Sea urchin harvest inside marine protected areas: an opportunity to investigate the effects of exploitation where trophic upgrading is achieved (#63164)

First submission

Guidance from your Editor

Please submit by **14 Sep 2021** for the benefit of the authors (and your $200 publishing discount) .

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

Author notes
Have you read the author notes on the guidance page?

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

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

Files

Download and review all files from the materials page.

10 Figure file(s)
3 Table file(s)
1 Raw data file(s)

Structure and Criteria

Structure your review

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

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

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

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

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

EXPERIMENTAL DESIGN

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

VALIDITY OF THE FINDINGS

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

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Sea urchin harvest inside marine protected areas: an opportunity to investigate the effects of exploitation where trophic upgrading is achieved

Giulia Ceccherelli Corresp., [1], **Pierantonio Addis** [2], **Fabrizio Atzori** [3], **Nicoletta Cadoni** [3], **Marco Casu** [1], **Stefania Coppa** [4], **Mario De Luca** [1], **Giuseppe Andre De Lucia** [4], **Simone Farina** [5], **Nicola Fois** [6], **Francesca Frau** [3], **Vittorio Gazale** [7], **Daniele Grech** [8], **Ivan Guala** [8], **Mariano Mariani** [9], **Massimo SG Marras** [10], **Augusto Navone** [11], **Arianna Pansini** [1], **Pieraugusto Panzalis** [11], **Federico Pinna** [1], **Alberto Ruiu** [9], **Fabio Scarpa** [1], **Luigi Piazzi** [1]

[1] University of Sassari, Sassari, Italy
[2] University of Cagliari, Cagliari, Italy
[3] Capo Carbonara – Villasimius Marine Protected Area, Villasimius (CA), Italy
[4] Istituto per lo studio degli Impatti Antropici e Sostenibilità in ambiente marino (IAS) – Consiglio Nazionale delle Ricerche (CNR), Torre Grande (OR), Italy
[5] SZN - Stazione Zoologica Anton Dohrn, Napoli, Italy
[6] AGRIS, Bonassai (SS), Italy
[7] Isola dell'Asinara Marine Protected Area, Porto Torres (SS), Italy
[8] International Marine Centre, Torre Grande (OR), Italy
[9] Capo Caccia – Isola Piana Marine Protected Area, Alghero (SS), Italy
[10] Penisola del Sinis - Isola di Mal di Ventre Marine Protected Area, Cabras (OR), Italy
[11] Tavolara Punta Coda Cavallo Marine Protected Area, Olbia (SS), Italy

Corresponding Author: Giulia Ceccherelli
Email address: cecche@uniss.it

Background. Marine protected areas (MPAs) have both positive effects of protection for the fisheries' target species and indirect negative effects for sea urchins. Moreover, often in MPAs sea urchin human harvest is restricted, but allowed. This study is aimed at estimating the effect of these restrictions on human harvest of the sea urchin *P. lividus* on the total and commercial abundances. Our hypothesis tested that sea urchins in restricted harvest (RH) sites are less abundant than those at no harvest (NH) and unrestricted (UH) sites because of natural and human predation cumulative effects. Accordingly, we expected the fasted regression in the RH sites, rather than in UH and NH sites.

Methods. At this aim, a collaborative database gained across five MPAs in Sardinia (Western Mediterranean, Italy) and areas outside was gathered collecting sea urchin abundance and size data in a total of 106 sites (33 NH, 37 RH and 36 UH). Furthermore, as estimates made in past monitoring efforts (since 2005) were available for 75 of the sampled sites, the rate of variation in the total sea urchin abundance was estimated at the NH, RH and UH sites.

Results. Results have highlighted that the least sea urchin total and commercial abundances were found in RH sites, likely for the cumulative effects of human harvest and natural predation. The overall rate of change in sea urchin abundance over time indicates that only NH conditions promoted the increase of sea urchin abundance and that current local management of the MPAs has driven towards a relevant regression of populations. Overall, results suggest that complex mechanisms may occur on sea urchin populations and the assessment of MPA effects on *P. lividus* populations would be crucial to guide management decisions on regulating harvest permits. Overall, the need to ban sea urchin harvest in the

MPAs to avoid extreme reductions is encouraged, as inside the MPAs sea urchin populations are likely under natural predation pressures for the trophic upgrading.

Sea urchin harvest inside marine protected areas: an opportunity to investigate the effects of exploitation where trophic upgrading is achieved

Giulia Ceccherelli[1], Pierantonio Addis[2], Fabrizio Atzori[3], Nicoletta Cadoni[3], Marco Casu[4], Stefania Coppa[5], Mario De Luca[1], Giuseppe Andrea de Lucia[5], Simone Farina[6], Nicola Fois[7], Francesca Frau[3], Vittorio Gazale[8], Daniele Grech[9], Ivan Guala[9], Mariano Mariani[10], Massimo SG Marras[11], Augusto Navone[12], Arianna Pansini[1], Pieraugusto Panzalis[12], Federico Pinna[1], Alberto Ruiu[10], Fabio Scarpa[4], Luigi Piazzi[1]

[1] Dipartimento di Chimica e Farmacia, Università di Sassari, Via Piandanna 4, 07100 Sassari (Italy)
[2] Dipartimento di Scienze della Vita e dell'Ambiente, Università di Cagliari, Via Fiorelli 1, 09126 Cagliari (Italy)
[3] Capo Carbonara – Villasimius Marine Protected Area, Via Roma 60, 09049 Villasimius, CA (Italy)
[4] Dipartimento di Medicina Veterinaria - Sez. Fisiologia della Nutrizione e Zoologia, Università di Sassari, 07100 Sassari (Italy)
[5] Istituto per lo studio degli Impatti Antropici e Sostenibilità in ambiente marino (IAS) – Consiglio Nazionale delle Ricerche (CNR), Loc. Sa Mardini, 09170 Torre Grande, OR (Italy)
[6] SZN - Stazione Zoologica Anton Dohrn, Villa Comunale Napoli (Italy)
[7] Agris - Agricultural Research Agency of Sardinia - Bonassai SS 291 km 18.6, 07100 Sassari (Italy)
[8] Isola dell'Asinara Marine Protected Area, via Ponte Romano 81, 07046 Porto Torres SS (Italy)
[9] IMC - International Marine Centre, Loc. Sa Mardini, 09170 Torre Grande, OR (Italy)
[10] Capo Caccia – Isola Piana Marine Protected Area, Loc. Tramariglio SP 55, 07041 Alghero, SS (Italy)
[11] Penisola del Sinis - Isola di Mal di Ventre Marine Protected Area, Corso Italia 108, 09072 Cabras, OR (Italy)
[12] Tavolara Punta Coda Cavallo Marine Protected Area, Via S. Giovanni 14, 07026 Olbia, SS (Italy)

Corresponding Author:
Giulia Ceccherelli[1]
Via Piandanna 4, 07100 Sassari, Italy
Email address: cecche@uniss.it

Abstract

Background. Marine protected areas (MPAs) have both positive effects of protection for the fisheries' target species and indirect negative effects for sea urchins. Moreover, often in MPAs sea urchin human harvest is restricted, but allowed. This study is aimed at estimating the effect of these restrictions on human harvest of the sea urchin *P. lividus* on the total and commercial abundances. Our hypothesis tested that sea urchins in restricted harvest (RH) sites are less abundant than those at no harvest (NH) and unrestricted (UH) sites because of natural and human predation cumulative effects. Accordingly, we expected the fasted regression in the RH sites, rather than in UH and NH sites.

Methods. At this aim, a collaborative database gained across five MPAs in Sardinia (Western Mediterranean, Italy) and areas outside was gathered collecting sea urchin abundance and size data in a total of 106 sites (33 NH, 37 RH and 36 UH). Furthermore, as estimates made in past monitoring efforts (since 2005) were available for 75 of the sampled sites, the rate of variation in the total sea urchin abundance was estimated at the NH, RH and UH sites.

Results. Results have highlighted that the least sea urchin total and commercial abundances were found in RH sites, likely for the cumulative effects of human harvest and natural predation. The overall rate of change in sea urchin abundance over time indicates that only NH conditions promoted the increase of sea urchin abundance and that current local management of the MPAs has driven towards a relevant regression of populations.

Overall, results suggest that complex mechanisms may occur on sea urchin populations and the assessment of MPA effects on *P. lividus* populations would be crucial to guide management decisions on regulating harvest permits. Overall, the need to ban sea urchin harvest in the MPAs to avoid extreme reductions is encouraged, as inside the MPAs sea urchin populations are likely under natural predation pressures for the trophic upgrading.

Introduction

Unsustainable harvesting is now the most prevalent issue affecting threatened marine species (Di Minin *et al.*, 2019). In fact, about one-third of commercial wild fish stocks are currently being overfished (FAO, 2016) and global marine fishery catches are declining (Pauly and Zeller, 2016). The general overexploitation of species has consequences on food webs and ecosystem functioning, firstly due largely to the widespread declines in marine predators. When high trophic level predators are removed from ecosystems the 'trophic downgrading' (*sensu* Estes *et al.*, 2011) leaves greater proportions of low trophic level species. This leads to an imbalance in the regulation of coastal systems (Britten *et al.*, 2014).

Marine protected areas (MPAs) have emerged as a promising management tool for the conservation and recovery of marine coastal ecosystems (Russ *et al.*, 2004; Gaines *et al.*, 2010; Giakoumi *et al.*, 2017). Although it was evidenced that the enforcement level is the essential requirement for the reestablishment of lost predatory interactions (Guidetti, 2006; Giakoumi *et al.*, 2017; Giakoumi *et al.*, 2018), encouraging data for managing the marine coastal environments have been provided even by small, well-enforced, fully protected (integral reserve) areas that have had relevant ecological effects (*i.e.* Guidetti *et al.*, 2008; Giakoumi *et al.*, 2017). In MPAs where reserve effectiveness has been achieved, the density of prey species, whether fish or invertebrates, can be drastically reduced by the increased abundance of predators (*e.g.* Willis and Anderson, 2003; Sala et al., 2013; Giakoumi *et al.*, 2017; Guidetti *et al.*, 2019).

In temperate reefs, sea urchins play a key role in the transmission of top-down effects (Pinnegar *et al.*, 2000; Filbee-Dexter and Scheibling, 2014; Ling *et al.*, 2015; Carr and Reed, 2016; Melis *et al.*, 2019). Despite the importance of recruitment and other conditions such as refuge availability, storms and temperature (Hereu *et a*l., 2012; Clemente *et al.*, 2013; Yeruham *et* al., 2015; Oliva *et al.*, 2016; Piazzi and Ceccherelli, 2017; Medrano *et* al., 2019; Farina *et al.*, 2020), sea urchin density is mainly controlled by predation through consumptive and non-consumptive effects (*e.g.* Sih *et al*., 1998; Guidetti, 2006; McClananhan *et al*., 2006; Hernández *et al*., 2007; Guidetti and Sala, 2007; Seytre *et al*., 2013; Pessarrodona *et al*., 2019). On the other hand, the benthic community structure is controlled by sea urchin grazing effects (*e.g.* Filbee-Dexter and Schibling, 2014; Piazzi and Ceccherelli, 2019).

In the Mediterranean, the sea urchin *Paracentrotus lividus* (Lamarck, 1816) (Echinoidea: Parechinidae) is a key herbivore of the shallow subtidal rocky habitats, playing a central role in the trophic cascade (Micheli *et al*., 2005; Giakoumi *et al*., 2012). Its high-density populations, due to the lack of predators (overexploited areas), can have dramatic effects on rocky macroalgal communities, producing barren grounds (Guidetti and Dulcjc, 2007; Gianguzza *et al*., 2011; Boada *et al*., 2017). However, in MPAs where the recovery of natural predators is widely achieved (Pinnegar *et al*., 2000; Guidetti *et al*., 2014), sea urchin abundance can be shaped by multiple predator effects, due to fish (Guidetti, 2005) and benthic invertebrates (Bonaviri *et al*., 2009, 2012; Boada *et al*., 2015; Farina *et al*., 2016). Predation mostly affects sea urchins up to 40 mm in size (Pessarrodona *et al*., 2019), therefore reserve effectiveness usually leads to higher frequency of large *P. lividus* compared to no protected areas (Hereu *et al*., 2005; Loi *et al*., 2017).

However, natural predation is not the only pressure controlling *P. lividus* populations. Since it is an edible species, human harvest of this sea urchin has recently intensified (Furesi *et al*., 2016), making *P. lividus* one of the most exploited benthic invertebrate species in the Mediterranean (Gianguzza *et al*., 2006; Ceccherelli *et al*., 2011). Thus, there is growing interest concerning the maintenance of *P. lividus* populations both for ecological and commercial aims. This interest has led to an increase in the knowledge of mechanisms regulating *P. lividus* abundances (*e.g.* Guidetti, 2004; Hereu *et al*., 2008; Ceccherelli *et al*., 2009; Prado *et al*., 2012; Boada *et al*., 2015; Oliva *et al*., 2016; Farina *et al*., 2018) in order to define sustainable harvest (*e.g*. Ceccherelli *et al*., 2011; Bertocci *et al*., 2014). The current regulation varies on a local scale and acts on the harvest season, the number of fishermen, the minimum size. Thus, the perception of an inherent trade-off between achieving conservation and fishing goals may be far from being reduced or eliminated (Gaines *et al*., 2010). Particularly severe conflicts may arise from multiple-use MPAs that are used for conservation purposes: their goal is to allow a variety of human activities that are managed comprehensively to support compatible uses while at the same time protecting key habitats and resources.

In Sardinia (central-western Mediterranean Sea, Italy), sea urchin roe is a common ingredient in several dishes and harvesting has been historically carried out both by professional and non-professional fishermen (Furesi *et al*., 2016). To minimise the risk of overexploitation the Regional Government of Sardinia has imposed restrictions on the commercial fishing of the edible sea urchin: i) by granting a limited number of firms (about 200) authorisation for this activity; ii) by limiting the fishing season from November to May; iii) by fixing daily catch quotas (1500 to 3000 sea urchins per day for each professional fisherman); and iv) by providing a minimum sea urchin size to harvest (test diameter of 50 mm without spines). These restrictions are effective on the whole Island, MPAs included, where a specific number of authorized fishermen have been addressed. However, each MPA, based on its own management plan, has independently allowed harvesting in partially protected zones (both B and C zones, according to the Italian designation) by allowing a fixed number of authorized professional fishermen. They are not given access to the fully protected zone (integral reserves, A zone) where harvest has never been allowed (Table 1). Therefore, the effectiveness of protection is not obvious since the effects of human and natural predation may detrimentally cumulate inside the MPAs where sea urchin harvest is allowed, while outside the MPAs (commonly overfished areas) the harvest is likely to be the pressure most affecting *P. lividus* populations. Moreover, both natural and manmade predation pressures should have the opposite shaping effect on the sea urchin population structure, as humans should exploit only large-sized individuals because of regulations (>50 mm) while fish attacks are more frequent on small-sized urchins (Guidetti

2004). Thus, complex mechanisms may occur and the assessment of MPA effects on *P. lividus* populations is crucial to guide management decisions on regulating sea urchin harvest permits (Coppa *et al*., 2021), with the intention of avoiding their local extinction. In particular, in Sardinia the demand for *P. lividus* has grown significantly in the last two decades (Furesi *et al*., 2016) so that studies have focused on the effect of harvest restrictions (*i.e*., Pais *et al*., 2007; Ceccherelli *et al*., 2011; Loi *et al*., 2017), and data are now available for observing patterns of change depending on the management. In this way, Sardinia may represent a suitable case to assess the management effectiveness of MPA management in the maintenance of sea urchin populations in order to obtaining useful information for the conservation of ecosystems functioning and the sustainable harvest of the resource.

The present study is aimed at comparing the *P. lividus* total (any size urchin) and commercial (only urchins larger than 50mm) abundance in different harvest conditions in Sardinia (Italy). This goal was achieved by two approaches: a spatial evaluation and a temporal evaluation. For the spatial evaluation, we compared total and commercial *P. lividus* abundance at sites with different harvest regulations using data collected in 2018-2019. The prediction we formulated was that the smallest densities of commercial sea urchins would be found where human harvest is allowed and where the harvest is restricted, compared to where the harvest is forbidden. Our prediction for the whole population of *P. lividus* was that the smallest total abundance of sea urchins would be found in protected zones where the effect of human harvest (even if restricted) and natural predation can cumulate. For the temporal evaluation, only the sites where past monitoring data on *P. lividus* abundance were available (overall since 2005) were considered, so that the variability of the total abundance of *P. lividus* over time was also estimated depending on the harvest level, with the expectation that the greatest changes would be found in areas where both human and natural predation have occurred. For both evaluations, a collaborative database was produced by integrating information taken at different times by several research institutions involved in monitoring Sardinian MPAs and non-protected areas.

Results can provide important information for addressing both the MPAs and Regional management of the sea urchin harvest and may also give insights into the successful management of any sustainable exploitation of resource in danger of being depleted.

Materials & Methods

Study locations

P. lividus abundance and size were assessed at 106 sites located along the coast of Sardinia (Italy, Mediterranean Sea, Fig. 1, Fig S1-S5): 33 no harvest sites (NH, harvest never been allowed), 37 restricted harvest sites (RH, exploitation of sea urchins is restricted by the MPA) and 36 harvested unrestricted sites (UH, no limits for an overall exploitation, outside the MPA) sites. The NH and RH sites are located in the main Sardinian MPAs (Table 1): Penisola del Sinis-Isola di Mal di Ventre (SN MPA), Capo Caccia-Isola Piana (CI MPA), Isola dell'Asinara (AS MPA), Tavolara Punta Coda Cavallo (TV MPA), and Capo Carbonara (CC MPA). These multiple-use MPAs differ significantly in their establishment dates, in the extension of zones with different degrees of protection (A, B and C zones), in reserve effectiveness and in their management of the sea urchin harvest (Table 1). However, their no-take areas (A zones) have recently shown a higher biomass of commercial fish compared to other protected areas (Natura 2000 sites) or unprotected sites (Guidetti *et al*., 2019). Each MPA management body has authorized a number of fishermen to harvest sea urchins inside the boundaries, therefore affecting pressure on the local *P. lividus* density and territorial use rights, as for example in the SN MPA (Coppa *et al*., 2021) and TV MPA (Table 1). Furthermore, in MPAs where sea urchin harvest is allowed the number of catches is monitored, but the data collected in the logbooks are unfortunately not reliable (*e.g.* Coppa *et al*., 2021). UH sites are located outside the MPAs, where the exploitation of sea urchins is regulated by the regional government, and urchins can be harvested by both professional and recreational fishermen (*i.e.* any permanent resident in Sardinia, is allowed to harvest up to 50 sea urchins per day). Therefore, outside the MPAs, sea urchins can indeed be harvested unrestrictedly, as there are no limits for an overall exploitation (except for the minimum size allowed) and often the only determining restriction on harvesting is the accessibility of sites (Ceccherelli *et al*., 2011).

Data collection

For the spatial evaluation, sampling was done between May 2018 and November 2019 at 106 sites (33, 37, and 36 for NH, RH and UH, respectively). At each site, sea urchin abundance was estimated visually in the field using 1 m^2 frames (randomly placed meters of distance apart) and the size of each individual (test diameter without spines) in the quadrat was measured with callipers to the closest mm. To obtain comparable data, values collected on rocky substratum at a depth of 5 m were selected from the available dataset: this led to dealing with a different number of quadrats (10-30) for each site, for an overall dataset of 886 quadrats.

For the temporal evaluation, only the sites for which past monitoring data (since 2005) were available were considered. Among these, based on the consistency in the methodology used (5m of depth using 1 m^2 quadrat size), 75 could be selected (32, 28, and 15 for NH, RH and UH, respectively).

For both evaluations the short temporal variability due to the month of sampling was neglected and data analyses were done on the average values obtained from quadrats (the sites were replicates). This allowed us to limit the exclusion of data (due to the unbalanced number of replicate quadrats), though it has prevented us from estimating the variability at the scale of the site.

Data analyses

Data were analyzed using univariate permutational analyses of variance based on Euclidean distance measure (Terlizzi et al., 2007; Anderson, 2001). In this analysis, P-values associated with F statistics are obtained by permutation (Clarke and Gorley, 2006). For the spatial evaluation, two one-way univariate permutational analysis of variance (PERMANOVAs) were run to estimate the effects of the harvesting conditions (NH, RH, and UH) on the total and commercial sea urchin abundances where the mean value at each site was used as replicate (n=33, 37, and 36, respectively). *A posteriori*, pair-wise tests were run to identify alternative hypotheses. For the temporal evaluation, a one-way univariate PARMANOVA was run to compare the rate of change in total urchin abundance at the different harvesting conditions (NH, RH, and UH), where the mean change/year at each site was used as replicate (32, 28, and 15, respectively).

The effect of the harvesting conditions was also visually examined by quantifying the natural logarithm of the ratio between the values of each response variable (*i.e* sea urchin total and commercial abundances) at NH and RH conditions versus UH conditions (response ratio ln RR, Micheli *et al*., 2004). With this approach, the observed effect is independent of the absolute abundance at each location. Positive RRs indicate greater values under either NH or RH than in UH conditions, whereas negative values indicate greater values in UH than in protected conditions (NH or RH). A ratio of zero, instead, means that similar values were found between protected and control conditions.

Results

The spatial evaluation has evidenced that *P. lividus* total and commercial abundances were significantly affected by the harvesting conditions, where NH is the condition that promoted the highest response (Fig. 2 and Table 2). Particularly, the lowest density of urchins was found inside the MPAs in the RH, rather than in the NH and UH, while commercial *P. lividus* was differently affected by the harvest: commercial abundance was ranked among harvesting conditions as being highest in the NH and lowest in the RH. In terms of ln RR, both sea urchin variables had a positive response in NH and a negative one in RH conditions (Fig. 3).

The temporal variability in the total urchin abundance has evidenced an overall decrease in sea urchin abundance since 2005 in NH, as well as in RH and UH conditions. This general pattern was derived from a graphical inspection of total urchin abundance in each condition over time (obtained by averaging all data available from all sites sampled), although the sample size has changed considerably (Fig. 4). However, the comparison of the rate of temporal variability in total *P. lividus* abundance (change in # of urchins/yr per site) among conditions has revealed different effects of harvesting conditions. In fact, there has been an overall increase (positive effect) in mean density per year in NH, whereas in RH and UH the urchin abundance has decreased (negative effect) in a similar manner (Table 3 and Fig. 5).

Discussion

A few clear results have been gained from this collaborative database. The spatial evaluation has highlighted differences between harvesting conditions. Although *P. lividus* total abundance is presently higher in NH conditions, evidence gained for RH, where values were even lower than in UH, suggests that the local management of the MPAs has driven the urchin density to be lower than in unprotected areas (UH). Although total urchin abundance was similar in NH and UH, relevant differences were revealed: in fact, the commercial sea urchin abundance was significantly higher in NH than in UH conditions, suggesting a natural predation effect in selecting large-sized individuals where no harvest is allowed (Pessarrodona *et al*., 2019). However, the overall type of RH effect on commercial abundance was again of extreme reduction compared to the other conditions, indicating that RH is the condition where the overall abundance of urchins and the commercial portion have regressed the most. Moreover, the same indication was gained from ln RR, as negative values (for both variables) were only found for the RH condition.

Therefore, the prediction that in RH human predation effects would cumulate with natural predation in RH has been proved true. This finding offers a further example of the unexpected effect of fishing when natural trophic webs are not considered (Scheffer *et al*., 2005). This phenomenon has been observed worldwide (Daskalov, 2002; Loh *et al*., 2015; Stuhldreier *et al*., 2015) and the increase in resource depletion has led to the development of holistic approaches to fisheries management (ecosystem-based fisheries management, Link, 2010) and multispecies models of predation, where trophic pressures vary and the assumption of constant natural mortality is neglected (Jurado-Molina *et al*., 2005; Kinzey and Punt, 2009). Moreover, recent investigations have explicitly highlighted how ignoring natural trophic interactions affects stock assessment model performance and fisheries management (Farina *et al*., 2020; Trijoulet *et al.,* 2020).

Understanding the *P. lividus* spatial variability in Sardinia can be greatly facilitated by the analysis of the change in abundance over time. Indeed, although there were wide differences in the encompassed time, a general overall decreasing pattern was observed. However, the analysis has evidenced that the temporal variability depended on the harvesting conditions, with a decreased rate in RH and UH conditions and an increased rate only at NH. This NH effect provides the precious indication that restrictions (and probably enforcement) allowed *P. lividus* abundance to increase and there are no environmental threats, such as global warming or acidification (Yeruham *et al*., 2015; Asnaghi *et al*., 2013; Asnaghi *et al*., 2020), that can justify the deep change in sea urchins that occurred in RH. Consequently, although context-dependent features related to the site such as nutrient supply, larvae dispersion and substrate characteristics affect sea urchin processes enormously (Pinna *et al*., 2012; Prado *et al*., 2012; Oliva *et al*., 2016), harvest restriction remains the most relevant driver affecting sea urchins.

Furthermore, the deep changes that have occurred over time are worrisome for the species conservation, as the general depletion of urchins may lead to a stable state by triggering some feed-back mechanisms (Filbee-Dexter and Schiebling, 2014; Guarnieri *et al*., 2020). Local density of adult sea urchins depends on the recruitment success and thus it is constrained by natural predation pressure (targeting the small-sized individuals, Guidetti and Sala, 2007). At the same time, recruitment depends on the occurrence of adults (Oliva *et al*.,

2016) and becomes impeded by human harvest (which removes the most effective reproducers, Loi *et al*., 2017). This scenario highlights the need for more in-depth knowledge of the fate of *P. lividus* coastal populations. In fact, although harvest and natural predation affect different portions of the same sea urchin populations, they might also be seen as synergistic pressures on the same resource. Overall, the rate of change in sea urchin density in RH and UH conditions calls for a better management: for the former, by effectively excluding human predation within the MPAs in order to restore the urchin populations, and for the latter, by defining harvest limits for a sustainable exploitation.

The use of MPAs for fisheries management has become popular in the last decades (*e.g.* Pelc *et al*., 2010; Di Lorenzo *et al*., 2020) as they can enhance fishery yield and improve stock sustainability through spillover effects. They increase adult density, and thus the production of eggs and larvae. However, to obtain such goals, an assessment of the spatial distribution of resources such as sea urchins, that have a complex spatial structure, is fundamental for addressing the spatial scales of management (Ouréns *et al*., 2015). Therefore, fishery management failures are often due to a mismatch between the spatial scale of exploited populations and the scale of their management. This might be the case in Sardinia, where wide areas of most of the MPAs (TV, CI and SN) have been offered to the fisheries for several years regardless of the size of the stocks actually available and the identification of metapopulations.

As a matter of fact, many wildlife populations are now well below equilibrium levels in many industrial countries, and humans provide their predominant preying control as food webs are so depleted that natural predators are lacking. However, humans can regulate themselves by defining catch limits, prohibiting the harvest of individuals of a certain size, and restricting hunting seasons. An interesting debate has recently arisen for sea urchins because the demand and economic interest are evidently contrasting with the species conservation and harvest sustainability. Because of the possible cumulating effects of multi predators on urchins, this should only be achieved by considering a stage-structure and predator-urchin modeling (Panja,

2018) in order to provide context-dependent estimates of urchin stock assessment. This would also possibly lead to considering whether setting the threshold size for urchin harvest should depend on the overall sea urchin abundance and population structure (*i.e.* proportion of adults). Efforts addressing such goals should be encouraged to ensure sustainable resource exploitation on the basis of natural mortality, whose rate is expected to increase with reserve effects. Therefore, appropriate conservation measures are needed to contrast unsustainable harvesting, especially where other restrictions are been taken to achieve trophic upgrading.

Conclusions

This study was aimed at estimating the effect of restrictions on the human harvest of the sea urchin *P. lividus.* By a spatial evaluation we tested the hypothesis that sea urchins total and commercial abundances in restricted harvest (RH, inside MPAs) sites were less abundant than those at no harvest (NH, MPA reserves) and unrestricted (UH, outside MPAs) sites because of natural and human predation cumulative effects. Expectations were met and the least sea urchin total and commercial abundances were found in RH sites. Furthermore, by a temporal evaluation, we evidenced the rate of change in sea urchin abundance over time indicating that only NH conditions promoted the increase of sea urchin abundance and that current local management of the MPAs has driven towards a relevant regression of populations. Overall, results suggest that complex mechanisms may occur on sea urchin populations and the assessment of MPA effects on *P. lividus* populations would be crucial to guide management decisions on regulating harvest permits. However, the need to ban sea urchin harvest in the MPAs to avoid extreme reductions is encouraged, as inside the MPAs sea urchin populations are likely under natural predation pressures for the trophic upgrading.

Acknowledgements

None

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32-46.

Asnaghi, V., Chiantore, M., Mangialajo, L., Gazeau, F., Francour, P., *et al*., 2013. Cascading effects of ocean acidification in a rocky subtidal community. *PLoS ONE* 8, *4*.

Asnaghi, V., Chindris, A., Leggieri, F., Scolamacchia, M., Brundu, G., *et al.,* 2020. Decreased pH impairs sea urchin resistance to predatory fish: a combined laboratory-field study to understand the fate of top down processes in future oceans. *Marine Environmental Research* 162, 105194.

Bertocci, I., Dominguez, R., Machado, I., Freitas, C., Domínguez Godino, J., *et al*., 2014. Multiple effects of harvesting on populations of the purple sea urchin *Paracentrotus lividus* in north Portugal. *Fisheries Research* 150, 60-65.

Boada, J., Arthur, R., Farina, S., Santana, Y., Mascaró, O., *et al*., 2015. Hotspots of predation persist outside marine reserves in the historically fished Mediterranean Sea. *Biological Conservation* 191, 67-74.

Boada, J., Arthur, R., Alonso, D., Pagès, J.F., Pessarrodona, A., *et al*., 2017. Immanent conditions determine imminent collapses: nutrient regimes define the resilience of macroalgal communities. *Proceedings of the Royal Society B* 284, 20162814.

Bonaviri, C., Vega Fernández, T., Badalamenti, F., Gianguzza, P., Di Lorenzo, M., 2009. Fish versus starfish predation in controlling sea urchin populations in Mediterranean rocky shores. *Marine Ecology Progress Series* 382, 129-138.

Bonaviri, C., Gianguzza, P., Pipitone, C., Hereu, B., 2012. Micropredation on sea urchins as a potential stabilizing process for rocky reefs. *Journal of Sea Research* 73, 18-23.

Britten, G.L., Dowd, M., Minto, C., Ferretti, F., Boero, F., *et al*., 2014. Predator decline leads to decreased stability in a coastal fish community. *Ecology Letters* 17, 1518-1525.

Carr, M., Reed, D., 2016. Shallow rocky reefs and kelp forests. p. 311-336. In: Ecosystem of California. Mooney, H., and Zavaleta, E. (Eds). University of California Press, Berkeley, California, USA.

Ceccherelli, G., Pinna, S., Sechi, N., 2009. Evaluating the effects of protection on *Paracentrotus lividus* distribution in two contrasting habitats. *Estuarine, Coastal and Shelf Science* 81, 59-64.

Ceccherelli, G., Pais, A., Pinna, S., Sechi, N., Chessa, L.A., 2011. Human impact on *Paracentrotus lividus*: the result of harvest restrictions and accessibility of locations. *Marine Biology* 158, 845-852.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User manual/tutorial. Plymouth, UK: PRIMER+E.

Clemente, S., Hernandez, JC, Montano-Moctezuma, G., Russel, M.P., Ebert, T.A., 2013. Predators of juvenile sea urchins and the effect of habitat refuges. *Marine Biology* 160, 579-590.

Coppa, S., Pronti, A., Massaro, G., Brundu, R., Camedda, A., Palazzo, L., Nobile, G., Pagliarino, E., de Lucia, G., 2021. Fishery management in a marine protected area with compliance gaps: socio-economic and biological insights as a first step on the path of sustainability. *Journal of Environmental Management* 280, 111754.

Daskalov, G.M., 2002. Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology Progress Series* 225, 53-63.

Di Lorenzo, M., Guidetti, P., Di Franco, A., Calò, A., Claudet, J., 2020. Assessing spillover from marine protected areas and its drivers: A meta-analytical approach. *Fish and Fisheries* 21, 906–915.

Di Minin, E., Brooks, T.M., Toivonen, T., Butchart, S.H.M., Heikinheimo, V., *et al*., 2019. Identifying global centers of unsustainable commercial harvesting of species. *Science*

Advances 5(4), eaau2879.

Estes, J., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., *et al*., 2011. Trophic downgrading of planet Earth. *Science* 333, 301-306.

FAO 2016. The State of World Fisheries and Aquaculture*.*

Farina, S., Quattrocchi, G., Guala, I., Cucco, A., 2018. Hydrodynamic patterns favouring sea urchin recruitment in coastal areas: a Mediterranean study case. *Marine Environmental Research* 139, 182-192.

Farina, S., Guala, I., Oliva, S., Piazzi, L., Pires da Silva, R., Ceccherelli, G., 2016. The seagrass effect turned upside down changes the prospective of sea urchin survival and landscape implications. *PLoS ONE* 11(10), e0164294.

Farina, S., Baroli, M., Brundu, R., Conforti, A., Cucco, A., De Falco, G., Guala, I., Guerzoni, S., Massaro, G., Quattrocchi, G., Romagnoni, G., Brambilla, W., 2020. The challenge of managing the commercial harvesting of the sea urchin *Paracentrotus lividus*: advanced approaches are required. *PeerJ* 8, e10093.

Filbee-Dexter, K., Schibling, R.E., 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series* 495, 1-25.

Furesi, R., Madau, F.A., Pulina. P., Sai, R., Pinna, M.G., Pais, A., 2016. Profitability and sustainability of edible sea urchin fishery in Sardinia (Italy). *Journal of Coastal Conservation* 20, 299-306.

Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Science of the United States of America* 107, 286–293.

Giakoumi, S., Cebrian, E., Kokkoris, G.D., Ballesteros, E., Sala, E., 2012. Relationships between fish, sea urchins and macroalgae: The structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. *Estuarine, Coastal and Shelf Science* 109, 1-10.

Giakoumi, S., Scianna, C., Plass-Johnson, J., Micheli, F., Grorud-Colvert, K., *et al*., 2017. Ecological effects of full and partial protection in the crowded Mediterranean Sea: A regional meta-analysis. *Scientific Reports* 7, 8940.

Giakoumi, S., McGowan, J., Mills, M., Beger, M., Bustamante, R.H., *et al*., 2018. Revisiting "success" and "failure" of Marine Protected Areas: a conservation scientist perspective. *Frontiers in Marine Science* 5, 223.

Gianguzza, P., Chiantore, M., Bonaviri, C., Cattaneo-Vietti, R., Vielmini, I., 2006. The effects of recreational *Paracentrotus lividus* fishing on distribution patterns of sea urchins at Ustica Island MPA (Western Mediterranean, Italy). *Fisheries Research* 81, 37-44.

Gianguzza, P., Agnetta, D., Bonaviri, C., Di Trapani, F., Visconti, G., *et al*., 2011. The rise of thermophilic sea urchins and the expansion of barren grounds in the Mediterranean Sea. *Chemistry and Ecology* 27, 129-134.

Guarnieri, G., Bevilacqua, S., Figueras, N., Tamburello, L., Fraschetti, S., 2020. Large-scale sea urchin culling drives the reduction of subtidal barren grounds in the Mediterranean Sea. *Frontiers in Marine Science* 7, 519.

Guidetti, P., 2004. Consumers of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, in shallow Mediterranean rocky reefs. *Helgoland Marine Research* 58, 110-116.

Guidetti, P., 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecological Applications* 16, 963-976.

Guidetti, P., Dulcic, J., 2007. Relationships among predatory fish, sea urchins and barrens in Mediterranean rocky reefs across a latitudinal gradient. *Marine Environmental Research* 63, 178-184.

Guidetti, P., Sala, E., 2007. Community-wide effects of marine reserves in the Mediterranean Sea. *Marine Ecology Progress Series* 335, 43-56.

Guidetti, P., Bussotti, S., Boero F., 2005. Evaluating the effects of protection on fish predators and sea urchins in shallow artificial rocky habitats: a case study in the northern Adriatic

Sea. *Marine Environmental Research* 59, 333-348.

Guidetti, P., Milazzo, M., Bussotti, S., Molinari, A., Murenu, M., *et al*., 2008. Italian marine reserve effectiveness: Does enforcement matter? *Biological Conservation* 141, 699-709.

Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., *et al*., 2014. Large-scale assessment of Mediterranean marine protected areas effects on fish assemblages. *PLoS ONE* 9, e91841.

Guidetti, P., Addis, P., Atzori, F., Bussotti, S., Calò, A., *et al*., 2019. Assessing the potential of marine Natura 2000 sites to produce ecosystem-wide effects in rocky reefs: a case study from Sardinia Island (Italy). *Aquatic Conservation: Marine and Freshwater Ecosystems* 29, 537-545.

Hereu, B., Zabala, M., Linares, C., Sala, E., 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Marine Biology* 146, 293-299.

Hereu, B., Zabala, M., Sala, E., 2008. Multiple controls of community structure and dynamics in a sublittoral marine environment. *Ecology*. 89, 3423-3435.

Hereu, B., Linares, C., Sala, E., Garrabou, J., Garcia-Rubies, A., Diaz, D., Zabala, M.. 2012. Multiple Processes Regulate Long-Term Population Dynamics of Sea Urchins on Mediterranean Rocky Reefs. *PLoS ONE* 7(5), e36901.

Hernández, J.C., Clemente, S., Sangil, C., Brito, A., 2007. Actual status of the sea urchin *Diadema* aff. *antillarum* populations and macroalgal cover in marine protected areas compared to a highly fished area (Canary Islands – eastern Atlantic Ocean). *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 1091-1108.

Jurado-Molina, J., Livingston, P.A., Ianelli, J.N., 2005. Incorporating predation interactions in a statistical catch-at-age model for a predator-prey system in the eastern Bering Sea. *Canadian Journal of Fisheries and Aquatic Science* 62, 1865-1873.

Kinzey, D., Punt, A.E., 2009. Multispecies and single-species models of fish population dynamics: comparing parameter estimates. *Natural Resource Modeling 22*, 67-104.

Ling, S., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., *et al*., 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B* 370, 20130269.

Link, J., 2010. Ecosystem-based fisheries management: Confronting tradeoffs. Cambridge University Press, Cambridge, UK.

Loh, T.L., McMurray, S.S., Henkel, T.P., Vicente, J., Pawlik, J.R., 2015. Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. *PeerJ*. 3, e901.

Loi, B., Guala, I., da Silva, R.P., Brundu, G., Baroli, M., 2017. Hard time to be parents? Sea urchin fishery shifts potential reproductive contribution of population onto the shoulders of the youngest. *PeerJ.* 5, e3067.

Medrano, A., Linares, C., Aspillaga, E., Capdevila, P., Montero-Serra, I., Pagès-Escolà, M., Hereu, B., 2019. No-take marine reserves control the recovery of sea urchin populations after mass mortality events. *Marine Environmental Research* 145, 147-174.

Melis, R., Ceccherelli, G., Piazzi, L., Rustici, M., 2019. Macroalgal forests and sea urchin barrens: structural complexity loss, fisheries exploitation and catastrophic regime shifts. *Ecological Complexity* 37, 32-37.

McClananhan, T.R., Verheij, E., Maina, J., 2006. Comparing the management effectiveness of a marine park and a multiple-use collaborative fisheries management area in east Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16, 147-165.

Micheli, F., Halpern, B.S., Botsford, L.W., Warner, R.R., 2004. Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications* 14, 1709-1723.

Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., *et al*., 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecological Monographs* 75, 81-102.

Oliva, S., Farina, S., Pinna, S., Guala, I., Agnetta, D., *et al*., 2016. Determinants of *Paracentrotus lividus* sea urchin recruitment under oligotrophic conditions: implications for conservation management. *Marine Environmental Research* 117, 13-20.

Ouréns, R., Naya, I., Freire, J., 2015. Mismatch between biological, exploitation, and governance scales and ineffective management of sea urchin (*Paracentrotus lividus*) fisheries in Galicia. *Marine Policy* 51, 13-20.

Pais, A., Chessa, L.A., Serra, S., Ruiu, A., Meloni, G., *et al*., 2007. The impact of commercial and recreational harvesting for *Paracentrotus lividus* on shallow rocky reef sea urchin communities in North-western Sardinia, Italy. *Estuarine, Coastal and Shelf Science* 73, 589-597.

Panja, P., 2018. Stability and dynamics of a fractional-order three-species predator-prey model. *Theory in Biosciences* 138, 251-259.

Pauly, D., Zeller, D., 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications* 7, 10244.

Pelc, R.A., Warner, R.R., Gaines, S.D., Paris, C.B., 2010. Detecting larval export from marine reserves. *Proceedings of the National Academy of Sciences* 107, 18266-18271.

Pessarrodona, A., Boada, J., Pagès, J., Arthur, R., Alcoverro, A., 2019. Consumptive and non-consumptive effects of predators vary with the onthogeny of their prey. *Ecology* 100, e02649.

Piazzi, L., Ceccherelli, G., 2017. Concomitance of oligotrophy and low grazing pressure is essential for the resilience of Mediterranean subtidal forests. *Marine Pollution Bulletin* 123, 197-204.

Piazzi, L., Ceccherelli, G., 2019. Effect of sea urchin human harvest in promoting canopy forming algae restoration. *Estuarine, Coastal and Shelf Science* 219, 273.

Pinna, S., Pais, A., Campus, P., Sechi, N., Ceccherelli, G., 2012. Habitat preferences of the sea urchin *Paracentrotus lividus*. *Marine Ecology Progress Series* 445, 173-180.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., *et al*., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation* 27, 179-200.

Prado, P., Tomas, F., Pinna, S., Farina, S., Roca, G., *et al*., 2012. Habitat and scale shape the demographic fate of the keystone sea urchin *Paracentrotus lividus* in Mediterranean macrophyte communities. *PLoS ONE* 7, e35170.

Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., White, A.T., 2004. Marine reserve benefits local fisheries. *Ecological Applications* 14, 597-606.

Sala, E., Costello, C., Dougherty, D., Heal, G., Kelleher, K., *et al*., 2013. A general business model for marine reserves. *PLoS ONE* 8, e58799.

Scheffer, M., Carpenter, S., de Young, B., 2005. Cascading effects of overfishing marine systems. *Trends in Ecology and Evolution* 20, 579-581.

Seytre, C., Vanderklift, M.A., Bodilis, P., Cottalorda, J.M., Gratiot, J., *et al*., 2013. Assessment of commercial and recreational fishing effects on trophic interactions in the Cap Roux area (north-western Mediterranean). *Aquatic Conservation: Marine and Freshwater Ecosystems* 23, 189-201.

Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predator effects. *Trends in Ecology and Evolution* 13, 350-355.

Stuhldreier, I., Bastian, P., Schönig, E., Wild, C., 2015. Effects of simulated eutrophication and overfishing on algae and invertebrate settlement in a coral reef of Koh Phangan, Gulf of Thailand. *Marine Pollution Bulletin* 92, 35-44.

Terlizzi, A., Anderson, M.J., Fraschetti, S., Benedetti-Cecchi, L., 2007. Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. *Marine Ecology Progress Series* 332, 25-39.

Trijoulet, V., Fay, G., Miller, T.J., 2020. Performance of a state-space multispecies model: what are the consequences of ignoring predation process errors in stock assessments? *Journal* *of Applied Ecology* 57, 121-135.

Willis, T.J., Anderson, M.J., 2003. Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Marine Ecology Progress Series* 257, 209-221.

Yeruham, A., Rilov, G., Shpigel, M., Abelson, A., 2015. Collapse of the echinoid *Paracentrotus lividus* populations in the Eastern Mediterranean: result of climate change? *Scientific Reports* 5, 13479.

Table 1(on next page)

MPA features in terms of: year of establishment and relative zonation (*i.e.* surface covered by different degree of protection); regulation of sea urchin harvest and fishery.

SN: Penisola del Sinis-Isola di Mal di Ventre, CI: Capo Caccia-Isola Piana, AS: Isola dell’Asinara, TV: Tavolara Punta Coda Cavallo and CC: Capo Carbonara. For each MPA the # of NH (no harvest=not allowed) and RH (restricted harvest=allowed, but restricted) sites useful for the current evaluation are also given.

	SN MPA	CI MPA	AS MPA	TV MPA	CC MPA
Year of establishment	1997	2002	1997	1997	1998
Area protected in A zone (Km^2)	3.5	0.4	5.4	5.3	1.0
Area protected in B zone (Km^2)	9.7	4.1	70.2	25.6	16.9
Area protected in C zone (Km^2)	229.2	20.5	32.4	127.9	66.0
Urchin harvest in A zone	NH	NH	NH	NH	NH
Urchin harvest in B zone	NH	RH	NH	RH	NH
Urchin harvest in C zone	RH	RH	NH	RH	NH
# Authorized urchin fishers through years in RH	282 (2005)	--	None	-	None
	276 (2007)	10 (2007)	None	-	None
	184 (2012)	10 (2012)	None	-	None
	119(2015)	10 (2015)	None	17 (2015)	None
	74 (2018)	10 (2018))	None	14 (2018)	None
	40 (2019)	10 (2019)	None	2 (2019)	None
Natural predators fishery in A zone	Not allowed	Not allowed	Not allowed	Not allowed	Not allowed
Natural predators fishery in B zone	Allowed	Allowed	Allowed	Allowed	Allowed
Natural predators fishery in C zone	Allowed	Allowed	Allowed	Allowed	Allowed
# NH sites for the spatial evaluation	6	1	19	2	5
# RH sites for the spatial evaluation	8	9	-	20	-

Table 2(on next page)

Spatial evaluation: PERMANOVA results on the effect of harvest type on total *P. lividus* abundance and commercial abundance. Significant results ($p<0.05$) are given in bold. Harvest: NH=no harvest, RH=restricted harvest and UH=unrestricted harvest.

		Total abundance		Commercial abundance	
	df	MS	Pseudo-F	MS	Pseudo-F
Harvest	2	34.99	**6.71**	12.30	**8.30**
Residual	103	5.21		1.48	
Pair wise tests		NH=UH>RH		NH>UH>RH	

Table 3(on next page)

Temporal evaluation: PERMANOVA results on the effect of harvest type on the variation rate of total *P. lividus* abundance (yr^{-1}). Harvest: NH=no harvest, RH=restricted harvest and UH=unrestricted harvest.

	variation in total abundance			
	df	MS	Pseudo-F	P
Harvest	2	1.51	4.54	**0.014**
Residual	72	0.33		
Pair wise test	NH>RH=UH			

Figure 1

Map of Sardinia Island with zonation in the studied MPAs. CI: Capo Caccia-Isola Piana, AS. Isola dell’Asinara, SN: Penisola del Sinis-Isola di Mal di Ventre, TV: Tavolara Punta Coda Cavallo, CC: Capo Carbonara.

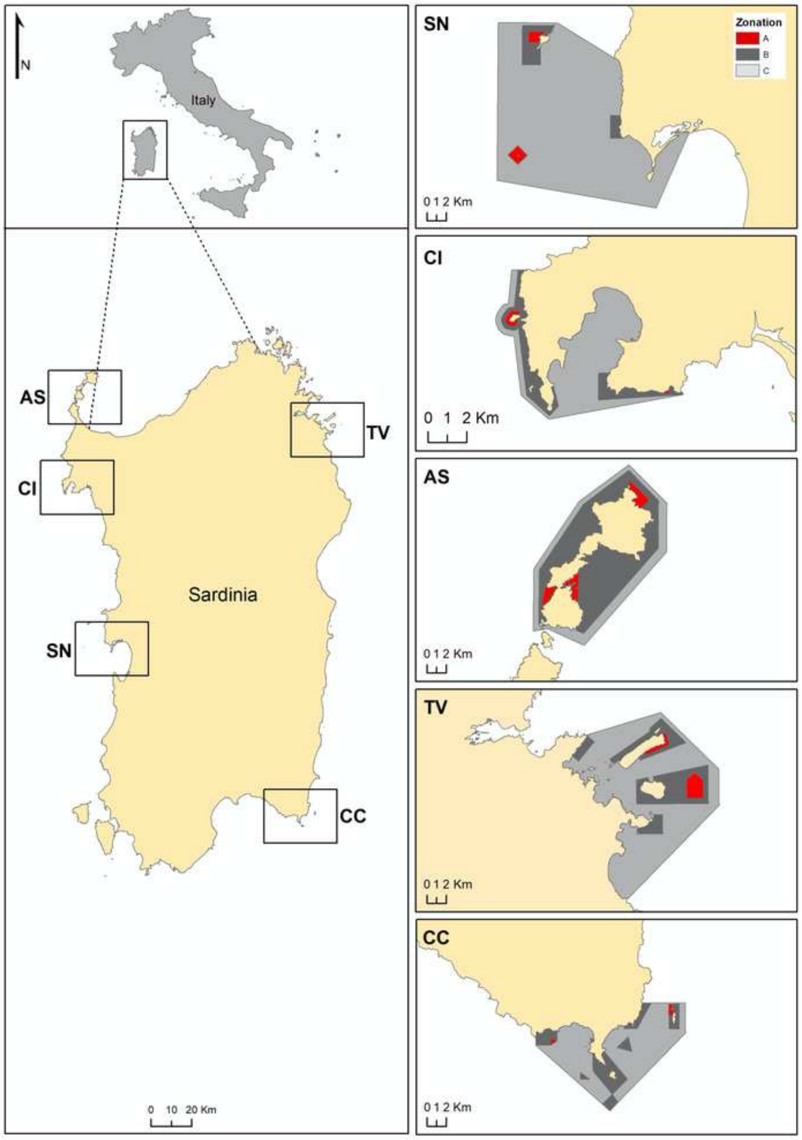
N
Italy
AS
TV
CI
Sardinia
SN
CC
0 10 20 Km
SN
Zonation
A
B
C
0 1 2 Km
CI
0 1 2 Km
AS
0 1 2 Km
TV
0 1 2 Km
CC
0 1 2 Km

Figure 1

Figure 2

Paracentrotus lividus. A) total and B) commercial abundance (mean+SE) at the NH (no harvest), RH (restricted harvest) and UH (unrestricted harvest) sites (n=33, 37, and 36, respectively).

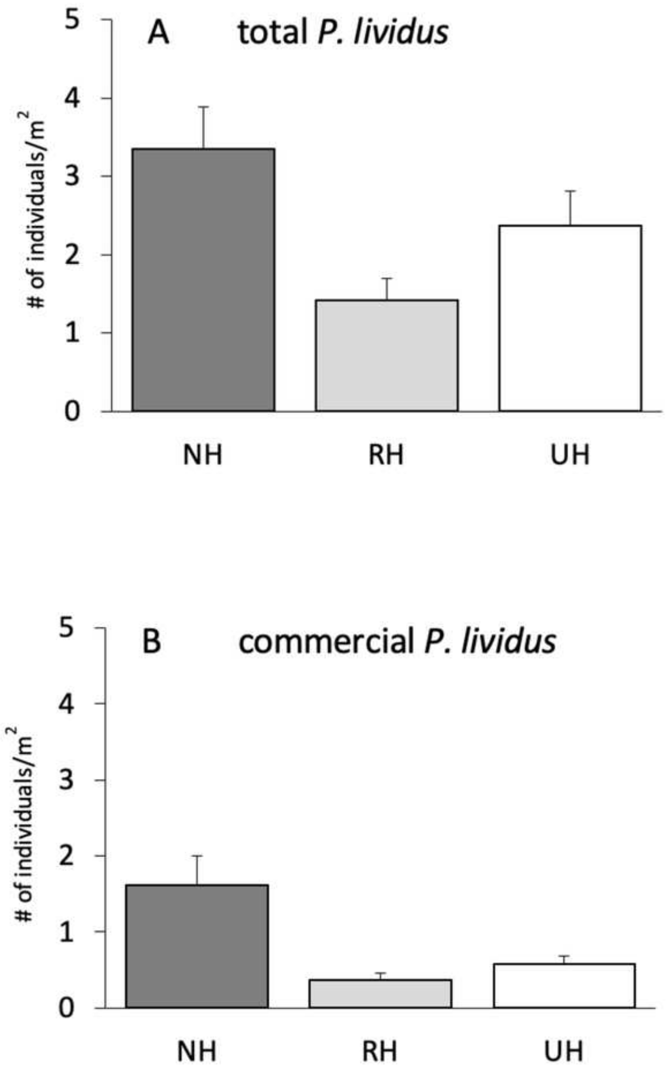
A total *P. lividus*
B commercial *P. lividus*
# of individuals/m²
0
1
2
3
4
5
NH
RH
UH

Figure 2

Figure 3

Paracentrotus lividus. Variability in the response of total abundance (solid) and commercial abundance (striped) to no harvest (NH) and restricted harvest (RH) conditions.

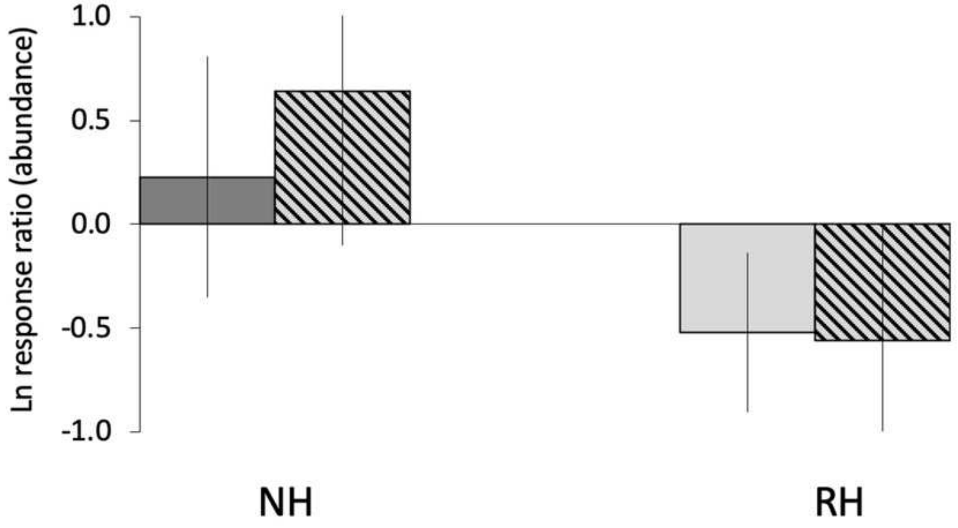

Figure 3

Figure 4

Paracentrotus lividus. Temporal variability in total abundance/m^2 at NH=no harvest, RH=restricted harvest and UH=unrestricted harvest conditions.

Numbers at the bottom of the histograms indicate the number of sites from which the mean (and SE) was calculated.

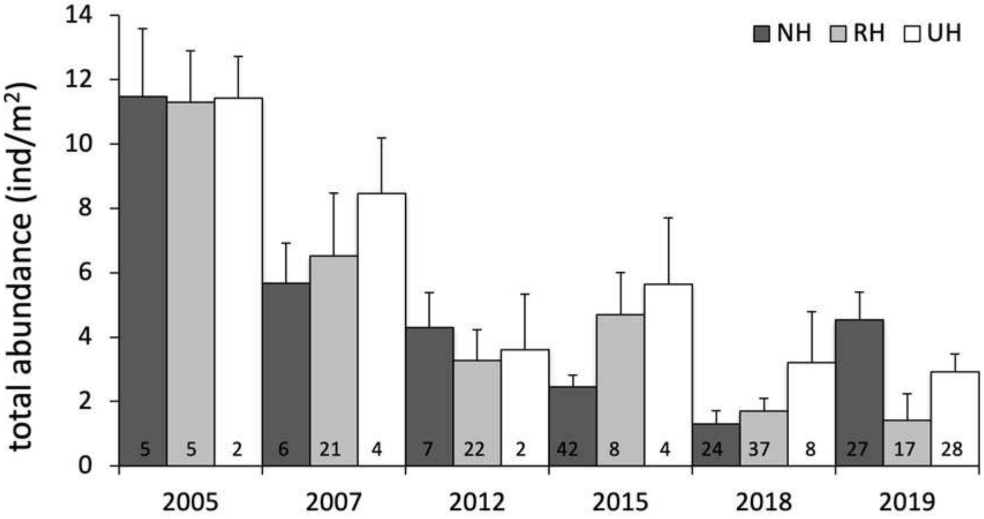
14
12
10
8
6
4
2
0
total abundance (ind/m²)
NH
RH
UH
5
5
2
6
21
4
7
22
2
42
8
4
24
37
8
27
17
28
2005
2007
2012
2015
2018
2019

Figure 4

Figure 5

Paracentrotus lividus. Rate of variation (mean+SE change in abundance of individuals/m^{2}yr) at NH (no harvest), RH (restricted harvest) and UH (unrestricted harvest) conditions (n=27, 28, and 13, respectively).

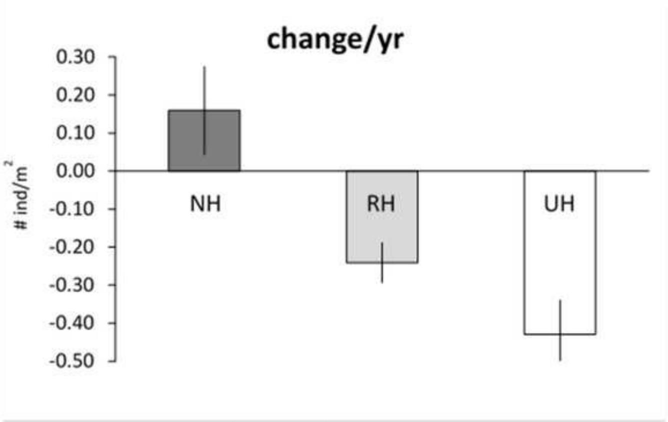

Figure 5