosystem-based management for fishing quota allocation. Therefore, the aim of this study is to provide evidence for the importance of a broader approach to the management of fisheries, targeting both sea urchins and their predators in the Peninsula of Sinis.

For this purpose, five fishing sectors were identified along the study area, each with specific environmental constraints that can differently influence the main ecological drivers of sea urchin population dynamics, such as recruitment and predation. Specifically, we looked at types of habitat (i.e. Calcareous rock substrate, Granite substrate, Basalt substrate, patchy and continuous meadows of *Posidonia oceanica*) as well as a pool of variables describing habitat spatial configuration (patch density, perimeter-to-area ratio, mean patch size, largest patch index and the interspersion/juxtaposition index) which strongly influence shelter and food availability for sea urchins (e.g. Hereu et al., 2005; Farina et al., 2017). A circulation model of bottom current speed is used to approximate coastal hydrodynamics that strongly influence larval diffusion and sea urchin settlement (Farina et al., 2018). Finally, predatory fish abundance provides approximative information about potential predation activity along the fishing sectors (Guidetti, 2007).

Specifically, differences in the density of sea urchins under commercial size (< 5 cm diameter size), recruit density (0-1 cm diameter size) and middle-sized sea urchin density (2-5 cm diameter size) are estimated in according to fishing sector and type of habitat. Due to the absence of a direct estimation of predation and recruitment rates in these years, the importance of local hydrodynamics on population recovery and of predator activity on population structure are evaluated as a relationship a) of the average bottom current speed to the density of recruits, and b) between the densities of predatory fish and middle-sized sea urchins, as the size-class range potentially vulnerable to fish predators. Finally, the influence of spatial configurations of rocky habitats on the density of sea urchins under commercial size (< 5 cm diameter size) is estimated.

Based on these criteria, this study emphasises the importance of advanced approaches to developing a scientifically sound, ecosystem-based fisheries management that embeds spatial and temporal environmental processes in the assessment of stock sustainability.

Material & Methods

Study Area

The study area encompasses 40 km of the West Coast of Sardinia (Italy) between the Gulf of Oristano and Su Pallosu Bay (Peninsula of Sinis) (Fig.2). This area include the local Marine Protected Area of “Penisola del Sinis, Isola di Mal di Ventre”, which was established in 1997 and covers a surface of 250 Km^2 (Fig. 2). The full protection area is 5 Km^2 (Guala et al., 2008), while the remaining zones are intensively frequented by fishermen (Pieraccini, Coppa & De Lucia, 2016). The study area is limited to the bathymetry of 5 ± 1m (mean depth at which the harvesters usually work) and it is subdivided into five fishing sectors (Table 1). Study sector 1 is identified in the portion of coast located outside the Marine Reserve from Su Pallosu Bay to the northern boundary of the Marine Reserve, including Cape Mannu (Fig.2). Sectors 2 and 3 encompass the stretch of coast inside the Marine Reserve that is exposed to the open sea, while sector 4 represents the Marine Reserve islands of Mal di Ventre and Catalano. Finally, sector 5, at the southern border of the Marine Reserve, includes part of the Gulf of Oristano.

The seabed of the study area is composed of bedrock of 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); and the Miocene and Quaternary Calcareous rocks located all along the study area coastline (Lecca & Carboni, 2007). These different types of substrate morphology influence the distribution of *Posidonia oceanica*; the meadow shows a patchy pattern where the matte is on the bedrock and a 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 *P. oceanica* shows a patchy meadow pattern in the rest of the study area (De Falco et al., 2008).

Along the coastal area, the average bottom current speed (Fig.3) strongly influences the abundance of sea urchin recruits (Farina et al., 2018). The water circulation in this area is mainly promoted by the action of the winds which are predominatly from the North-West, the Mistral wind, and from the South-West, the Libeccio wind, with average speeds of 7 m/s and with peaks around 20 m/s (Zecchetto et al., 2016). Such two prevalent wind regimes may generate intense flows towards the 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 to 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.

Within the sectors, on the basis of the occurrence of different rocky substrates and *Posidonia oceanica* meadows, the environmental areas inhabited by sea urchins are defined as types of habitat (Abercrombie, Hickman & Johnson, 1966): Calcareous rock (CR), Granite (GR), Basalt (BA), *Posidonia oceanica* patchy meadow (PM) and *Posidonia oceanica* continuous meadow (CM).

Environmental constraints

The geomorphology was described through habitat mapping (Fig. 2). Available data consisted of morpho-bathymetric data, aerial images 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) that was developed by researchers from the Italian National Research Council within the framework of the RITMARE research 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 by imposing clear boundaries between different morphotypes (Fig. 2) to provide representations of how are they structured. Habitats alternate heterogeneously along the coast. A pool of variables describing the basic characteristic of their spatial configuration was estimated in each sector with the free software Fragstats 4.1 (McGarial & Marks, 1995). The estimated variables are Patch Density on the total landscape area (PD, patch/Km^2), Perimeter-to-area ratio (P/A ratio, 1/m), Mean Patch Size (MPS, Km^2), the Largest Patch Index (LPI, %) as the percentage of landscape area occupied by the largest patch of a class and Interspersion/Juxtaposition Index (IJI, %) which measures the degree of aggregation or "clumpiness" of a map based on adjacency of patches (O'Neill et al., 1988) (Table 2).

The average bottom current speed in the investigated area was obtained by means of a numerical modelling previously applicated in Farina et al., (2018). A three-dimensional hydrodynamic and wind wave model, SHYFEM-WWM (Umgiesser et al., 2004), previously used to reproduce the wind-wave and the 3D water circulation in the Western Sardinian Sea (Cucco et al., 2006, 2016; De Falco et al., 2008), was adopted.

In Farina et al., (2018), the authors reported the model solution for the biennium 2009 and 2010 since it is highly representative of the climate in the Sinis Peninsula (see Appendix 1 in there). The same solutions were used here to describe the water circulation in the first 10 meters of water depth. Hourly data of the sea water speed at the bottom were averaged between January and June, corresponding to the period of active local recruitment (Table 1; Fig.3) (Prado et al., 2012; Farina et al., 2018).

Finally, from a multi-year series of fish biomass data recollection, we extrapolated the abundance of sea urchin predatory fish for each sector from 2004 to 2007 with the exception of sector 5 (Marra et al., 2016). In these years, the reserve effect on fish biomass was not evident and no significant differences were detected between inside and outside the Marine Reserve with the exception of the sea bream that were more abundant inside (Marra et al., 2016; Table.1). Data represent the abundance of the commercial sea breams *Diplodus spp.*, *Sparus aurata* and Labrid *Coris julis*, in the shallow water over the rocky bottoms (5 metres in depth) collected using Underwater Visual Census (Table 1) (Marra et al., 2016).

Sea urchin population structure

Sea urchin population structure was estimated for each type of habitat in the study sectors from a multi-year series of data from 2004 to 2007 (before the population collapsed). During this period, 79 samplings were carried out following a standard protocol at depths between 2 and 10 m (Guala et al., 2008). Data were collected as previously described in Farina et al. (2018). Specifically, for each site and type of habitat, sea urchin density was estimated as the number of individuals per square meter (ind/m^2) and the sizes of the individuals (without spines) were measured with callipers to the closest mm.

For the statistical analysis, we define recruits as individuals with a diameter ≤ 1 cm that survived until approximately one year after their settlement (Ouréns et al., 2013) and middle-sized sea urchins as individuals of size class range 2-5 cm (diameter size), vulnerable to predatory fish. Recruits and middle-sized sea urchins together constitute the under commercial size. Sea urchins larger than 5 cm diameter represent the commercial stock and this size-class range is not considered in the analysis since its density was already reduced to low values by human activity before 2007 (Pieraccini, Coppa & De Lucia, 2016).

Sea urchin population density and structure are estimated for each type of habitat and sector for before their collapse (Table 3, Fig.4). We carried out an analysis of variance of the sea urchin density for the under-commercial-sized (< 5cm diameter test), recruit-sized (0-1 cm diameter size) and middle-sized sea urchins (2-5 cm diameter test) function of "sector" and "habitat" as fixed factors. Assumptions of normal distribution and homogeneity of response variables were tested using D'Agostino-Pearson and Cochran's tests. The densities of sea urchins under commercial size and those of the middle-size followed a normal distribution with unbalanced replicates and were analysed with General Linear Model with Gaussian family distribution (Zuur et al., 2009). Whereas, given the non-normal distribution and the high amount of zeros in recruit density, the analysis of variance of recruits was performed with General Linear Model with Negative Binomial Distribution and certain zero Inflation in order to avoid biased parameter estimates and standard errors (Zuur et al., 2009). All the model validations are provided graphically (see Supplementary material).

Relationship between population structure and environmental conditions

Spearman's rank correlation coefficient as a non-parametric measure of rank correlation was carried out between non-normal distribution values of recruit density and the average bottom current speed, while Pearson's rank correlation, as a parametric linear regression test, was used to estimate the statistical relationship between normally distributed values of density for middle-sized sea urchins and the density of predatory fish.

The Generalized Linear Model (GLM) with Poisson family distribution was performed in order to assess the influences of a pool of variables representing the basic configuration of the rocky habitats on total sea urchin density for those under the commercial size. Patch Density, Perimeter-to-area ratio, Mean Patch Size, Largest Patch Index and Interspersion/Juxtaposition Index (IJI, %) are previously estimated (see above) and used as predictors for sea urchins density (commercial stock excluded). The *stepwise forward regression* technique was used to select the more conservative model (Whittingham et al., 2006).

Given the lack of data on fish visual census in *Posidonia oceanica* and since recruits are considerably underestimated inside meadows (Oliva et al., 2016), the patchy meadow and continuous meadow types of habitats were excluded *a priori* from all these analyses. Analyses were performed using R Studio (R Core Team, 2014).

Results

Environmental constraints

Sector 1 is the largest sector with an area of 12.7 Km^2 (Fig.2). The average current speed was 0.05 ± 0.003 m/s (Fig.3) which was the slowest current measured in the recruitment period (from January to June; see Table 1). Conversely, sector 4 is the smallest sector with a total area of 3.8 Km^2 (Fig.2) and the highest predatory fish abundance of 84.6 ± 12.6 ind/ 125m^2 (Table 1). Sectors 2 and 3 extend 5.1 Km^2 and 4.4 Km^2 respectively (Fig.2) with intermediate values for both bottom current speed average and predatory fish abundance (see Table 1 and Fig.3). Finally, sector 5 covers a total area of 11.9 Km^2 with a similar bottom current speed average for sector 3, while data on predatory fish abundance was not available (Table 1).

In sector 1, *Posidonia oceanica* patchy meadow (PM-1) is the most extended habitat with a surface of 7.2 Km^2, while Calcareous rock (CR-1) covers 4.5 km^2 with a Patch Density of 1.0 per Km^2 . In sector 2, Calcareous rock (CR-2) presents the most extensive surface of the habitats in the sector with the highest patch aggregation (98.9% of IJI) of all the habitats in the study area (see Table 2).

In sector 3, *Posidonia oceanica* patchy meadow (PM-3) and Calcareous rock (CR-3) cover a surface of 2 and 1 Km^2 respectively and both habitats present a Patch Density of 0.32 per Km^2 (Table 2). Basalt (BA-3) is distributed over 0.1 km^2 in both sectors 3 and 4. In Sector 4, Granite (GR-4) covers 1.8 Km^2 (Table 2). Finally, in sector 5 *Posidonia oceanica* continuous meadow (CM-5) represents 11.1 Km^2 of the surface in the sector with the largest patch covering 42.6% of the total area (Table 2) . Continuous meadow is also present in sector 4 but sea urchins have never been sampled there. A variable proportion of sandy bottom is present in all the sectors with the exception of sector 4.

Sea urchin population structure

Sector 1, located outside the Marine Reserve, presented the highest sea urchin density of 9.9 ± 1.1 ind/m^2 , but the lowest proportion of commercial stock (15.1%; Table 1). Inside the Marine Reserve, sea urchin density ranged from the low density of sector 5 of 2.5 ± 0.2 ind/m^2, with a proportion of 20% commercial stock, to the high density of 9.8 ± 1.2 ind/m^2 in sector 4 and with a proportion of commercial stock of 28.7% (Table 1).

The density of specimens under commercial size differ significantly between habitats ($p\text{-value} < 0.001$) and between sectors ($p\text{-value} = 0.02$; Table 4a). Among the types of habitat, the highest sea urchin density for specimens under commercial size was found in CR-1: 16.3 ± 1.4 ind/m^2 (Figure 4, Table 3). High values were also found in CR-2, CR-3 (10.6 ±1.3 and 10.1 ±0.8 ind/m^2 respectively) and in GR-4 (11±1.1 ind/m^2). Otherwise, the lowest sea urchin density was estimated in correspondence to CM-5 (Table 3).

Densities for both recruits and middle-sized sea urchins were significantly different among habitats and sectors (p-values < 0.001; Fig. 4 and Table 4b and 4c). Recruits were significantly more abundant in sector 1 and sector 4 where they were 3.6 ±0.6 ind/m^2 in CR-1, 1.9 ±0.6 ind/m^2 in GR-4 and 1.5 ±1.1 ind/m^2 in BA-4 (Table 3 and 4b). Meanwhile, no recruits were found in PM-1, PM-2, BA-3 and CM-5 (Fig.4, Table 3). The highest average value of density for middle-sized sea urchins was found in CR-1 at (7.2 ±0.8 ind/m). Average density values for CR-2 and CR-3 (6.3 ±0.9 ind/m^2 and 5.4 ±0.7 ind/m^2 respectively) were higher than for BA-3, BA-4 and GR-4 (3.1 ±1.1, 0.5 ±0.2 ind/m^2 and 3.3 ±0.8 ind/m^2 respectively) (Table 3). In CM-5, the density of middle-sized sea urchins was 1.9 ± 0.5 ind/m^2 (Fig.4, Table 3).

Relationship between population structure and environmental conditions

Values of recruit density in rocky habitats (Calcareous rocky, Basalt and Granite) follow a non-normal distribution due to the high number of sampled zeros. Accordingly, Speraman's non-parametrical rank correlation test was performed between recruit density and average bottom current speed and a negative significant relationship was found (Spearman's rank correlation p-value = 0.002932; *rho* = -0.3972998; Fig.5a). The density of middle-sized sea urchins following normal distribution was correlated to the predatory fish density using Peason's correlation test and the variables resulted in a significant negative correlation (Pearson's correlation p-value = 0.04268, *correlation coefficient* = -0.5118654; Fig. 5b).

The General Linear Model highlights high significant influences of Patch Density (PD; p-value< 0.001) and significant influence of the Mean Patch Size (MPS; p-value<0.001) on sea urchin density for specimens under commercial size. The proportion of the variance explained by the Minimal Adequate Model is roughly 50% (see Table 5 and Fig. S5).

Discussion

During the sampling period done between 2004 and 2007, conspicuous differences in sea urchin density were found across fishing sectors and types of habitat. In general rocky habitats of Calcareous rock, Basalt and Granite supported larger sea urchin populations than the habitats of *Posidonia oceanica*.

Excluding the commercial stock whose density was distorted by intensive fishing, the sea urchin density for specimens under commercial size in rocky habitats was significantly higher in Calcareous rock. Moreover, considering results obtained from the analysis on the spatial configuration, the high values of patch density and mean patch size seem to further increase the sea urchin density in Calcareous rock of sector 1.

Although sector 1 was outside the Marine Reserve and had the lowest proportion of commercial stock, Calcareous rock in this sector presented a large extension surface (4.5 Km^2) with high Patch Density (one patch per Km^2) which supported a density of sea urchin under commercial size approximately twice that of calcareous rock in sectors 2 and 3. Specifically, recruit density in Calcareous rock of sector 1 was 6 and 4 times higher than in the Calcareous rock of sectors 2 and 3 respectively. It was approximately 2 and 2.5 times higher respectively than in the Granite and Basalt of sector 4. Also, the density of middle-sized sea urchins resulted significantly higher in Calcareous rock (sectors 1,2,3); it was more than 2 times higher here than in Basalt and Granite (sector 4). Finally, in the *Posidonia oceanica* patchy meadows, recruit density was negligible everywhere. This was also found to be true for the middle –sized sea urchins in the continuous meadow of sector 5.

Population structures analysed responded to the high variability of the environmental constraints observed along this stretch of coast. From January to June, when the spawning events occur (Loi et al., 2017) and settlement is supposed to be over (estimating 20-30 days for the planktonic phase once the eggs are fertilized, Lozano et al., 1995), the average bottom current speed was slowest in sector 1. It was almost half the speed of sectors 2 and 4 and a third less than in sectors 3 and 5. The weak, negative correlation between recruits and bottom current speed is a distant approximation of the real influence of hydrodinamics on population recruitment. This correlation was performed due to the lack of data on larvae and settlers during these years. In general, the influence of current on recruitment can serve as an indicator of effective connectivity between areas (Romagnoni et al., 2020). However, sea urchin density during the post-settlement phase experiences important decreases due to predators (Hereu, Zabala & Sala, 2008). Accordingly, bottom current speed should be more closely correlated to larvae and settlers than to recruits. The low values of the average bottom current speed (< 0.1 m/s) correspond to recruit densities above 3.5 ind/m^2. It is interesting to notice that the average bottom current speed on the Calcareous rock of sector 1 is always under this critical threshold. In fact, this condition seems to support the existence of local standing circulation structures that determine a higher regime of natural recruitment (Farina et al., 2018).

After recruitment, predation is the second main process regulating sea urchin population structure on a local scale (Guidetti, 2004; Hereu, Zabala & Sala, 2008; Boada et al., 2015). Adult sea urchins are effectively preyed on by few fish species, especially the sea breams *Diplodus spp* and *Sparus aurata* which are targeted by artisanal fisheries (Guidetti, 2006). During 2004-2007, there was an evident negative correlation between the abundances of predatory fish and middle-sized sea urchins.

Low abundances of predatory fish were found outside the Marine Reserve in sector 1, most likely due to the strong pressure exerted by recreational spear fishermen (Marra et al., 2016). Conversely, in sector 4- Islands inside the Marine Reserve- the density of sea breams was higher than in the other sectors during these years (Marra et al. 2016).

Although no reserve effect was evident and no differences in fish biomass between inside and outside the Marine Reserve were detected during this period, the reduced accessibility of the islands compared to the other coastal sectors could have offered the local community of sea bream more protection from recreational spear fishermen, making them more abundant. Consistently with this theory, the lowest density of middle-sized sea urchins was found in Sector 4, supporting the possibility of a higher level of predation in this area.

Moreover, predator activity is generally influenced by an increase in habitat edges (Bender, Contreras & Fahrig, 1998; Kondoh, 2003; Prado et al., 2008; Farina et al., 2017). This is typically caused by fragmentation processes, which generally result in increasing habitat complexity as patch perimeter- to- area ratios increase (Ranney, Bruner & Levenson, 1981). The opposite condition is designed by the calcareous rock in sector 1. High-density patches with very large surfaces dampen visual predation of fish providing efficient shelters to middle-sized sea urchins and recruits as well (Hereu et al., 2005).

Our results suggest how environmental constraints exert an important influence on sea urchin population dynamics and population structures and are not quite as homogenous as it might seem along this stretch of coast. Thus, a management plan for sustainable harvesting should start from the assumption that the sea urchin population in this region could be composed of multiple, smaller populations with their own population dynamics.

The long, planktonic early life-stage (between 20-30 days according to Lozano et al., 1995) makes sea urchin populations demographically open (López et al., 1998; Morgan et al., 2000; Prado et al., 2012; Treml et al., 2012). Populations are connected via a process of larval dispersion (Knight & Landres, 2002) that could be strongly dependent on the bottom current speed. A connectivity system among local populations could be generated where “source” populations supplement “sink” populations via dispersing individuals determining a rescue effect that should be considered crucial when planning management for sustainable fisheries. This is especially important for conservation requirements in a Marine Reserve (Paterno et al., 2017) and it is a point to be developed urgently in future research proposals for this area.

The strength of local connectivity depends strongly on the abundance of reproducers in populations. Since commercial harvesting depletes the main reproducers, middle-sized sea urchins play an important the population’s recovery (Loi et al., 2017). However, this size class is also highly vulnerable to predators. For this reason, its harvesting should be more restricted in conditions of high predation activity. This could be the case of the Islands of sector 4, where the sea urchin population seemed to suffer a higher predation pressure than in the other sectors, and the harvesting should be more restricted as consequence.

Farina et al. (2009, 2014) found high proportions of middle-sized sea urchins in patchy meadows in accordance with the efficient shelter that *Posidonia oceanica* leaves provide from the visual mechanism of predatory fish. However, the three-dimensional structure of large seagrass meadows can become a 'death trap' in the presence of high densities of bottom predators (Farina et al., 2014, 2016; Schmidt & Kuijper, 2015). Sector 5, in the Gulf of Oristano, is characterized by a large, continuous meadow of *Posidonia oceanica* (De Falco et al., 2008). Here, the low density of *P. lividus* could be related to the abundance of whelks (e.g. *Hexalplex trunculus*, authors pers. obs.), which is probably related to the adjacent mussel farms (Inglis & Gust, 2003) and known as effective predators of sea urchins (Farina et al., 2016).

Fisheries that aim to provide long-term sustainable exploitation of resources should take into consideration not only the monitoring of stock density but also of population dynamics, its ecological drivers and what they depend on, as well as the effects and dynamics of fisheries (Hilborn & Walters, 1992). Accordingly, a clear understanding about the processes regulating realistic population dynamics on a relevant spatial and temporal scale is a prerequisite of any management strategy. Our results identify spatial heterogeneity in population dynamics and stock abundance related to local conditions. We highlight the importance of developing a broader management approach to fisheries targeting both sea urchins and their predators. Although the rates of recruitment and predation were unknown the period before the population collapse, this study suggests how these mechanisms are of crucial importance to ensure long-term sustainable exploitation of the resource. Despite the highly limited approximations that are carried out in this study, natural relationships have been demonstrated to exist between sea urchin population dynamics, their ecological drivers and the environmental constraints along this stretch of coast.

In this system, the continuous and inexorable decrease of the natural resource since 2007 has been followed by frantic adjustments in management measures. Simulations obtained by fisheries models with an ecosystem approach allow for the testing of alternative management strategies (Christensen & Walters, 2004; Fulton et al., 2004; Spedicato et al., 2010). This could foster a systemic territorial planning geared to supporting sustainable use of the fishing resources. This approach relies strongly on the basic understanding of population dynamics, its spatial structure, and its interaction with other elements of the ecosystem. These elements should lead to specific measures for regulating the fishing effort on specific components of the populations (for example, to reduce harvesting of the most productive age classes or areas).

The Peninsula of Sinis offers a unique case study, where ecological and economic information and data is building up, and the involved stakeholders, including small-scale fisheries organizations, Marine Reserve and local administration are demanding a science-based management system. There is currently momentum toward the implementation of a long-term vision which entails a data collection procedure aiming to provide management strategies for the sustainable management of sea urchin fisheries. These would combine the objectives of conservation of ecological features and of traditional and socio-economics values. Moreover, achieving sustainable fishing of both resources -sea urchins and sea breams- will enhance, as a cascade effect, the conservation prospective for macrophyte communities, which are pivotal for ensuring a high environmental quality and support nursery of other benthic species.

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Figure 1

Diagram describing sea urchin population dynamics.

Letters represent different life stages 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.

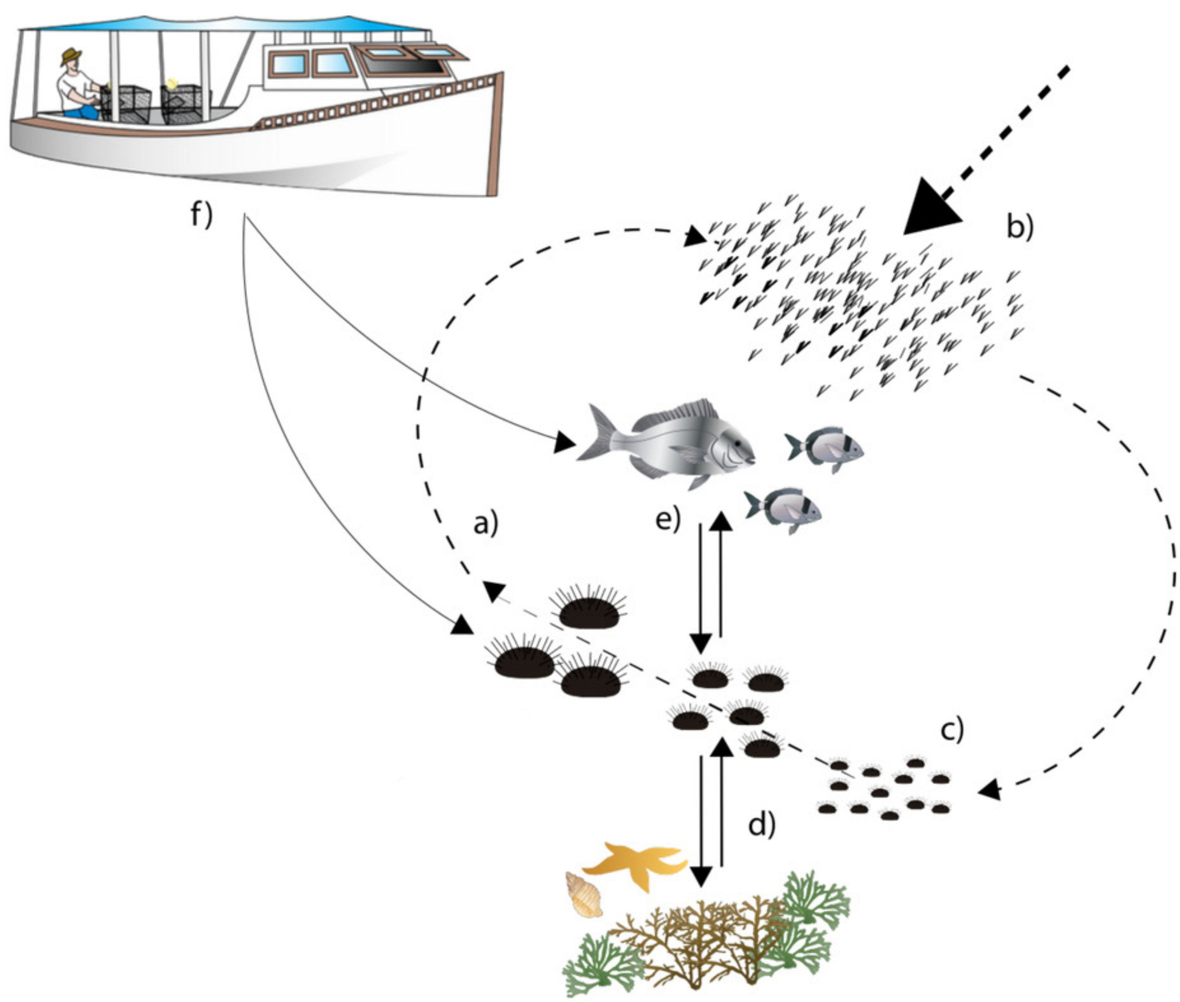


Figure 2

Detailed digital mapping of geomorphology in the study area

Colours indicatedifferent sectors and types 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 sandy bottom (in yellow).

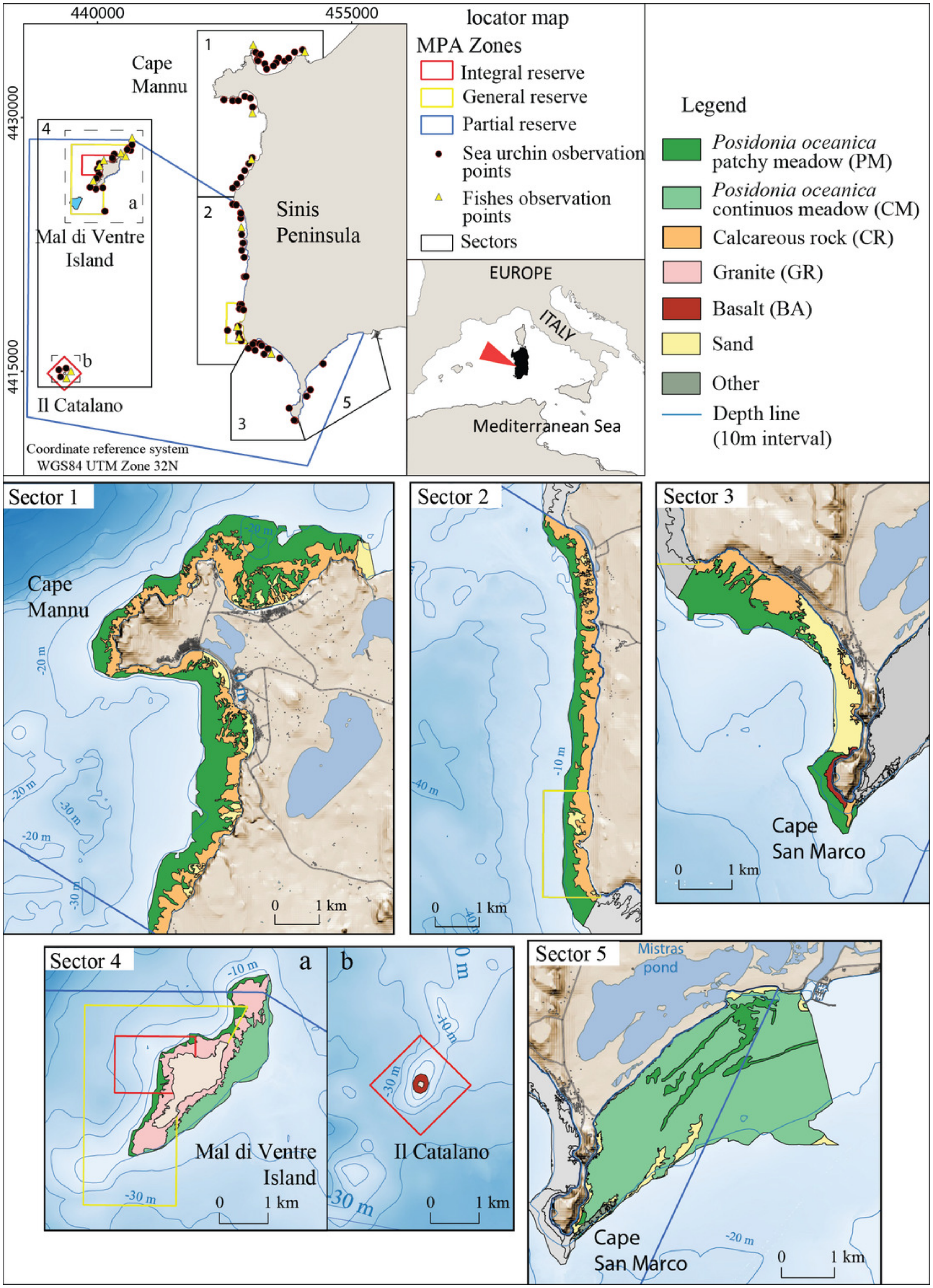
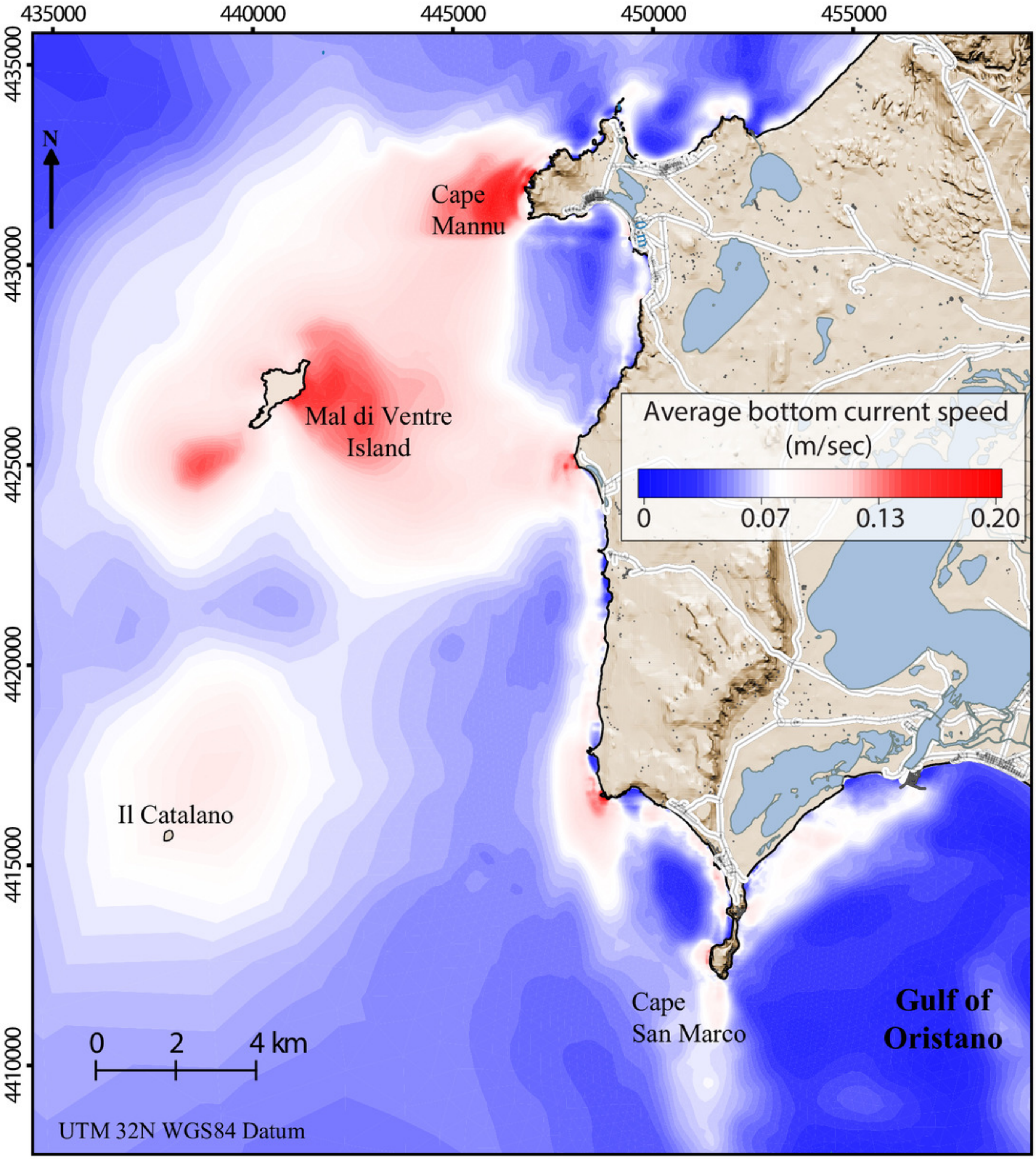

440000
455000
4430000
4415000
Cape Mannu
Mal di Ventre Island
Il Catalano
Sinis Peninsula
Coordinate reference system WGS84 UTM Zone 32N
locator map
MPA Zones
Integral reserve
General reserve
Partial reserve
Sea urchin osbervation points
Fishes observation points
Sectors
EUROPE
ITALY
Mediterranean Sea
Legend
Posidonia oceanica patchy meadow (PM)
Posidonia oceanica continuos meadow (CM)
Calcareous rock (CR)
Granite (GR)
Basalt (BA)
Sand
Other
Depth line (10m interval)
Sector 1
Sector 2
Sector 3
Sector 4
Sector 5
Cape San Marco
Mistras pond
0 1 km

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).



435000
440000
445000
450000
455000
4435000
4430000
4425000
4420000
4415000
4410000
N
Cape Mannu
Mal di Ventre Island
Average bottom current speed (m/sec)
0
0.07
0.13
0.20
Il Catalano
Cape San Marco
Gulf of Oristano
0 2 4 km
UTM 32N WGS84 Datum

Figure 4

Graphs representing different population structures.

Populations of each type of habitat in each sector: 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

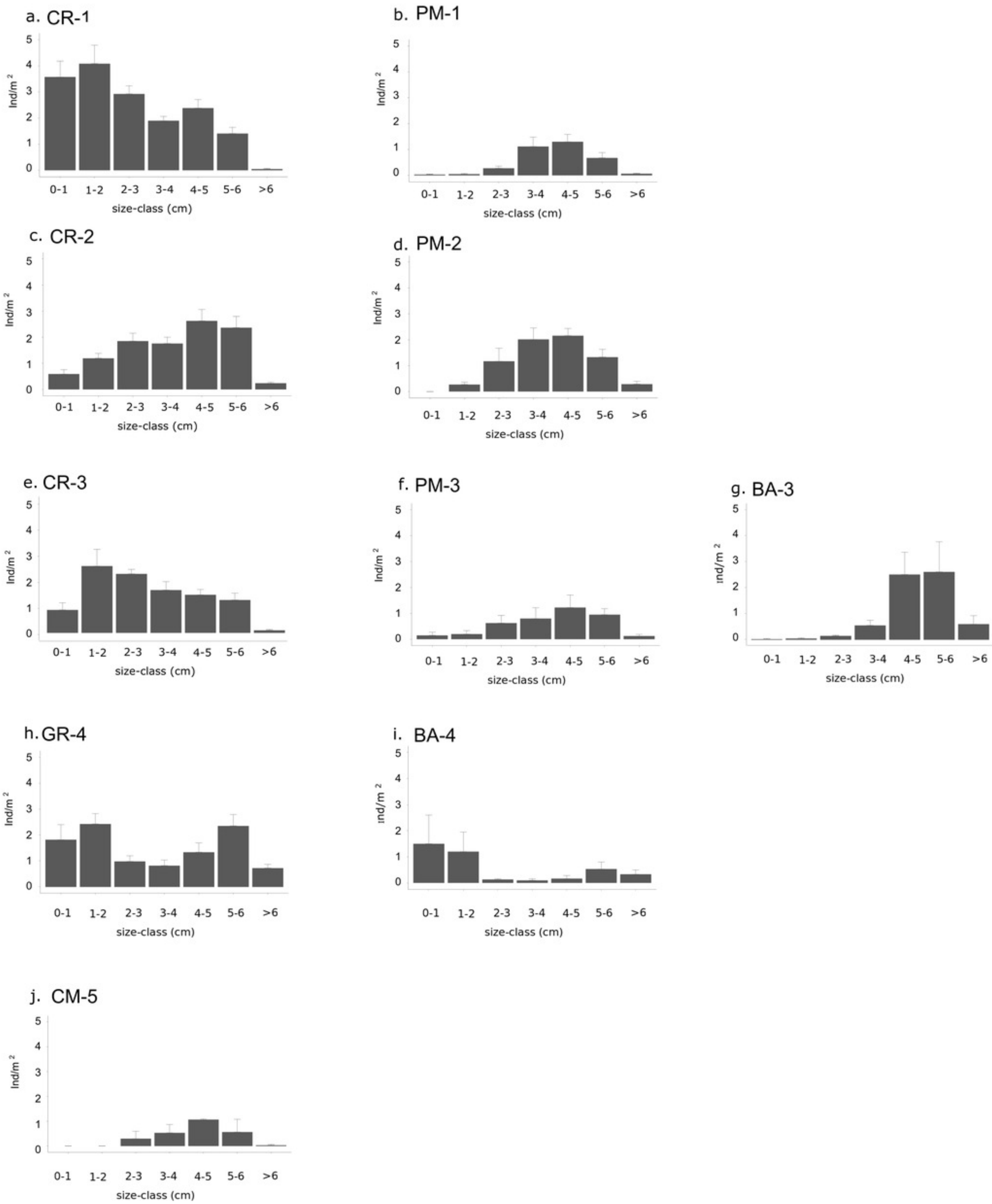


Figure 5

Graphs representing relationships between sea urchin densities and environmental constraints.

In rocky habitats a) density of recruits is correlated with the average bottom current speed (Spearman's rank correlation) and b) density of middle-sized sea urchins with predatory fish density (Pearson’s correlation) 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.

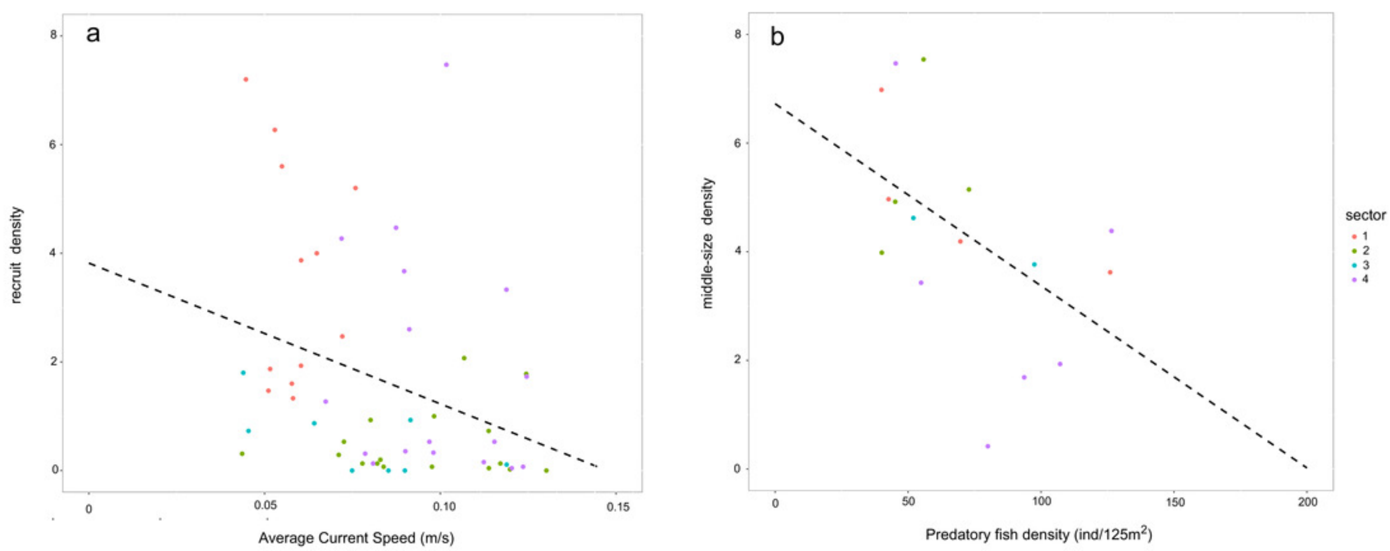


Table 1(on next page)

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

Sector	Total area (Km^2)	Average Current Speed (m/s)	Average predatory fish (ind/125m^2)	Total sea urchin density	Stock proportion (%)
1	12.7	0.05 ±0.003	69.6 ± 20	9.9 ±1.1	15.1 ±2.3
2	5.1	0.09 ±0.004	53.5 ± 7.2	8.9 ±1.3	23.3 ±2.2
3	4.3	0.07 ±0.007	74.8 ± 22.8	6.9 ±1.5	28.7 ±4.7
4	3.8	0.10 ±0.004	84.6 ± 12.6	7.5 ±1.7	27.8 ±3.6
5	11.9	0.07 ±0.003	-	2.5 ±0.2	20.0 ±1.8

Table 2(on next page)

Spatial configuration of sampled habitats for each study sector.

Dash means no samplings were carried out.

Sector	Habitat	code	Nº of samplings	Area (Km^2)	PD (n/Km^2)	P/A ratio (1/m)	MPS (Km^2)	LPI (%)	IJI (%)
1	Calcareous Rock	CR-1	12	4.5	1.01	21.1	0.10	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	0.05	0.3	0.18	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	-	-	-	-	-

Table 3 (on next page)

Densities of sea urchin size-classes representing population structures.

Mean sea urchins densities of the size-class range representing population structure in the different types of habitat. Size-class ranges 0-1cm and 2-5cm diameter represent recruits and middle-sized sea urchins respectively, whereas commercial stock size densities are represented beyond the dotted line and are not included in the analysis.

Sector	Habitat	0-1cm	1-2cm	2-3cm	3-4cm	4-5cm	stock 5-6cm	>6cm
1	Calcareous Rock	3.6±0.6	4.1±0.7	2.9±0.3	1.9±0.2	2.4±0.3	1.4±0.2	0
1	Patchy Meadow	0	0	0.3±0.1	1.1±0.4	1.3±0.3	0.7±0.2	0.1±0
2	Calcareous Rock	0.6±0.2	1.2±0.2	1.9±0.3	1.8±0.2	2.6±0.4	2.4±0.4	0.2±0.1
2	Patchy Meadow	0	0.3±0.1	1.2±0.5	2±0.4	2.1±0.3	1.3±0.3	0.3±0.1
3	Calcareous Rock	0.9±0.3	2.5±0.6	2.3±0.2	1.6±0.3	1.5±0.2	1.2±0.3	0.1±0
3	Patchy Meadow	0.1±0.1	0.2±0.1	0.6±0.3	0.8±0.4	1.2±0.5	1±0.2	0.1±0.1
3	Basalt	0	0.1±0	0.1±0	0.5±0.2	2.5±0.9	2.6±1.1	0.6±0.3
4	Granite	1.9±0.6	2.6±0.4	1±0.2	0.9±0.2	1.4±0.4	2.5±0.5	0.8±0.1
4	Basalt	1.5±1.1	1.2±0.7	0.2±0	0.1±0.1	0.2±0.1	0.5±0.3	0.3±0.2
5	Continuous Meadow	0	0	0.3±0.3	0.5±0.3	1.1±0	0.6±0.5	0

Table 4(on next page)

Analysis of deviance table GLM model

a) density of under-commercial-size, b) density of recruit and c) density of middle-size sea urchins in function of Sector and Habitat as fixed factors. DF: degrees of freedom, DR: deviance residual, F: F statistics, P: probability of Type I error.

a. Response variable	**Factor**	**DF**	**DR**	**F-value**	**p-value**
Density of under-commercial size	Sector	4	193.29	3.2592	**0.01638**
	Habitat	3	801.33	18.0157	**8.534e-09**
	Residual	79			
b. Response variable	**Factor**	**DF**	**MS**	**F-value**	**p-value**
Density of recruit	Sector	3	44.68	6.038	**0.00103**
	Habitat	3	101.21	13.677	**4.26e-07**
	Residual	69	7.40		
c. Response variable	**Factor**	**DF**	**DR**	**F-value**	**p-value**
Density of middle-size	Sector	4	125.61	5.1458	**0.0010676**
	Habitat	3	130.73	7.1410	**0.0002935**
	Residual	78			

Table 5(on next page)

Generalized Linear Model (GLM) showing the effects of the assessed explanatory variables on the density of commercial under-sized classes (TD<5cm).

The Minimal Adequate Model (AIC=290.8; R-square = 0.468) was obtained starting from Full Model (AIC=295.5; R-square=0.476) through the stepwise forward regression technique (Anova p-value=0.55). Coefficient estimates (Estimate), standard errors (SE), z-values, and significance levels (p-value) for variables are provided for fixed effects. Significant effects are given in bold.

Full Model					
Response variable	**Effect**	**Estimate**	**SE**	**z-value**	**p-value**
	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
Minimal Adequate Model					
Response variable	**Effect**	**Estimate**	**SE**	**z-value**	**p-value**
Sea urchin density	MPS	0.3758	0.0861	4.365	**1.27e-05**
	PD	1.1459	0.1381	8.300	**2e-16**