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Distribution of sea urchin barrens in shallow algal communities along the eastern Adriatic coast

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Abstract

The sea urchins *Paracentrotus lividus* and *Arbacia lixula* are important herbivores in algal communities of the infralittoral rocky bottoms in the Mediterranean Sea. However, grazing by sea urchins that outweighs natural algal recruitment processes might result in the formation of barrens, which are areas dominated by urchins and coralline algae. We present the results of the first large-scale mapping of sea urchin barrens and analyses of sea urchins' impact on the main algal communities across 1955.5 km of rocky coastline on the eastern side of the Adriatic Sea (Croatia). Since mapping was performed over a geographically wide area and covered a representative quantity of approximately 40% of the coastline of the central part of the Adriatic Sea, the results could be considered to reflect the general situation in that area of the eastern Adriatic coast. Mapping revealed that sea urchin barrens are present along over 35% of the coastline, while the complete absence of algal cover was recorded in 8% of the inspected area. Communities with canopy-forming algae, which are the most valuable shallow-water communities of the Mediterranean Sea, represent the largest proportion of the observed coastline and are affected by sea urchins in over 28% of their extent. Among other factors, the extensive harvesting of date mussels (*Lithophaga lithophaga*) in the 1970s, 1980s, and early 1990s is likely one of the main activities that resulted in exceptional sea urchin expansion via the removal of micropredators and establishment of shelters for subadult urchins.

Keywords: sea urchins; *Paracentrotus lividus*; *Arbacia lixula*; sea urchin barrens; algal communities; Adriatic Sea.

Introduction

Sea urchins are one of the most important herbivores in shallow algal communities worldwide and serve an important role in shaping the shallow benthic communities of rocky reefs (Paine & Vadas, 1969; Bulleri *et al.*, 1999; Ling *et al.*, 2015). The ecology of such communities, including their algal composition, can be disrupted if grazing by sea urchins outweighs natural algal recruitment and growth processes. This can result in a habitat shift from photophilic biocenoses rich in erect algal species to habitats dominated by encrusting coralline algae, known as sea urchin barrens (Lawrence, 1975; Harrold & Pearse, 1987; Pearse, 2006). Barrens are typically inhabited by dense populations of one or two sea urchin species, mainly represented by individuals of smaller body size, and overall biodiversity is low with a complete absence of erect algae (Ling & Johnson, 2009; Filbee-Dexter & Scheibling, 2014). The degraded state of a rocky reef community can remain stable for long periods, sometimes over decades, due to several mechanisms that prevent recovery of the algae, most notably continuous grazing by sea urchins (Knowlton, 2004; Gagnon *et al.*, 2004; Wright *et al.*, 2005). Additionally, sea urchin barrens are suitable sites for the settlement of new sea urchin larvae due to the lack of micropredation, which significantly affects their settlement in well-developed algal communities (Bonaviri *et al.*, 2012). However, a decline in sea urchin density due to factors such as disease, storms, predation, human harvesting and culling, among others, can lead to the recovery of the reef community that had developed prior to the barren state (Ebeling *et al.*, 1985; Leinaas & Christie, 1996; Scheibling *et al.*, 1999; Lafferty, 2004; Guarnieri *et al.*, 2020; Miller *et al.*, 2022). Most investigated sea barrens occur in kelp grounds along temperate coastlines worldwide, and were often caused by the overgrazing of sea urchins belonging to two genera: *Strongylocentrotus* and *Centrostephanus* (Sala *et al.*, 1998; Steneck *et al.*, 2002; Filbee-Dexter & Scheibling, 2014).

Although information on the mechanisms leading to the formation of barrens within the Mediterranean Sea remains scarce, human activities such as date mussel (*Lithophaga lithophaga*) harvesting, the overfishing of species that prey on sea urchins, the spread of invasive species, and climate change could act as triggers for the development of barren states (Guidetti *et al.*, 2003; Guidetti & Dulčić, 2007; Guidetti, 2011; Gianguzza *et al.*, 2011; Giakoumi, 2014; Ling *et al.*, 2015).

In the Mediterranean Sea, several sea urchin species are commonly found in infralittoral rocky bottoms, where they feed on various algal species; however, two species are responsible for the formation of sea urchin barrens: *Paracentrotus lividus* (Lamarck, 1816) and *Arbacia lixula* (Linnaeus, 1758). Both species are widely distributed in the Mediterranean Sea and the Adriatic Sea (Zavodnik & Šimunović, 1997). While *P. lividus* serves an important role in creating barren grounds, especially in *Cystoseira* canopies, *A. lixula* serves an important role in maintaining a barren state (Bonaviri *et al.*, 2011; Agnetta *et al.*, 2015). Although barrens seem to be widely present along the Mediterranean coast, little information is available on their spatial extent.

Along the eastern coast of the Adriatic Sea, which is mostly rocky, algal infralittoral communities with canopy-forming algae are typical communities of the photophilic bottoms (Pérès & Gamulin Brida, 1973). They have been placed on the European Red List of Habitats and listed as one of the most important habitats, forming extended canopies rich in biodiversity and serving as important refugia and subsistence areas for many organisms (Cheminée *et al.*, 2013; Gubbay *et al.*, 2016).

Since 2010, Croatia has been continuously monitoring the ecological status of its water bodies according to the Water Framework Directive (Council Directive 2008/56/EC 2008). One of the biological quality elements for coastal water bodies is macroalgae, which are monitored using the CARLIT (cartography of littoral rocky-shore communities) method, developed for monitoring shallow rocky reef communities (Ballesteros *et al.*, 2007; Nikolić *et al.*, 2013). During the implementation phase, when the CARLIT method was applied on 300 km of coastline, it was determined that 23% of the investigated coastline was severely impacted by sea urchin overgrazing (Nikolić *et al.*, 2013). Since 2011, we have applied the CARLIT method on a wide coastal area of Croatia while also collecting data on sea urchin barrens. Based on this spatially extensive mapping, the current study presents an assessment of the extent of sea urchin barrens as well as the impacts of sea urchins on the main shallow rocky communities along the Croatian portion of the Adriatic Sea coastline. We also discuss possible factors that might be connected to the formation of the extensive sea urchin barrens that we recorded.

Materials and Methods

To assess the quantitative extent of the sea urchin barrens and their qualitative impact on the algal community, a total of 1955.5 km of rocky coastline was mapped at depths of between around 0 and 3 m during the spring season from 2011 to 2021 along the Croatian portion of the central Adriatic Sea (hereafter: central Adriatic Sea) (Fig. 1).

Mapping of the sea urchin barrens was performed

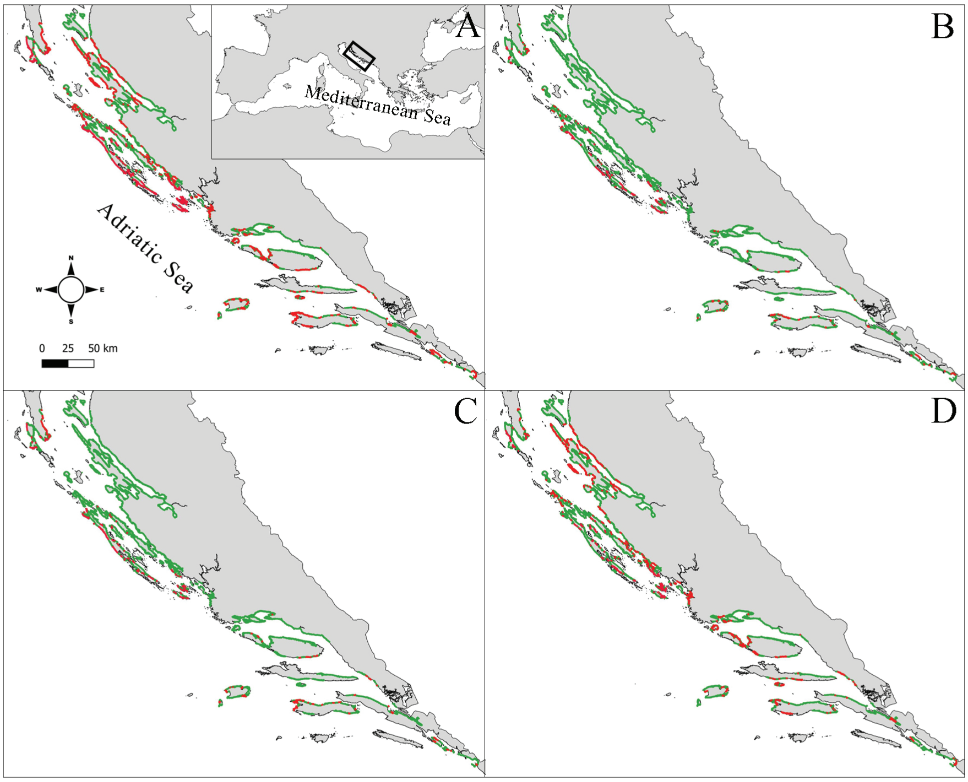

Fig. 1: Coastline investigated in this study to determine the quantitative extent of different sea urchin barren categories. A. Green line – coastline without sea urchin impact; red line – coastline with sea urchin impact (including all three categories of barrens). B. Green line – coastline without Category 1 sea urchin barrens; red line – coastline with Category 1 sea urchin barrens. C. Green line – coastline without Category 2 sea urchin barrens; red line – coastline with Category 2 sea urchin barrens. D. Green line – coastline without Category 3 sea urchin barrens; red line – coastline with Category 3 sea urchin barrens.

along with the implementation of the Water Framework Directive for the biological quality element macroalgae using the CARLIT method. The CARLIT method is based on observations of shallow-water benthic communities (from 0 to approximately 1 m depth) that are consequently ecologically validated and used for the assessment of coastal water quality (Ballesteros *et al.*, 2007).

Mapping was performed from a rubber boat (length: 3.8 m), which was driven slowly close to the shore. To ensure good visibility of the sea bottom, research was performed during calm weather. Data collection was only performed, where possible, along the rocky coastline that extends to a bottom depth of at least 3 m. However, due to the varying sea bottom topography, in some cases of wide areas with shallow waters, we only considered the part of the sea bottom that could be observed from the boat when driven close to shore. Tidal oscillations in the area of observation were minimal, and rarely above 0.5 m (Buljan & Zore-Armanda, 1971).

The presence and categories of sea urchin barrens were noted on printed Google maps (1:15000 scale). Due to the inability to distinguish sea urchin species (*P. lividus* and *A. lixula*) from the boat, the impacts of both species were considered cumulatively.

The quantitative impact of sea urchins, which represents the spatial extent of their barrens, was visually assessed and mapped as an average along 50-m-long sections of coastline at depths of between 0 and 3 m. This coastal segment represents the minimum length of assessment in the CARLIT methodology and was also applied in our study. The extent of barrens was defined using three categories:

Category 1 - patches of bare rocks with sea urchins covering less than 30% of the surface within the algal community along the assessed length of coastline;

Category 2 - bare rocks with sea urchins covering 30–60% of the surface within the algal community along the assessed length of coastline;

Category 3 - bare rocks with sea urchins covering more than 60% of the surface within the algal community along the assessed length of coastline.

The total length of coastline of each impact category was expressed as a percentage of the entire mapped coastline.

Regarding qualitative analyses of the impact, data on observed community type highlighted a parallel with mapping of the quantitative extent of sea urchin barrens when using the same methodology. We distinguished four community types: photophilic non-canopy-forming algae; photophilic canopy-forming algae; sciaphilic non-canopy-forming algae; "other communities" (e.g., port communities, undetermined community types, or communities not based on algae).

The quantitative and qualitative impacts of sea urchins on each of the three algal communities were analyzed separately, while "other communities" were not considered.

All field data were stored and analyzed in a GIS database (Oracle 12 with Locator Extension), and visualizations of the results were created using the GeoServer map server and the OpenLayers framework.

In terms of algal classification and nomenclature, we followed the current taxonomic arrangement of AlgaeBase (Guiry & Guiry, 2023).

Results

Based on the field mapping of sea urchin barrens over 1955.5 km along the investigated coastline in Croatia, we determined the quantitative (spatial) and qualitative impacts (on different algal communities) of the sea urchins.

The extent of the most severe impact (Category 3) encompasses 21%, while Categories 2 and 1 represent 8 and 6% of the mapped coastline, respectively (Fig. 1B-D, Table 1). Considering all three categories cumulatively, sea urchin barrens are present on 35% of the mapped coastline (Fig. 1A).

Considering each of the algal communities separately, the largest impact within a community (41%), including all of the impact categories, was detected in photophilic algal communities composed of non-canopy-forming algae. A nearly equal percentage of the impacted coastline length has communities with photophilic canopy-forming algae (28%) and communities with sciaphilic non-canopy-forming algae (27%) (Table 2).

Communities with canopy-forming algae, including protected algae from the genus *Cystoseira sensu lato* (*Gongolaria barbata* (Stackhouse) Kuntze, *Cystoseira compressa* (Esper) Gerloff & Nizamuddin, *Cystoseira corniculata* (Turner) Zanardini, *Cystoseira crinitophilla* Ercegović, and *Cystoseira spicata* Ercegović), represent

Table 1. Extents of coastline under different categories of barrens along the investigated coastline (total: 1955.5 km) of the central Adriatic Sea. Category 1 – patches of bare rocks with sea urchins covering less than 30% of the surface within the algal community along the assessed length of coastline; Category 2 – bare rocks with sea urchins covering 30–60% of the surface within the algal community along the assessed length of coastline; Category 3 – bare rocks with sea urchins covering more than 60% of the surface within the algal community along the assessed length of coastline.

Total observed coastline:		**1955.5 km**	
Observed coastline impacted by sea urchin grazing	Category 1	124.3 km	6%
	Category 2	154.0 km	8%
	Category 3	418.1 km	21%
	Sum of all categories	696.4 km	35%

Table 2. Total coastline extent of each algal community and their proportions under sea urchin impact (including all three categories of barrens) along the investigated coastline (total: 1955.5 km) of the central Adriatic Sea.

Algal community	Total extent (km)	Total extent under barrens (km)	Proportion under barrens (%)
Photophilic non-canopy-forming algae	709.2	288.6	41
Photophilic canopy-forming algae	840.5	232.0	28
Sciaphilic non-canopy-forming algae	78.9	21.7	27

the largest proportion of the observed coastline, with a total of 840.5 km (Table 2).

The area of coastline with a complete absence of algal cover due to extensive overgrazing was recorded as 150.4 km, which represents 8% of the mapped coastline. Due to a complete lack of algal cover, we were unable to link any of the communities and perform an impact assessment of those parts of the coastline. The remaining length of 176.5 km, which was not included within the combined totals of the three algal communities and total overgrazed area, represents the proportion of "other communities," which are not considered in the quality assessment.

Since our mapping has covered spatially different and extensive areas, the presented results reflect the general situation in the central area of the eastern Adriatic coast. In total, we mapped approximately 40% of the considered area.

Discussion

The rocky coast of the eastern Adriatic Sea represents the best possible substrate for the extensive development of shallow photophilic communities with canopy-forming algae, such as *Cystoseira s.l. and Sargassum* spp. It is one of the most valuable but also highly vulnerable shallow-water Mediterranean communities (Gubbay *et al.*, 2016). This community used to be present along 60% of the observed coastline (both rocky and non-rocky) during assessments conducted in the 1960s along 1300 km of the Croatian coastline (Špan, 1969). This is the first investigation since then, which has shown that –similar to other regions in the Mediterranean Sea– this section of the coastline has been dramatically deteriorating due to many different impacts (Thibaut *et al.*, 2005; Tamburello *et al.*, 2022).

Based on the present study, sea urchin expansion is likely the most important deteriorating factor since it has a dramatic effect on algal communities on a wide spatial scale in the rocky eastern Adriatic Sea. We have demonstrated that along more than one-third of the observed coastline at depths of 0 to 3 m, sea urchins have developed barrens. The deterioration of benthic communities, which was classified as Category 3 (bare rocks with sea urchins covering more than 60% of the surface), is present along 21% of the inspected coastline.

Compared to the situation during the 1960s, the deterioration of the photophilic canopy-forming algae community is obvious (43 *vs.* 60% of the coastline). Since nearly one-third (28%) of this community is now degraded by various extents of overgrazing by sea urchins (Table 2), only 31% of the remaining inspected coastline might be considered an area with a photophilic canopy-forming algae community that has no detectable sea urchin impact. Interestingly, a study conducted in the 1960s did not make any remarks regarding the impact of sea urchins along the 60% of the coastline occupied by photophilic canopy-forming algae at the time (Špan, 1969).

Contrary to the overall presence of sea urchins in the central Adriatic, along the western Istrian coast (North Adriatic, Croatia), sea urchins were considered rare in research conducted during the 2010-2013 period (Iveša *et al.*, 2016). Only in the southern part of the Istrian Peninsula were higher densities of sea urchins observed together with the appearance of barrens, which were absent or in low abundance along the central and northern parts of the peninsula. Barrens are most commonly formed by *P. lividus*, while *A. lixula* is generally a rare species in the northernmost part of the Adriatic (Zavodnik & Šimunović, 1997), and was found in small quantities and only in a few areas along the southern part of the Istrian Peninsula (Iveša *et al.*, 2016).

In the central Adriatic Sea, different algal assemblages are not equally affected by sea urchins (Table 2). The communities of photophilic non-canopy-forming algae are the most impacted, with a total of 41% of the coastline under this type of community being affected. Notably, communities dominated by *Cystoseira s.l.* (canopy-forming algae) showed greater resilience to sea urchin grazing (Table 2). This is likely due to food preferences since *Cystoseira s.l.* seems to be less preferred when compared to algae with soft thalli (Tsiaga *et al.*, 1998). In fact, sea urchins in *Cystoseira s.l.* communities first consume the lower algal layer and branches of the Fucales; thus, only the main axes of those algae remain on the completely overgrazed bare rock (personal observation).

Several factors are likely responsible for such dense and widespread sea urchin settlements along the central Adriatic Sea. Among the globally recognized mechanisms that might control or reduce the sea urchin population density (Boudouresque & Verlaque, 2001; Uthicke *et al.*, 2009; Hereu *et al.*, 2012; Yeruham *et al.*, 2015; Iveša *et al.*, 2016; Miller *et al.*, 2022), some have more important roles, such as the depletion of sea urchin predators, harvesting of date mussels leading to habitat modification and the concurrent removal of micropredators. Additionally, the traditional avoidance of sea urchin consumption and minimal interest in their commercial exploitation (until recently) have also influenced the situation.

As a possible factor in reducing species abundance, the commercial fishing of sea urchins is not as intense in Croatia as it is in some Mediterranean countries, where *P. lividus* is an important commercial species that is harvested for its gonads (Keesing & Hall, 1998). In many harvesting sites throughout the Mediterranean, commercial sea urchin species, especially *P. lividus*, are in significant decline (Boudouresque & Verlaque, 2001; Pais *et al.*, 2007). Notably, removing sea urchins from algal communities can lead to their recovery (Bulleri *et al.*, 1999; Miller *et al.*, 2022). This could be a possible scenario in Croatia since the commercial harvesting of *P. lividus* has been increasing over the last few years and is expected to increase further. Another problem is the size of individual *P. lividus* in the barrens –especially in completely overgrazed areas– which are mostly under the *minimum* allowable size for capture (personal observation). Therefore, such areas are not of interest for professional harvesting. Moreover, such a barren state dominated by encrusting coralline algae and small sea urchins may persist for decades (Filbee-Dexter & Scheibling, 2014).

Another species abundant in the central part of the eastern Adriatic coast, *A. lixula*, is not of commercial interest and thus may not be controlled by commercial harvesting. The increase in global sea temperature also has a positive effect on the abundance of this thermophilic species (Francour *et al.*, 1994; Guidetti & Dulčić, 2007).

One activity that could have resulted in sea urchin expansion along the eastern Adriatic coast is the date mussel fishery. This fishery was widespread and intense in the area of investigation in the 1970s, 1980s, and early 1990s, until the legal protection of this species in 1994. Although violations of the law continue to occur in this regard (Devescovi & Iveša, 2008; personal observation), the extent of harvesting is incomparable to the period before protection, when it was a legal fishery activity. There is not a square meter of shallow rocky bottom around populated areas that has not been physically damaged by date mussel harvesting. Date mussel fishermen were able to collect over 15 kg/day in one dive in areas rich with this species (personal communication). Harvesting of this species was also allowed as part of recreational fishing. Collecting date mussels was an almost traditional activity during leisure time on the sea in Croatia, which stands in stark contrast to the almost total avoidance of sea urchin consumption. Date mussel collection resulted in the tremendous direct morphological and biological devastation of the rocky coastline but also indirectly affected sea urchin expansion. The connection between date mussel harvesting, increased sea urchin settlement, and the appearance of barrens was previously observed on the Italian coast (Guidetti *et al.*, 2003). Here, we assume that the removal of sea urchin micropredators during the date mussel harvesting process was the underlying mechanism of this connection. Namely, a well-developed algal community is inhabited by numerous small invertebrates but also small fishes, particularly labrids. Small fishes, together with micropredators mainly composed of small crustaceans, consume newly settled sea urchins after their larval planktonic stage, thereby limiting their proliferation (Kabasakal, 2001; Bonaviri *et al.*, 2012). The extensive harvesting of date mussels led to a change in habitat and subsequent trophic cascade due to the drastic removal of algal cover, consequently resulting in the removal of associated fauna (Fanelli *et al.*, 1994). Sea urchin larvae might have settled and thrived at increased densities within such predator-free benthic environments.

The removal of date mussels leaves empty holes in stones, which are optimal nursery sites for subadult sea urchins (Guidetti, 2011), providing them with protection during growth from larger predators such as sparid fish (*Diplodus* spp.) and sea stars *Marthasterias glacialis* (Guidetti, 2004; Bonaviri *et al.*, 2009). Additionally, during the period of intense mussel harvesting, sparids were also overfished (Stagličić *et al.*, 2011), while sea stars have never been abundant and also became heavily collected by tourists (personal observation). In this manner, date mussel harvest zones have become a core zone for sea urchin expansion into adjacent areas with healthy algal communities. In the barren areas with well-established adult sea urchin populations, recruitment is even more successful due to their protection behavior since older and larger sea urchins serve as a physical shelter for juveniles to hide from predators (Sala *et al.*, 1998). Abundant sea urchin populations also generate more larvae, which will consequently increase the likelihood of their successful settlement and the formation of new barren areas.

The impoverishment of shallow-water algal communities, especially those with canopy-forming algae, in the central part of the eastern Adriatic Sea, must be seriously considered. Following degradation, natural recovery can take decades due to low dispersal capacity (Riquet *et al.*, 2021).

Apart from the effects of sea urchins, these communities are also threatened by pollution, eutrophication, shoreline construction (including the development of gravel beaches over initially rocky bottoms), and the spread of alien species.

Shallow-water algal communities serve as nursery grounds for many species of littoral fishes, including those of commercial interest (Cheminée *et al.*, 2013). The deterioration of the photophilic canopy-forming algae community, rich in terms of its number of species (Ballesteros, 1990a, b; Cheminée, 2013; Bedini *et al.*, 2014), must have profound negative impacts on shallow-water biodiversity overall.

Some of the *Cystoseira s.l.* species that develop only in the zone impacted by sea urchins are strictly protected under Annex I of the Bern Convention, while the Barcelona Convention's Mediterranean Action Plan identifies the conservation of all but one species as a priority. The photophilic community with canopy-forming algae is listed in the European Red List of Habitats. Many of the impacted and degraded sites are part of the Natura 2000 protected network, with this community representing a component of the reef habitat type according to the

EU Habitats Directive. Considering what has occurred in the northwestern Mediterranean –and what is likely to occur in many other areas of the Mediterranean where communities composed of the genus *Cystoseira s.l.* are now virtually gone (Thibaut *et al.*, 2005; Tamburello *et al.*, 2022)– Croatia and the European Union have a responsibility to undertake actions that should protect the remaining shallow-water forests. Notably, the culling of sea urchins can be considered the most efficient method available due to its high efficiency and relatively low cost (Guarnieri *et al.*, 2020).

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