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A natural population of the European flat oyster (*Ostrea edulis* Linnaeus, 1758) in the northern Adriatic Sea: Changes over time and restoration potential

Daria EZGETA-BALIĆ[1], Ratko CVITANIĆ[1,2], Nedo VRGOČ[1], Damir MEDVEŠEK[1], Jelena NEJAŠMIĆ[1,2], Melita PEHARDA[1], Barbara ZORICA[1], Nika STAGLIČIĆ[1], and Niko BUJAS[1,2]

[1]Institute of Oceanography and Fisheries, Split, Croatia
[2] Faculty of Science, University of Zagreb, Zagreb, Croatia

Corresponding author: Ratko CVITANIĆ; cvitanic@izor.hr

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Abstract

The European flat oyster (*Ostrea edulis* Linnaeus, 1758) is a native bivalve of high ecological and economic importance in European marine ecosystems. Overexploitation, combined with widespread disease outbreaks in the 1970s, has caused a severe decline throughout its historical range, leaving many populations critically depleted or functionally extinct. This study assesses the status of remnant natural *O. edulis* populations inhabiting deeper subtidal habitats (~30 m depth) in the northern Adriatic Sea, a region where *O. edulis* was abundant until relatively recently but has shown a pronounced decline over the last decade. We combined an extensive literature review with field surveys using beam trawl sampling and observations from a remotely operated vehicle (ROV). Analyses focused on oyster distribution, biomass indices, natural settlement substrates, and associated macrobenthic communities. Our results indicate a substantial decline in *O. edulis* biomass over the past decade, although small remnant populations persist within the study area. ROV surveys conducted at sites where fishing pressure has been eliminated, including historically abundant grounds, reveal no clear signs of population recovery. These findings suggest that reduced fishing pressure alone is insufficient to restore *O. edulis* populations. The results highlight the need for coordinated, region-wide monitoring and emphasise the importance of habitat availability, recruitment dynamics, and interactions with local aquaculture practices when developing effective conservation and restoration strategies for *O. edulis* in the Adriatic Sea.

Keywords: *Ostrea edulis*; European flat oyster; Adriatic Sea; Population status; Subtidal habitat; Conservation ecology; Oyster beds; Biomass indices.

Introduction

The European flat oyster (*Ostrea edulis* Linnaeus, 1758) is a native bivalve species of high ecological and economic importance across European marine ecosystems and exists in aquaculture and natural populations. In its natural habitat, *O. edulis* acts as an ecosystem engineer, forming complex reef structures that provide habitat for numerous marine organisms. These reefs enhance local biodiversity, serve as nursery grounds for fish and invertebrates, and improve water quality through filtration (Pogoda *et al.*, 2019). Historically, the species has been widespread throughout European seas, from Norway to Morocco along the Atlantic coast and throughout the Mediterranean Sea to the Black Sea, where it was abundant in coastal and sublittoral waters (Kerckhof *et al.*, 2018; Pogoda *et al.*, 2019; Hayer *et al.*, 2021; Thurstan *et al.*, 2024; zu Ermgassen *et al.*, 2025). Within this broad range, *O. edulis* occupies diverse habitats, from the lower intertidal zone to subtidal depths of ~80 m (Perry & Jackson, 2017). However, this important fishery resource has experienced a significant decline across most of its range, and some regional populations are now severely depleted and even functionally extinct. The observed decline over the past century is due to multiple, often interacting, factors, including disease, overfishing, habitat degradation, and pollution (Helmer *et al.*, 2019; Pouvreau *et al.*, 2023; Thurstan *et al.*, 2024; zu Ermgassen *et al.*, 2025). Natural populations have been subjected to intense fishing pressure because *O. edulis* has a high market value and is viewed as a delicacy.

A large disease outbreak in the 1970s, associated with the parasites *Marteilia refringens* Grizel, Comps, Bonami, Cousserans, Duthoit, and Le Pennec, 1974 and *Bonamia ostreae* Pichot, Comps, Tigé, Grizel, and Rabouin, 1980, had significantly negative impact on *O. edulis* populations (Gosling, 2008; Beck *et al.*, 2011; Helmer *et al.*, 2019). These parasites devastated wild and cultured *O.*

edulis, with bonamiosis causing up to 90% mortality in infected groups (Culloty & Mulcahy, 2007). The parasites continue to affect natural populations today. Some *O. edulis* beds now show degrees of innate resistance after decades of exposure, whereas others remain vulnerable (Vera *et al.*, 2019). Although recent research has focused more on Atlantic populations, Mediterranean populations face similar conservation challenges, with ongoing threats from overfishing, habitat degradation, water contamination, disease, and inadequate management. To mitigate commercial losses from parasite-induced mortality, the Pacific oyster (*Magallana gigas* (Thunberg, 1793), formerly *Crassostrea gigas*) was introduced into European aquaculture in 1970s, and its production has steadily increased since then (Gosling, 2008). The presence of *O. edulis* adults in aquaculture contributes to the wild *O. edulis* population, as larvae settle naturally. Replacing *O. edulis* with another species could further reduce the supply of *O. edulis* larvae in the environment, particularly given the high recorded larviphagy of *M. gigas* (Ezgeta-Balić *et al.*, 2020).

Despite the occurrence of disease in the Mediterranean, *O. edulis* aquaculture has persisted in Croatia, where it retains cultural and economic significance. Historically, cultivated populations in the eastern Adriatic Sea have benefited from the absence of the major *O. edulis* parasites that drove stock collapses in northern Europe during the late 1960s and 1970s, mostly due to a ban on spat imports from Western Europe (Horvath *et al.*, 2013). Nowadays, *O. edulis* is cultivated at several locations along the Croatian part of the eastern Adriatic coast, with the main production areas located in Lim Bay, Medulin Bay, the Krka River estuary, and Mali Ston Bay. Although production remains relatively modest compared to other European countries, a clear upward trend has been observed in recent years. Production increased from approximately 52 tonnes in 2015 to around 93 tonnes in 2023. Despite these comparatively low quantities, especially when contrasted with leading producers such as France (approximately 1,254 tonnes), available data indicate that Croatia currently ranks as the fifth largest producer of *O. edulis* in the European Union (EU), following France, Ireland, Spain, and the Netherlands (Eurostat, 2026).

The Adriatic Sea represents one of the regions where *O. edulis* natural populations persist (Cocci *et al.*, 2020; Stagličić *et al.*, 2020). Nevertheless, Mediterranean populations are not entirely free from disease: *B. ostreae* and *Bonamia exitiosa* Hine, Cochennec-Laureau, and Berthe, 2001 have been documented in the Adriatic since the 1990s in natural populations along the central and southern parts of the western Adriatic coast (Narcisi *et al.*, 2010; Cocci *et al.*, 2020), as well as in cultivated populations along the northern and central eastern Adriatic coast (Oraić *et al.*, 2021). Preliminary parasite analyses from natural populations in the Croatian northern Adriatic Sea were negative for *B. ostreae*, *B. exitiosa*, and *M. refringens* (Ezgeta-Balić, unpublished data).

While aquaculture populations have been relatively well studied in the Croatian Adriatic region, little is known about the status, distribution, and ecological characteristics of natural *O. edulis* populations in the Adriatic Sea. Early studies primarily provided qualitative observations, indicating that populations were sparse and of low economic importance (Morović, 1959; Grubišić, 1967, cited in Hrs-Brenko, 1974; Hrs-Brenko, 1974, 1979). Historical records also suggest a decline of once locally abundant populations, such as those in the Karin Sea, likely due to overexploitation and environmental changes. Although the species has been reported in several areas of the Adriatic Sea (e.g., Legac & Hrs-Brenko, 1982; Bolotin *et al.*, 1993), these studies generally lack quantitative data. More recent work by Peharda *et al.* (2010) provided quantitative insights, showing that *O. edulis* occurs at various locations along the eastern Adriatic coast but at low densities with a highly patchy distribution, even within small geographic areas such as Kaštela Bay (maximum observed biomass was 72.06 g m^{-2}, with a density of 2.027 individuals m^{-2}). However, their survey employed a hydraulic dredge designed primarily to catch infaunal soft-bottom bivalves, so the data for *O. edulis* should be considered indicative rather than definitive. Overall, available evidence indicates that natural *O. edulis* populations in the Adriatic are poorly characterised. Despite sporadic references confirming their presence, systematic research on their abundance, spatial structure, and ecological status remains largely absent, underscoring a major knowledge gap in the understanding of wild *O. edulis* resources in the region.

On the Croatian Adriatic coast, the species is harvested by scuba divers, and there is also a large fishing ground offshore of western Istria, where beam trawlers ("rampon") operate. Ten years ago, Croatia was the leading EU member for *O. edulis* harvest, peaking at 513 tonnes per year in 2015 – nearly the entire EU catch (Fig. 1). However, Croatian landings declined sharply in subsequent years, falling to less than 20 tonnes by 2024. Over the same period, catches in Denmark, Ireland, Italy, and France increased but varied over the years. In 2024, Italy reported the highest recorded catch (~150 tonnes), followed by Ireland (~70 tonnes), Spain (~40 tonnes), and France (~35 tonnes) (Eurostat, 2025). Fishing activities are often considered one of the main drivers of oyster-reef declines in several regions. Historically, Croatian aquaculture production has satisfied local demand, so natural *O. edulis* populations were less exploited. However, following Croatia's accession to the EU, access to the wider EU market increased demand, leading to more intensive harvesting of natural populations. The decreases recorded over the past decade (Ezgeta-Balić *et al.*, 2021) raise concerns about the status and prospects for the conservation and restoration of wild *O. edulis* populations.

This study focused on natural *O. edulis* populations inhabiting deeper subtidal grounds (~30 m) in the northern Adriatic Sea. Although these populations have long represented a rare example of persistence in the region, recent observations indicate a marked decline in abundance over the past decade. The primary objective of this research was to assess the status of these natural populations and to evaluate temporal changes over the last two decades, based on available historical data combined with

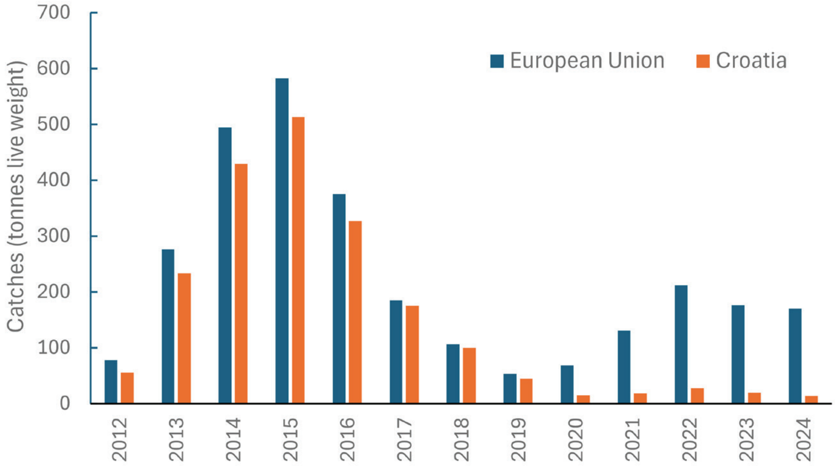

Fig. 1: Officially reported annual catches of *Ostrea edulis* in the European Union and Croatia (Eurostat, 2025).

new field observations. By addressing a critical knowledge gap regarding deep subtidal populations, this study aimed to provide a scientific basis for informed management, conservation, and potential restoration measures for *O. edulis* in the Adriatic Sea.

Material and Methods

Distribution and biomass indices of O. edulis *– beam-trawl surveys*

Beam-trawl surveys were carried out in the Croatian northern Adriatic Sea (Fig. 2A), specifically within fishing zone A and a small part of zone H – areas where beam-trawl fishing is permitted (Official Gazette 48/2015, 12/2016; Suppl. Fig. S1). The dataset includes *O. edulis* catch data collected on several occasions from 2008 to 2024 and comprises two distinct subsets: (i) catches obtained during commercial beam-trawl fishing activities (2008 and 2013) and (ii) catch collected during targeted scientific surveys (2017–2018 and 2022–2024). In both cases, scientists were onboard and analysed catches according to the protocol described below.

In the survey area, the beam trawl primarily targets scallops, oysters, common sole, other flatfishes, and cephalopods such as cuttlefish and musky octopus (Ezgeta-Balić *et al.*, 2021). The 2008 and 2013 samples were collected on fishing grounds chosen by fishers during routine commercial trips, whereas the scientific surveys were conducted at stations selected by researchers to meet specific research objectives. The survey conducted in 2017–2018 aimed to assess differences in the catch composition of beam-trawl fisheries between areas where this gear is permitted and nearby areas where it is prohibited, considering different distances from the coastline (for more details, see Ezgeta-Balić *et al.*, 2021). For the purposes of the present study, only *O. edulis* data were extracted from both commercial fishing trips by onboard scientific observers. The 2022–2024 surveys focused explicitly on *O. edulis*, aiming to cover a broader geographic area to gain better insight into the distribution of this species. Considering the different aims of the surveys conducted prior to 2022 and those conducted during 2022–2024, which were designed to cover a broader geographical range and assess the current distribution and presence of *O. edulis*, the study had limitations in terms of direct spatial comparisons. Beam trawl surveys are subject to methodological constraints, including variable weather conditions affecting tow direction, other fishing or transport activities in the area, and underwater structures that may damage gear or reduce sampling efficiency and therefore need to be avoided. Despite these limitations, the survey still provided valuable and generally comparable information on species occurrence and distribution patterns across the study area. Although data were collected under commercial and scientific settings, the same gear type, mesh size, and onboard sampling protocol were applied across all sampling occasions, ensuring methodological consistency.

All trawling was performed by a commercial vessel equipped with a two-beam trawl fitted with 40-mm diamond mesh (80-mm stretched mesh). Table 1 summarises the main characteristics of the sampling dynamics and the hauls. The haul duration varied based on the catch amount, the technical limitations of the vessel, and the seabed characteristics, but commercial hauls in this area typically last 20–30 min. For each haul, the start and end position (latitude, longitude), depth, haul duration, and vessel speed were recorded. In total, 252 hauls were analysed (43 in 2008, 62 in 2013, 60 in 2017 and 2018, and 87 in the period 2022–2024). All sampling locations are shown in Figure 2B.

After each haul, the catch was sorted on deck, and all commercially important species, including *O. edulis*, were separated. Shell length was measured to the nearest millimetre with digital callipers, and whole-animal mass was recorded to the nearest gram with an electronic scale (in 2024) or total biomass of the species per haul was measured (all other sampling occasions). All *O. edulis* specimens collected during the scientific surveys were returned to the sea immediately after measurement. To ensure comparability among sampling periods, all catch data were standardised to biomass per unit area (kg km^{-2}). Biomass was standardised to area using a swept-area method. Vessel speed was converted from nautical miles per hour (kn) to kilometres per hour (km h^{-1}). The swept

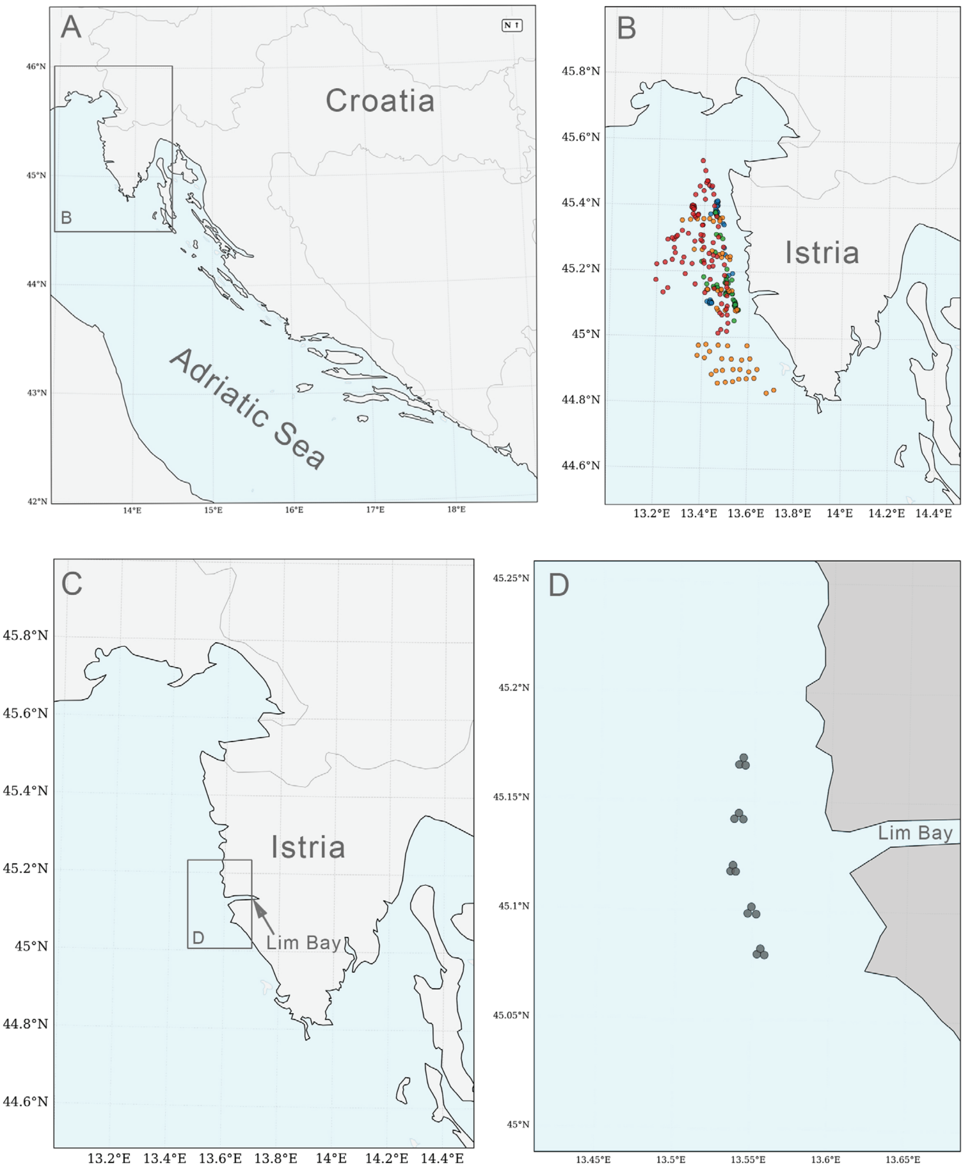

Fig. 2: The study areas and sampling design in the northern Adriatic Sea. (A) Location of the survey area. (B) The beam-trawl sampling stations. The dots indicate surveys conducted in 2008 (blue), 2013 (green), 2017–2018 (orange), and 2022–2024 (red). (C) Remotely operated vehicle (ROV) survey area. (D) Spatial distribution and location of the ROV transects.

Table 1. Specifications of beam-trawl hauls (mean ± standard deviation) conducted during various surveys in the northern Adriatic Sea from 2008 to 2024.

	2008	**2013**	**2017–2018**	**2022–2024**
Survey type	Regular fishing activity	Regular fishing activity	Scientific survey	Scientific survey
Sampling season	Jun (3 days)	Apr/Jun/Aug/Dec (total of 4 days)	Oct (2 days per year)	May/Jun (total of 6 days)
Speed (kn)	4.0 ± 0.2	3.9 ± 0.1	5.2 ± 0.4	4.6 ± 0.5
Duration (min)	20 ± 3	24 ± 7	11 ± 4	22 ± 5
Haul length (km)	2.6 ± 0.4	2.9 ± 0.9	1.7 ± 0.7	3.1 ± 0.9

area (A) for each haul was calculated as:

$$A = v \times t \times w,$$

where v is vessel speed (km h^{-1}), t is haul duration (h), and w is the beam trawl width (expressed in km). Biomass per unit area was then calculated by dividing the total catch biomass (wet weight) by the estimated swept area. In addition to calculating the exact biomass per unit area, stations were grouped into the following categories: 0.1–50.0 kg km^{-2}; 50.1–200.0 kg km^{-2}; 200.1–500.0 kg km^{-2}; 500.1–1000.0 kg km^{-2}; 1000.1–3000.0 kg km^{-2}; and >3000 kg km^{-2}.

Additional analyses were conducted during the 2024 survey. Most of the specimens collected during this survey were single, independent individuals. To determine the substrate or object to which these individuals were attached, each specimen was examined. The attachment substrate was determined visually onboard immediately after collection. When the attachment substrate was clearly identifiable, it was recorded to the lowest possible taxonomic level (e.g., oysters, scallops). Specimens attached to bivalve shells of unidentified origin were classified as "other bivalves." If oysters were detached or the attachment substrate could not be determined, they were classified as "other."

Remotely operated vehicle (ROV) survey of O. edulis *distribution*

To assess the present status of *O. edulis* on grounds that were highly productive in 2013 but are now closed to beam-trawl fishing, a ROV survey was conducted in October 2024. A QYSEA FIFISH E-MASTER NAVI ROV, fitted with 10,000-lumen LED lights and a 4K camera (1/1.8″ sensor, 146° field of view), was deployed at five sites selected from historical abundance records. At each site, three 200-m transects approximately 1 m wide were filmed at a depth of 20-30 m (Fig. 2B and D). Video footage from every transect was analysed, and the presence or absence of *O. edulis* was noted.

Biodiversity of benthic and fish communities in the study area

To assess potential differences in benthic community composition in relation to *O. edulis* population density, macrozoobenthos discarded from the beam trawl was subsampled at 10 selected stations during the 2024 survey. At each station, approximately 6 kg of macrozoobenthos was randomly subsampled from the beam-trawl catch and analysed (except one station where a larger subsample was processed). Each subsample was sorted to the lowest practicable taxonomic level, and abundance and biomass were determined for each taxon. To allow comparisons among stations, abundance and biomass data for all macrozoobenthic taxa were standardised to a 6-kg sample. Differences in macrozoobenthic community composition, in terms of biomass and abundance, were tested using one-way analysis of similarity (ANOSIM) (PRIMER Plymouth Marine Laboratories, UK; Clarke & Warwick, 1994) after square root transformation of the data, with the *O. edulis* biomass index as the factor. Based on the *O. edulis* biomass index at each station, three categories were defined: (i) *O. edulis* absent; (ii) biomass index between 0.1 and 50.0 kg m^{-2}; and (iii) biomass index between 50.1 and 200.0 kg m^{-2} (in 2024, biomass remained below 200 kg km^{-2} at all stations). For all sampling stations, the entire beam-trawl commercial catch was analysed, whereby all commercially important species from the entire catch were identified and their total biomass measured.

Results

Distribution and biomass of O. edulis *– beam trawl survey*

The four sampling periods differed in survey context and sampling effort yet together allowed an assessment of the spatial distribution and biomass of *O. edulis* in the study area. In 2008, 43 stations were sampled during commercial beam-trawl activities, with *O. edulis* absent at 32 stations (Fig. 3A). When present, the biomass ranged 1.27–460.63 kg km^{-2}. Biomass ranged 0.1–to 50.0 kg km^{-2} at most stations where *O. edulis* was present, while only two stations had biomass in the range of 200.1–500.0 kg km^{-2}.

In 2013, 62 stations were sampled during commercial fishing, and *O. edulis* was recorded at all locations (Fig. 3B). Biomass ranged 19.64–3937.97 kg km^{-2}, indicating a generally higher abundance compared to 2008. Most stations exhibited biomass between 200 and 3,000 kg km^{-2}, including 23 stations in the 500–1,000 kg km^{-2} range and 24 stations in the 1,000–3,000 kg km^{-2} range. Only two stations had biomass below 50 kg km^{-2}, and five stations exceeded 3,000 kg km^{-2}.

During the 2017–2018 scientific survey, 60 stations were sampled, and *O. edulis* was absent from 33 stations (Fig. 3C). At stations where *O. edulis* was present, biomass ranged 1.24–294.71 kg km^{-2}. In 2017, in an area where beam-trawl fishing is permitted, *O. edulis* biomass was generally low to moderate, with values below 50 kg km^{-2} at eight stations, 50–200 kg km^{-2} at nine stations, and 200–500 kg km^{-2} at four stations. No biomass values exceeded 500 kg km^{-2}. In contrast, the 2018 survey, conducted in an area where beam-trawl fishing is prohibited, recorded *O. edulis* at lower biomass levels. Of the 27 sampled stations, biomass was below 50 kg km^{-2} at three stations and between 50 and 200 kg km^{-2} at two stations, with no stations exceeding 200 kg km^{-2}.

The 2022–2024 surveys focused specifically on *O. edulis* and included 87 stations. *Ostrea edulis* was absent from 27 stations (five in 2022, 12 in 2023, and 10 in 2024), while biomass at the other stations ranged 0.34–583.63 kg km^{-2} (Fig. 3D). Biomass levels varied among years: in 2022, values ranged from less than 50 to 200 kg km^{-2}; in 2023, biomass reached higher levels, includ-

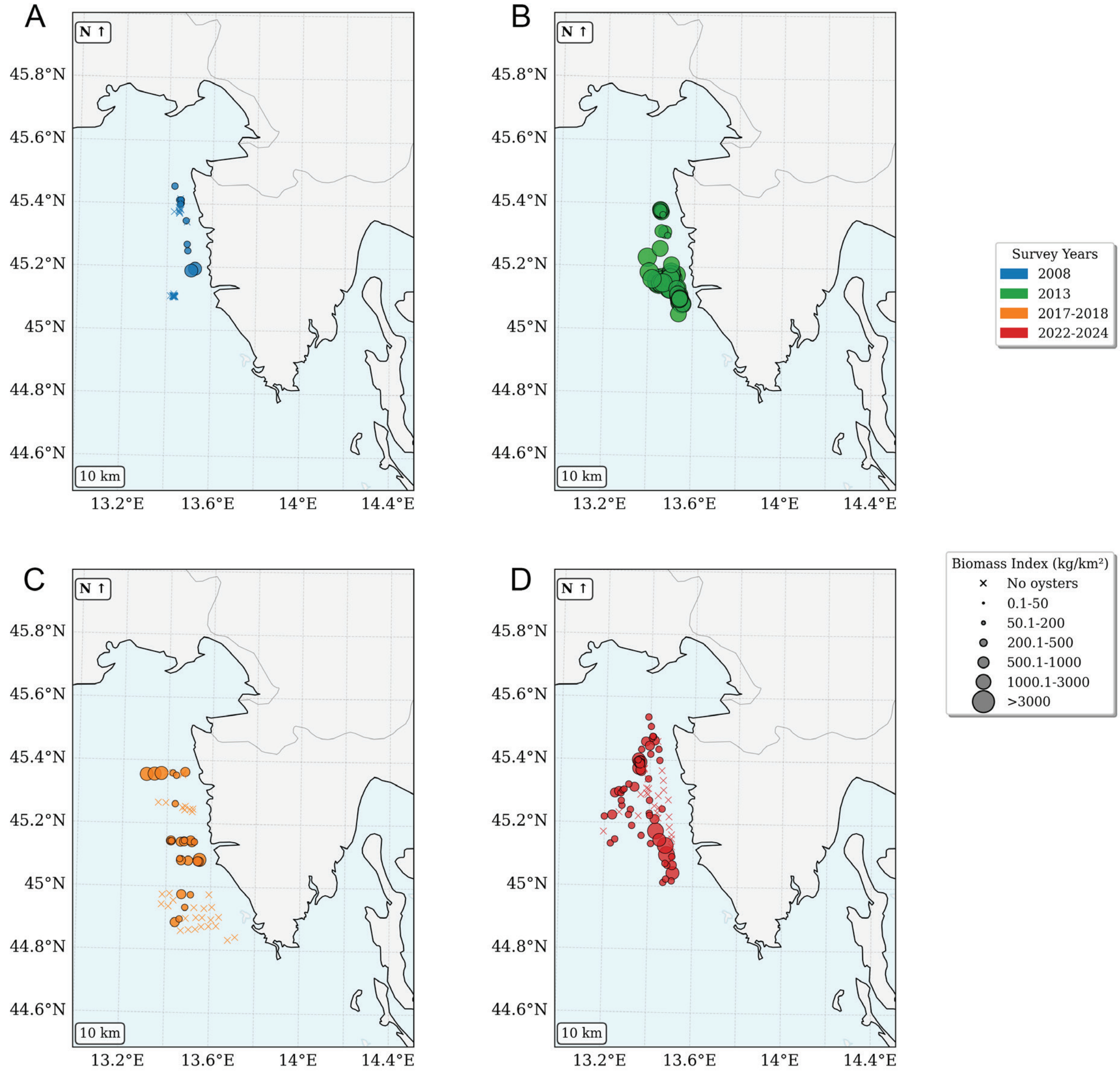

Fig. 3: *Ostrea edulis* biomass indices from surveys conducted in (A) 2008, (B) 2013, (C) 2017–2018, and (D) 2022–2024.

ing stations with 200–500 kg km^{-2} (at five stations) and 500–1,000 kg km^{-2} (at three stations); in 2024, biomass remained below 200 kg km^{-2} at all stations.

Despite differences in survey design across years, the use of standardised sampling protocols allowed for a general comparison of trends over time. Overall, the results indicated pronounced interannual and spatial variability in the occurrence and biomass of native *O. edulis* populations, with the highest biomass observed in 2013.

The size distribution of *O. edulis* specimens during the 2022–2024 surveys is shown in Figure 4. The mean (± standard deviation) shell length was 66.2 ± 13.3 mm in 2022, 73.2 ± 11.4 mm in 2023, and 70.6 ± 20.1 mm in 2024.

Distribution of O. edulis *– ROV survey*

The ROV survey from areas where fishing activities had not been conducted for several years revealed no visible presence of *O. edulis*, either as individual specimens emerging from the sediment or as oyster clumps. Overall, the video footage showed predominantly soft-bottom sediments with low benthic biodiversity, with some locations dominated by species of Ophiuroidea (Fig. 5).

O. edulis *settlement substrates under natural conditions*

A total of 150 live *O. edulis* were examined settlement substrate (Fig. 6). Most individuals (n = 78) were attached to the shells of the queen scallop (*Aequipecten opercularis* (Linnaeus, 1758)). In four instances, the scallop was still alive, while all other *O. edulis* were attached to empty shells. Tewnty-four individuals were attached to variegated scallops [*Mimachlamys varia* (Linnaeus, 1758)], one of which was alive. Fewer *O. edulis* were settled on other bivalve shells, including conspecific oyster shells (n = 6), pen shells (n = 5), and one unidentified bivalve shell. In 36 cases, the attachment substrate could not be determined.

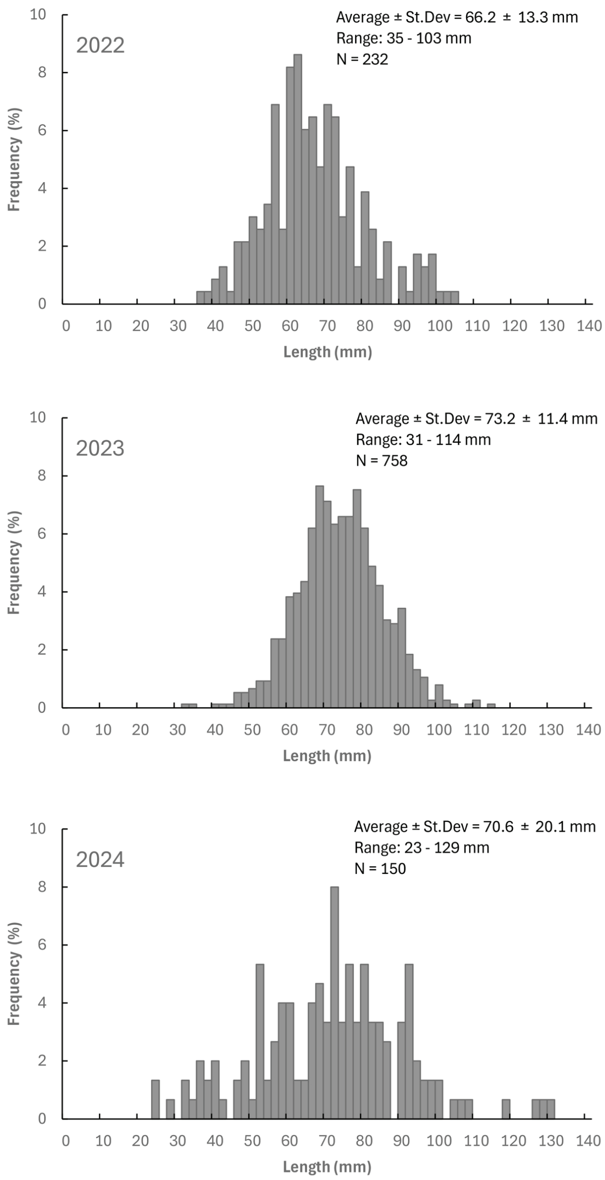

Fig. 4: Length distribution of *Ostrea edulis* during the survey period 2022–2024 in the northern Adriatic Sea.

Biodiversity of macrozoobenthos, cephalopods, and fish communities in the study area

Analysis of the macrozoobenthos at 10 stations revealed a total of 68 species comprising 16 Echinodermata, 19 Mollusca, 12 Arthropoda, 11 Porifera, two Annelida, seven Tunicata, and one1 Cnidaria (Suppl. Table S1). The primary aim of the macrozoobenthos analysis was to investigate whether community composition differed in areas with varying *O. edulis* abundance. However, none of the micro-locations met the criteria for oyster reefs during the survey, so the stations were compared based solely on the three predefined ranges of the *O. edulis* biomass index. The ANOSIM revealed no significant differences in macrozoobenthos community composition relative to the *O. edulis* biomass index, neither for macrozoobenthos biomass (Global R = −0.249, p = 0.973) nor abundance (Global R = −0.281, p = 0.992).

Across the entire study area, the commercial beam-trawl catch included 15 fish species, four mollusc species, and two crustacean species. The species exhibiting the highest abundance and biomass were the common sole (*Solea solea* Linnaeus, 1758) and the Mediterranean scallop (*Pecten jacobaeus* Linnaeus, 1758). As the primary aim of this study was not to investigate the composition of commercial species, only summary data are provided in Supplementary Table S2.

Discussion

The present study provides new insights into the occurrence and spatial distribution of *O. edulis* in offshore areas of the Croatian northern Adriatic coast. The Adriatic Sea still represents a region where this native bivalve species is considered generally widespread, yet it remains poorly documented. Despite its long history in local aquaculture and fisheries, little is known about the abundance, population structure, or long-term dynamics of natural *O. edulis* populations in the eastern Adriatic Sea. Thurstan *et*

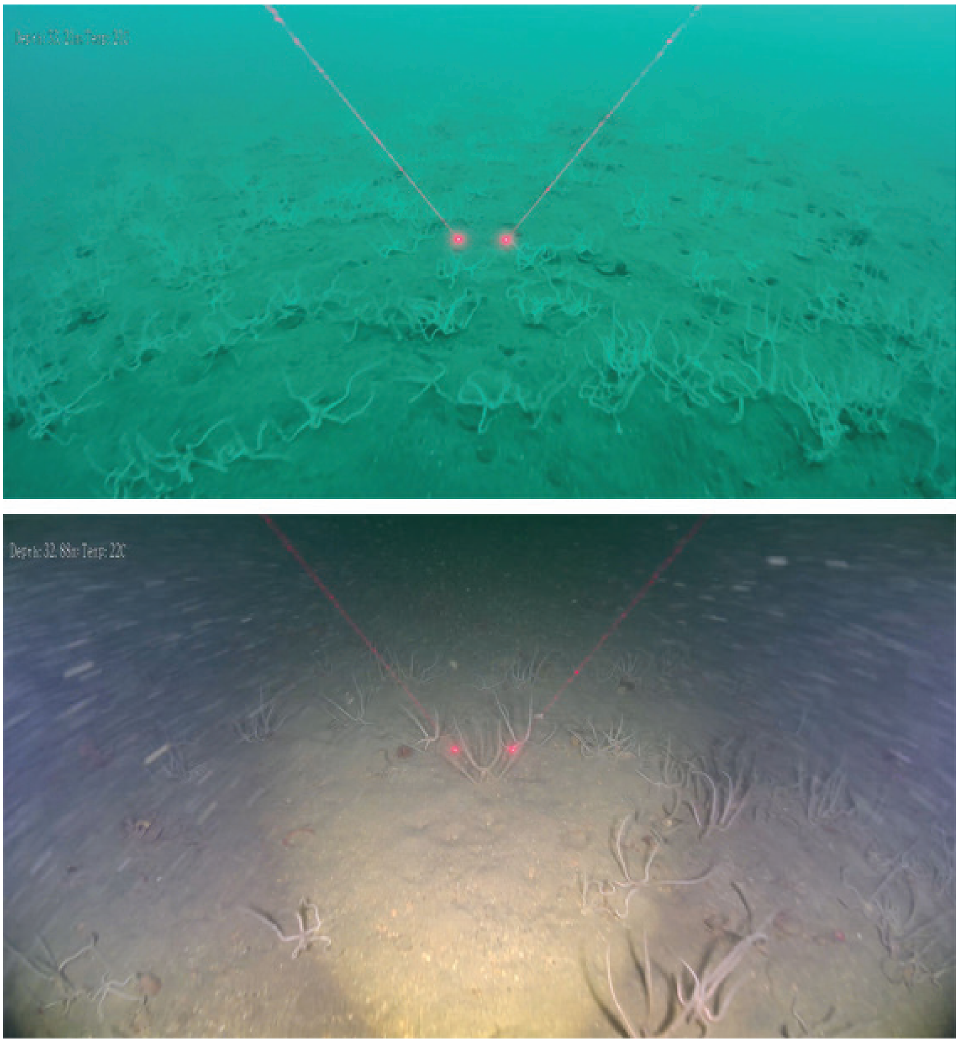

Fig. 5: Seafloor imagery acquired by a remotely operated vehicle in the study area of the northern Adriatic Sea. Photo credit: Daria Ezgeta-Balić.

al. (2024) also confirmed the lack of data for the eastern Adriatic coast: their literature review indicated there are only sporadic records of *O. edulis* on the Croatian Adriatic coast. Based on historical sources, there are only two locations for which there is high confidence regarding the presence of oyster reefs – one in the northern Adriatic region and one in the middle Adriatic region – although the possible size of these reefs remains unknown. Furthermore, several additional locations in the middle and central Adriatic regions showed the possible presence of oyster reefs, but with low confidence. However, the offshore region of the Croatian northern Adriatic coast was not identified as an area of historical oyster-reef presence, whereas the present study suggests that *O. edulis* were present in this region relatively recently. Notably, Thurstan *et al.* (2024) suggested high confidence in the presence of historical reefs along the Italian coast of the northern Adriatic Sea. Photo credit: Daria Ezgeta-Balić., with some reefs extending several kilometres in length. This confirms that the northern Adriatic Sea was historically suitable for supporting dense populations of *O. edulis*.

Moving from the historical context to the present, there was an evident pattern of decrease in many European *O. edulis* populations (Tully & Clarke, 2012; Thorngren *et al.*, 2019; zu Ermgassen *et al.*, 2025). A pronounced decline in the presence and abundance of *O. edulis* driven by intensive exploitation has been reported in many other regions (e.g., Smyth *et al.*, 2009). Spatial differences in *O. edulis* distribution in the northern Adriatic Sea are not solely related to fishing activities, as low abundance of *O. edulis* has also been recorded in non-fishing areas (Ezgeta-Balić *et al.*, 2021). Nevertheless, the observed decrease in abundance within beam-trawl fishing areas is likely related to high catches recorded over the past decade (Fig. 1, Eurostat, 2025). Although a sharp decrease in *O. edulis* biomass across the survey area has been evident since 2013, direct comparisons of abundance and biomass at specific locations over time are not entirely possible. Nevertheless, official catch statistics support the conclusion that this species is currently less abundant in the region than in the past. A comparison of biomass data from the northernmost survey location in 2008 and 2013 indicates that areas where *O. edulis* was absent or with a low biomass index in 2008 supported a higher biomass index in 2013. This pattern may suggest that *O. edulis* settled in this region during the past two decades; however, due to the lack of historical data, this interpretation remains speculative. Additionally, the inherently patchy distribution of oysters (Thorngren *et al.*, 2017) further limits the ability to draw broad-scale conclusions.

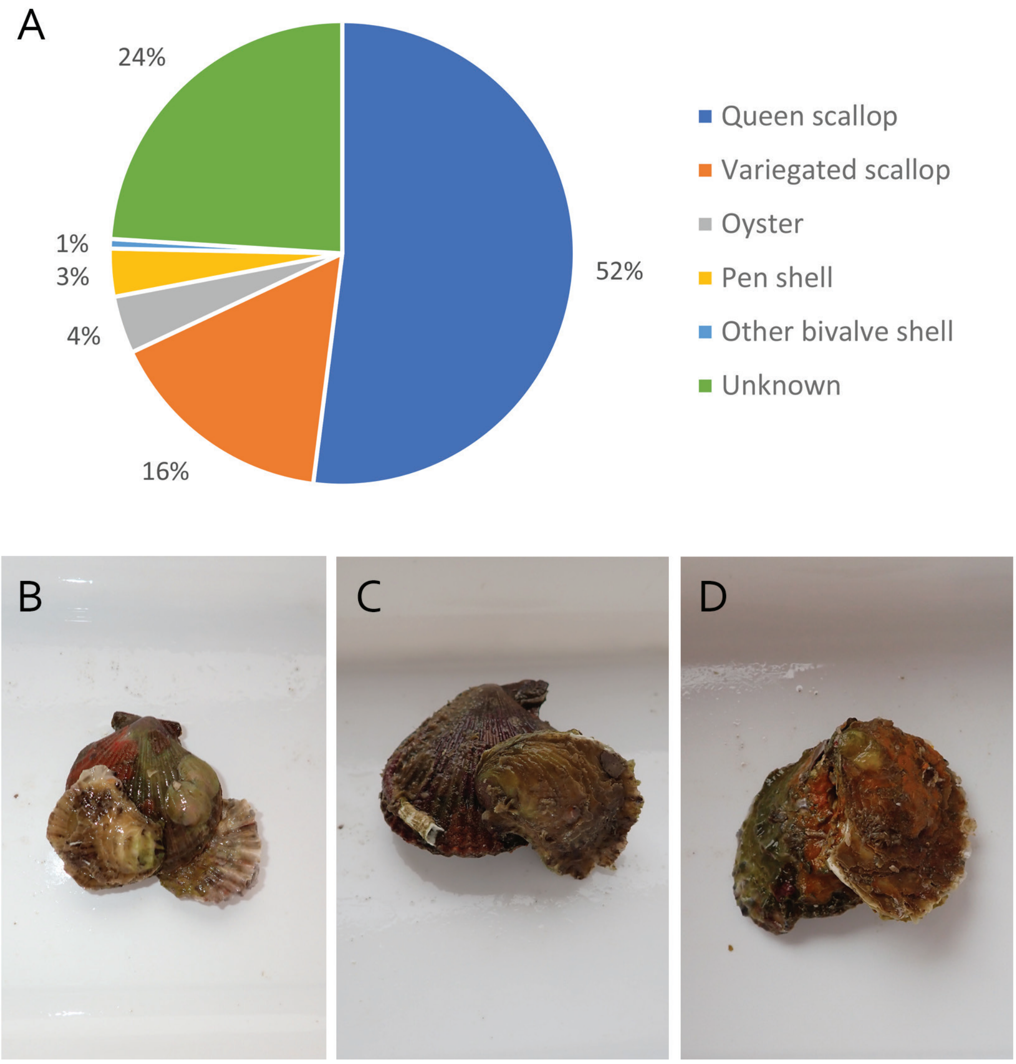

Fig. 6: Results of settlement substrate analysis for *Ostrea edulis* collected in the northern Adriatic Sea during the survey in 2024. Photo credit: Ratko Cvitanić.

Despite these limitations, the biomass index indicates that, prior to the recorded decline, there was higher *O. edulis* biomass in the central part of the western Istrian coast. The biomass index was highest near Lim Bay, a prominent oyster and mussel aquaculture region along the western Istrian coast and within Croatia (Benović, 1997). This pattern may reflect larval spill-over from aquaculture sites, as bivalve aquaculture has been shown to play an important role in sustaining populations in adjacent areas (Norrie *et al.*, 2020). Consistently, surveys of shallow coastal areas along the western coast of Istria have reported generally low *O. edulis* densities but with the highest average densities occurring in the Lim Bay area (Stagličić *et al.*, 2020). Using visual census methods along a north-south coastal gradient from the surface to a depth of 6 m, Stagličić *et al.* (2020) recorded low population densities throughout the survey area, mostly < 1 individual m^{-2}, with a mean density of 0.1 ± 0.02 individuals m^{-2}) and a maximum of 4 individuals m^{-2}.

Although our study covered a large spatial scale, the beam-trawl method did not allow us to categorise *O. edulis* habitats according to the stages proposed by Preston *et al.* (2021). Because beam-trawl catches represent a larger survey area and *O. edulis* exhibits a patchy distribution (Thorngren *et al.*, 2017), the spatial arrangement of the captured individuals remains unknown. It remains unclear whether *O. edulis* during periods of high abundance, such as in 2013, occurred in small or large clusters, or solely as single individuals or pairs. However, the analysis of *O. edulis* settlement substrates in 2024 showed that most *O. edulis* were attached individually to empty shells of scallop species, with only a small portion attached to other oysters. This pattern indicates that *O. edulis* does not form dense clusters in the study area but instead occurs as isolated individuals or in very low-density assemblages. According to Preston *et al.* (2021), such oyster habitats are characterised by low habitat resilience and reduced biodiversity.

This finding is further supported by the ROV survey, during which no *O. edulis* clusters or visible individuals were observed. Given that the ROV survey was conducted in an area not trawled in recent years and given the proximity to Lim Bay, where oyster aquaculture is present, some level of natural recovery or reef formation might have been expected. However, the absence of detectable oysters suggests that such recovery has not occurred. Several studies have demonstrated that a fishing ban alone is insufficient to promote the recovery of bivalve populations (e.g., Fariñas-Franco *et al.*, 2018; Helmer *et al.*, 2019). Based on demographic data, there was a lack of oyster recruitment after two years of a fishery ban and a reduced fishing season in preceding years (Helmer *et al.*, 2019). Even a longer period – seven years after the implementation of a fishing ban using a "protection alone" approach – was insufficient to promote the natural recovery of highly degraded biogenic reefs (Fariñas-Franco *et al.*, 2018). The lack of a positive effect (e.g., recruitment and settlement) on *O. edulis* populations may result from one or a combination of the following factors: (i) reduced reproductive success at the individual level, potentially associated with impaired gametogenesis such as oocyte atresia; (ii) low population density, which may lead to reduced or unsuccessful fertilisation; (iii) limited or absent larval supply from surrounding areas (e.g., Lim Bay); (iv) increased larval mortality during the pelagic phase; and (v) the absence or scarcity of suitable substrate for larval settlement. *Ostrea edulis* is a larviparous species in which females release eggs into the mantle cavity, where they are fertilised by male gametes received from the water column and brooded for up to 10 days before larvae are released into the surrounding water (Eagling *et al.*, 2017; Helmer *et al.*, 2019). Therefore, population density is a stronger determinant for successful *O. edulis* reproduction than for the reproduction of species in which both sexes release gametes directly into the water column (Helmer *et al.*, 2019). The settlement stage is also a critical phase in the life cycle of bivalves, as larvae released into the water column are influenced by various biotic and abiotic factors, including the substrate type (Jonsson *et al.*, 1991; André *et al.*, 1993). The combination of low overall abundance in some study regions, the complete absence in other regions along the west coast of Istria, and the lack of suitable attachment substrates detected during the ROV survey likely represents a bottleneck for the recovery of *O. edulis* populations in this region.

In marine restoration, a key question is which approach should be applied: passive (e.g., restoring hydrology and sediment characteristics) or active (e.g., introducing living plants or oysters to form biogenic habitats) (Barrett *et al.*, 2024). Passive restoration alone in areas of low oyster abundance appears to have only minimal effectiveness (Barrett *et al.*, 2024). Based on our data, a combined passive-active restoration approach should be considered in the regions of the northern Adriatic Sea where *O. edulis* has historically been abundant and fishing is no longer performed. However, prior to any intervention, additional research is required, some of which is currently underway (e.g., larval distribution modelling and settlement substrate testing).

In addition to the data on *O. edulis*, this study provides information on other species inhabiting the study area. Oyster reefs are known to support high biodiversity (Kennon *et al.*, 2023; Smith *et al.*, 2023). However, oyster-reef habitats were not recorded during the 2024 survey. Given that the analysed composition of macrozoobenthic communities in our study did not show statistically significant differences, the data presented here may serve as a baseline for areas where *O. edulis* was absent or present at low abundances, thereby enabling future comparisons in the context of potential restoration activities. Beyond general biodiversity patterns, biotic interactions represent another key factor influencing the success of oyster restoration. Predation has been identified as an important challenge in restoration efforts (Tedford & Castorani, 2022), so information on the occurrence of species that may act as bivalve predators (e.g., *Hexaplex trunculus* (Linnaeus, 1758); Morton *et al.*, 2007) is relevant for the planning and implementation of restoration measures. Although our study did not aim to assess potential mortality due to predation by species such as *H. trunculus*, this factor should be taken into account in future studies.

We identified several positive aspects of the *O. edulis* population in the Croatian northern Adriatic region. First, the length-frequency distribution from beam-trawl surveys along the west coast of Istria showed the presence of young, small specimens, suggesting successful reproduction and settlement where suitable substrate is available. Second, the sampled *O. edulis* tested negative for parasites responsible for diseases such as bonamiosis and marteiliosis (Ezgeta-Balić, unpublished data).

Finally, oyster aquaculture is focused exclusively on *O. edulis*, which may promote a larval spillover effect. Notably, Croatia does not cultivate *M. gigas*; the absence of this non-native, invasive species in local aquaculture likely reduces competitive pressure on natural *O. edulis* populations and may contribute to the continued presence of this species along the coastline. *Magallana gigas* has not been officially introduced into Croatian aquaculture, although short experimental trials have established intertidal populations in the northern Adriatic Sea, particularly on the west coast of Istria (Filić & Krajnović-Ozretić, 1978). Recent studies indicate that the two oyster species under natural conditions do not compete for space in the Adriatic Sea: *M. gigas* is almost exclusively intertidal in this region, whereas *O. edulis* inhabits subtidal zones from just below the surface to a depth of nearly 40 m (Stagličić *et al.*, 2020; Ezgeta-Balić *et al.*, 2021).

Harvesting practices also shape the population status of *O. edulis*. Harvesting by beam trawl is allowed only in a small portion of Croatian territorial waters along the western Istrian coast and part of the Exclusive Economic Zone (Official Gazette 48/2015, 12/2016). In the rest of the Adriatic Sea, *O. edulis* is collected exclusively by divers, a less destructive method. Notably, bivalves can be legally placed on the market only if collected from designated, monitored zones, which cover a relatively small portion of the coastline (Ministry of Agriculture, Forestry and Fisheries, 2024). These regulatory restrictions likely limit large-scale exploitation and may help preserve smaller, scattered *O. edulis* natural populations. While the existence of illegal, unreported, and unregulated fishing cannot be fully excluded, its overall impact is likely limited, especially given the availability of *O. edulis* from aquaculture.

Although there have been limited formal scientific surveys, numerous opportunistic observations indicate that *O. edulis* is more widely distributed than is currently documented. During various diving operations, artificial

Fig. 7: Marine litter serving as a settlement substrate for *Ostrea edulis*. The photograph shows an automobile tire retrieved from the sea during a cleanup action in Omiš, Croatia (June 2024). Photo credit: Daria Ezgeta-Balić.

structures, such as mooring lines, ropes, and other submerged elements, sometimes host *O. edulis* aggregations. The recurring presence of *O. edulis* on substrates considered marine litter, such as items collected during clean-up actions (e.g., observations from Omiš, Croatia; Fig. 7), provides further evidence of its broad distribution. This also suggests that suitable settlement surfaces are readily occupied when available. With the aim of collecting data across a broader geographic range, a citizen science initiative has been established (https://oesurvey.vercel.app/en), which is expected to provide more information on the distribution of *O. edulis* in the coming years. Through a dedicated application, divers, recreational fishers, boaters, and other sea users can report *O. edulis* sightings, upload geolocated data, and contribute photographs. The information collected through this platform will enable more accurate mapping of the species' distribution and help identify priority areas for future scientific surveys and protection. This approach has the potential to fill critical knowledge gaps and support long-term monitoring, conservation, and management efforts.

In conclusion, our study provides a valuable contribution to understanding the status of *O. edulis* in the Croatian sector of the northern Adriatic Sea. The results underscore the need for systematic, region-wide assessments of *O. edulis* populations across the eastern Adriatic coast. The integration of field surveys, molecular tools, and citizen science will be essential for developing a comprehensive understanding of population dynamics, thereby supporting effective management, conservation, and potential restoration of this ecologically and economically important species. Our findings indicate that reduced fishing pressure alone is insufficient to restore *O. edulis* populations. They also highlight the importance of considering local aquaculture practices (with a focus on native species), habitat availability, and recruitment dynamics when designing strategies to ensure the long-term persistence of natural populations in the region. At a time when Croatia is developing its National Nature Restoration Plan, studies such as this are particularly important, as they contribute to a better understanding of existing challenges and can provide a baseline for future actions. Bivalve-dominated seabed habitats (shellfish reefs) are among those identified as priorities for restoration. By addressing critical knowledge gaps, this research contributes to broader efforts aimed at preserving *O. edulis* populations across the Adriatic and Mediterranean Seas.

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Supplementary Data

The following supplementary information is available online for the article:

Fig. S1: (A) Fishing zones in the eastern Adriatic Sea. (B) Fishing zones in which beam-trawl fishing is permitted (shown in green); however, according to Ezgeta Balić et al. (2021), beam-trawl fisheries are conducted almost exclusively in fishing zone A and only sporadically in zone H. Original map source: *Official Gazette* 144/2005 *Pravilnik o granicama u ribolovnom moru Republike Hrvatske*.

Table S1. List of macrobenthos species found in discard subsamples from the 10 analysed stations during the 2024 survey.

Table S2. Commercial fish, crustacean, and mollusc species caught across the entire survey area in the 2024 survey.