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Effects of environmental change on *Echinocyamus pusillus* in Holocene sediment records from the northern Adriatic Sea

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ZUSAMMENFASSUNG

Die Auswirkungen langfristiger menschlicher Stressfaktoren auf die Populationen benthischer Meeresorganismen sind im Allgemeinen schwer zu evaluieren, da nur wenige systematische Langzeitdaten vorliegen. Die jüngsten fossilen Archive, die in marinen Sedimentproben erhalten sind, stellen ein wichtiges historisches Archiv dar, das ermöglicht, die ökologischen Auswirkungen natürlicher Umweltveränderungen während des Holozäns zu verfolgen und den Zustand von Populationen vor dem Beginn menschlicher Einflüsse zu rekonstruieren. Die meisten Studien, die diese paläoökologischen Archive nutzen, konzentrieren sich jedoch auf Mikrofossilien- oder Molluskengemeinschaften, während die Dynamik anderer wichtiger Komponenten mariner Ökosysteme, wie z.B. die der Echinodermata, nur begrenzt Studien vor. In dieser Arbeit werden die gut erhaltenen Gehäuse des infaunalen clypeasteroiden Seeigels, *Echinocyamus pusillus,* in Sedimentkernen aus der nördlichen Adria untersucht. Die Untersuchung dieser paläoökologischen Archive ermöglicht neue Einblicke in die langfristige Populationsdynamik und die ökologischen Reaktionen dieser weit verbreiteten Art. Wir untersuchen Trends in der Größe und Häufigkeit der Gehäuse von *Echinocyamus pusillus* und setzen diese in Beziehung zu den sedimentologischen Bedingungen, während der letzten ~ 11.000 Jahre in der nördlichen Adria, wo die küstennahen marinen Lebensräume über einen langen Zeitraum menschlichen Einflüssen ausgesetzt waren. Wir kombinieren diese Daten mit Radiokarbondatierungen mehrerer Exemplare, um ökologische Signale aus den zeitlich durchmischten Ablagerungen zu extrahieren. Sedimentkerne und Sedimentoberflächenproben von vier Stationen decken verschiedene benthische Habitate ab und dokumentieren Umweltveränderungen während der postglazialen Transgression und des holozänen Meeresspiegelstillstands. Dies wurde bereits durch Veränderungen in den Molluskengemeinschaften und durch geochemische Proxydaten belegt. Die Ergebnisse dieser Arbeit deuten auf erhebliche Schwankungen in der Häufigkeit von *E. pusillus* hin, jedoch auf bemerkenswert stabile Gehäusegrößen über die letzten Jahrtausende und über die verschiedenen Stationen hinweg. Darüber hinaus deuten die Ergebnisse der Altersdatierung darauf hin, dass in der obersten, durchmischten Sedimentschicht kaum Gehäuse aus dem späten 19. und 20. Jahrhundert vorhanden sind. Dies deutet auf einen starken Rückgang der Gehäuseproduktion und damit der Populationsdichte in den letzten 200 Jahren hin. Dieses Muster kann mit dem Beginn starker Umweltveränderungen wie Sedimentsiltation, Eutrophierung und häufigeren

hypoxischen Ereignissen in Verbindung gebracht werden. Der rasche Rückgang der Populationen während dieser Zeit, zusammen mit der zeitlichen Durchmischung der fossilen Bestände in den Sedimentkernen, könnte daher das Fehlen von Veränderungen in der Körpergröße erklären. Unsere Ergebnisse bilden eine grundlegende Basis für die Evaluierung der zeitlichen und regionalen Veränderungen der Körpergröße und des Vorkommens von *E. pusillus* in der nördlichen Adria. Schließlich können sie mit modernen systematischen Aufzeichnungen und Fossildaten aus anderen Regionen verglichen werden, um die natürliche Variabilität der Populationen von den Folgen der jüngsten Intensivierung menschlicher Einflüsse zu unterscheiden.

ABSTRACT

The consequences of prolonged human stressors on populations of marine benthic species are generally difficult to assess due to the paucity of long-term monitoring data. The youngest fossil record, preserved in marine sediment cores and grab samples, provides a rich historical archive that allows tracking ecological responses to natural environmental changes during the Holocene and reconstructing the state of populations prior to the onset of anthropogenic impacts. However, most studies using these paleoecological records focus on microfossil or mollusc assemblages, and only limited knowledge is available on the responses of other key components of marine ecosystems, such as echinoids. This study presents a novel record of well-preserved tests of the infaunal clypeasteroid *Echinocyamus pusillus* from Holocene marine sediment cores, which provide new insights into the long-term population dynamics and ecological responses of this widely distributed echinoid. We investigate trends in test size and abundance of *E. pusillus* and relate them to sedimentological conditions during the last ~11,000 years in the shallow northern Adriatic Sea, where coastal marine habitats have been under prolonged anthropogenic pressure. We combine these data with radiocarbon dating of multiple specimens to extract ecological signals from time-averaged assemblages. The sediment cores and grab samples collected from four stations, which cover different benthic habitats, document environmental changes during the post-glacial transgression and Holocene sea-level stillstand, as evidenced by shifts in molluscan assemblages and geochemical proxy records. The data suggest significant fluctuations in *E. pusillus* abundance but remarkably stable test sizes over the past millennia and across sampling stations. Moreover, the age-dating results indicate a paucity of dead tests originating from the late 19th and 20th centuries in the surface mixed layer. This points to a strong decline in test production and thus population densities over the past ~200 years. This pattern can be linked to the onset of pronounced environmental changes, including siltation, eutrophication, and increased frequency of hypoxic events. Rapid decline of populations during that time combined with temporal mixing of fossil assemblages may thus explain the overall lack of body size shifts observed in sediment cores. Our results provide a fundamental baseline for evaluating temporal and spatial changes in body size and abundance of *E. pusillus* in the northern Adriatic Sea. They can be compared with recent monitoring and fossil data from other areas and serve to disentangle natural population variability from responses to recent intensification of human impact.

1 INTRODUCTION

The reconstruction of the ecological baseline state of marine benthic species based on paleoecological data prior to the rapid onset of anthropogenic environmental change is an important approach to differentiate between natural population variability and human-induced impacts, and to guide conservation efforts (Dietl et al., 2015; Kidwell, 2015). It is particularly important because contemporary ecological monitoring studies often capture populations that have already been altered throughout the last decades to millennia (e.g. Lotze et al., 2006).

Conservation paleobiology aims to approach and overcome the problem of what constitutes a pristine community state by using geohistorical data to establish a baseline state as a reference for the evaluation of recent ecological shifts and their consequences for ecosystems. Therefore, the youngest fossil record, preserved as death assemblages in sediment cores and grab samples, provide a unique historical archive that goes back much further than ecological observations, offering essential data that can serve as reference for management decisions in marine conservation and can inform restoration targets (Dietl et al., 2015; Kidwell, 2015). Death assemblages represent time-averaged accumulations of skeletal remains that are naturally preserved in a temporally coarse manner. However, our increasing understanding of this data type enables documentation of both historical and anthropogenically altered community states. As such, death assemblages are a valuable resource for assessing the present state of ecosystems and for predicting their future responses to anthropogenic impacts (Kidwell & Tomašových, 2013).

Coastal marine ecosystems of the northern Adriatic Sea have been affected by climate change and human activities for millennia (Coll et al., 2008; Lotze et al., 2011; Kowalewski et al., 2015). However, eutrophication, seasonal hypoxia, trawling, overfishing, and pollution rapidly intensified since the industrial revolution, causing significant changes in marine communities, especially over the last decades (e.g., Justić, 1991; Stachowitsch, 1991; Ferretti et al., 2013). The impact of these long-lasting stressors on populations of marine species is often difficult to assess due to paucity of long-term monitoring data, specifically for small-bodied and non-commercial taxa. Most studies using macrofossil palaeoecological records to reconstruct composition of pre-impact benthic communities in

the northern Adriatic focused on molluscan assemblages (e.g., Schnedl et al., 2018; Gallmetzer et al., 2019), and only a few traced changes in population size structure of individual species (e.g., Peharda et al., 2002; Tomšić et al., 2010; Fuksi et al., 2018; Tomašových et al., 2020a; Cheli et al., 2021). In contrast, very little is known about the long-term responses of other major components of the northern Adriatic marine ecosystems like Echinoidea and their temporal shifts in body size. Both regular and irregular echinoids play a crucial role as benthic faunal components, especially in shallow marine ecosystems. Regular echinoids, important grazers on hard substrata, and irregular echinoids, acting as deposit feeders and bioturbators, have a significant impact on the structuring of marine communities and functioning of benthic ecosystems (e.g. Sammarco, 1982; Nebelsick, 1996, 2020; Lohrer et al., 2005).

The quantitative and qualitative evaluation of the ecology of echinoid assemblages based on geohistorical records faces challenges due to the loss of information in sediment cores resulting from taphonomic alterations of skeletal remains in death assemblages, leading to potential inaccuracies in the interpretation of historical shifts in living assemblages (Greenstein, 1989; Donovan, 1991; Gischler, 2010; Kowalewski et al., 2018; Nawrot et al., 2022). Grun & Kowalewski's (2022) observations on living and dead clypeasteroid and spatangoid echinoids, collected via SCUBA dives, indicate that the comparison of living and dead irregular echinoid assemblages can provide a fossil record with high spatial and compositional fidelity. But as they concluded, the causal factors of the high accuracy of this data could either imply the long-term persistence of local echinoid populations or the rapid disintegration of echinoid tests, which may hinder post-mortem transportation and the formation of time-averaged death assemblages (Grun & Kowalewski, 2022). Therefore, it remains uncertain how this high fidelity of surface accumulations of dead tests translates into subsurface sedimentary records. Due to these limitations, there is a paucity of research focusing on the conservation paleobiology of echinoids, especially studies that depend on long-term sedimentary records.

Although fragmented skeletal components like spines or isolated test plates of sea urchins in sediment cores can be employed to reconstruct the baseline abundance and composition of echinoid assemblages (Cramer et al., 2018), the analysis of body size poses challenges due to the inherent limitations of single skeletal elements. This creates a knowledge gap between various ecologically significant taxa, since body size changes can serve as a crucial proxy for tracking environmental shifts during natural (Martindale & Aberhan, 2017; Foster et al., 2020) and anthropogenic (Levin et al., 2009; Fuksi et al.,

2018) disturbances and can also predict recent extinction risks, for example of marine molluscs (Payne et al., 2016).

The aim of this study is to describe the stratigraphic and spatial distribution of a minute infaunal clypeasteroid, *Echinocyamus pusillus*, in the Holocene fossil record of the northern Adriatic Sea and to relate it to abiotic and biotic factors, based on test size-frequency distributions and environmental proxy data. To gain insights into the ecological response of this species in benthic ecosystems, a comprehensive analysis was conducted on multiple grab samples and sediment cores, spanning the past ~ 10,000 years, and containing numerous whole and fragmented tests.

1.1 *Echinocyamus pusillus*

Echinocyamus pusillus (Fig. 1) exhibits a widespread distribution across the Atlantic Ocean and the Mediterranean Sea (Mortensen, 1950; Zavodnik, 2003). This clypeateroid lives infaunally and burrows through the sediment, ranging from shallow waters down to a water depth of 1,250 m (Ghiold, 1982). It displays a preference for medium to coarse-grained sand, with maximum densities observed in sediments with a median grain size of 500-550 µm and low mud content, not exceeding 10% (Degraer et al., 2006). Very common occurrences of specimens in the northeastern Adriatic Sea near to the coast of Rovinj, Croatia, were documented from shallow waters down to ~ 35 m in biogenic calcareous sands collected in the year 1970 (Ernst et al., 1973). But it is unclear whether

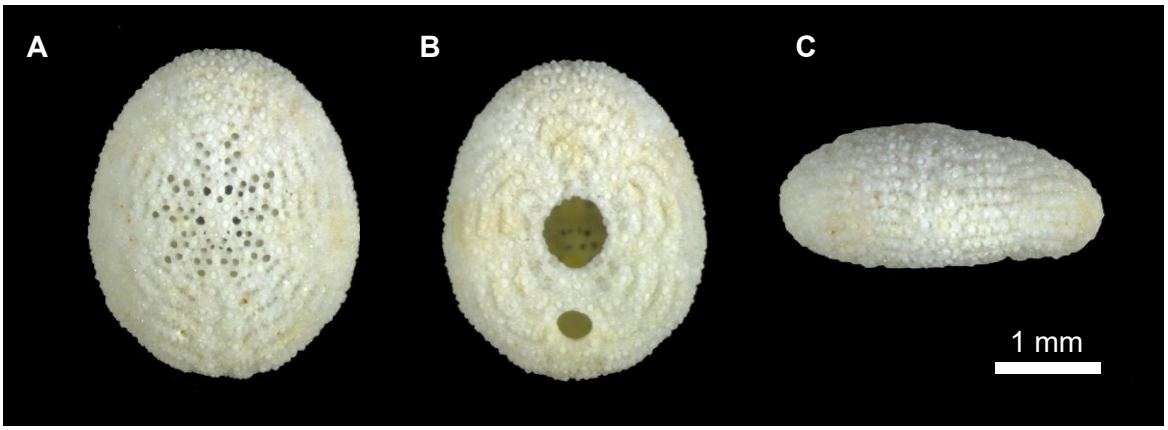

Figure 1 – Stereomicroscope photographs showing the aboral (A), oral (B), and lateral view (C) side of a dead test of E. pusillus. Lateral view (C) shows the anterior end to the right.

the specimens were dead or alive at the time of sampling. However, reports of living *E. pusillus* in the Adriatic are scarce, e.g. another report by Vatova (1943) mentions only a few specimens in the same area. Alternatively, it can also be common in seagrass meadows as observed in samples from the rhizomes of *Posidonia* in southern Cyprus, which contained abundant live *E. pusillus* (Martin Zuschin, personal communication).

The test is varying in length between 2-10 mm and is entirely covered by minute spines and has an oval to sub-elliptical outline (Ghiold, 1982). Unlike sand dollars, the spines have a passive function in the feeding and burrowing process and possibly serve a defensive purpose similar to those of regular sea urchins (Ghiold, 1982). This echinoid employs surface ciliary currents to move particles, but not towards its mouth, suggesting that they may have other purposes, such as assisting in respiration or cleaning (Ghiold, 1982). In turn *E. pusillus* involves primarily the podia in climbing, burrowing, righting and probably feeding (Ghiold, 1982). The slightly depressed and centrally located peristome (mouth) and much smaller periproct (after), located close to the posterior, are on the oral (ventral) side of the test (Fig. 1). When viewed in lateral section, the test displays a convex curvature, resembling a structurally efficient dome construction (Telford, 1985; Grun & Nebelsick, 2018). The high intrinsic preservation potential of *E. pusillus* tests is attributed to the presence of several skeletal reinforcement structures, such as circumferential ridges, plate interlocks, sutural and plate thickening and notably well-developed radial buttresses (Telford, 1985). Those characteristics and its small size in general make the test structurally very resistant.

Consequently, *Echinocyamus* represents a model taxon well-suited for quantitative analysis of abundance and size structure of echinoid populations in both recent environments and fossil sedimentary records (Nebelsick & Kowalewski, 1999; Złotnik & Ceranka, 2005; Ceranka, 2007; Grun et al., 2014; Grun et al., 2017; Grun & Nebelsick, 2018; Warwick & Pearce, 2020). *E. pusillus* may be under-sampled in living assemblages due to its very small size in coarse sediments, inconspicuous nature, and methodological problems associated with its extraction from the sediment (Warwick & Pearce, 2020). However, its excellent preservation potential contributes to its frequent presence in both recent and fossil death assemblages.

The objective of this thesis is to test whether anthropogenic impacts, such as eutrophication, increased frequency of seasonal hypoxia, and siltation over the last century have resulted in a significant decline in abundance and changes of body size of

E. pusillus in the northern Adriatic Sea. To establish a reliable baseline state of its population, it is also essential to evaluate the resolution of palaeoecological records. This assessment is necessary since sediment cores can contain death assemblages that are time-averaged over periods spanning decades to millennia. Hence, radiocarbon dating of *E. pusillus* tests was employed to estimate the degree of time averaging of its death assemblages.

2 MATERIAL AND METHODS

2.1 Study area

The northern Adriatic Sea is a relatively shallow (average depth is 35 m) and young epeiric sea flooded during the last ~ 11,000 years during the Holocene transgression. The prevailing counterclockwise currents lead to an asymmetrical distribution of sediments and nutrients (Fig. 2), with oligotrophic waters in the eastern regions, and meso- to eutrophic conditions in the western and northern areas, due to the inflow of the Po River (Fig. 2) and other rivers along the western margin, contributing to high nutrient and sediment input (McKinney, 2007; Zuschin & Stachowitsch, 2009). Primary production in the northern Adriatic Sea ranks among the highest in the Mediterranean (Turley, 1999) and is characterized by seasonal stratification of the water column in summer and strong mixing in winter caused by storms (Giani et al., 2012). The seafloor is generally formed by fine-grained sands, silts and clays on the inner shelf, and relict Pleistocene sands on the outer shelf (Frignani et al., 2005).

Human settlement and colonization have impacted the coastal areas of the northern Adriatic Sea since ancient times (Turney & Brown, 2007) and for more than a century, the practice of bottom trawling and dredging has been employed in this area, causing sediment destabilization (Pranovi et al., 2000). Furthermore, the twentieth century increase in anthropogenic eutrophication combined with the stratification of the water column during summer to mid-autumn has led to more frequent occurrences of short-term hypoxic and anoxic events (Justić, 1991). These events are often accompanied by mucilage events, which contribute to mass mortalities of benthic communities in the region (Stachowitsch, 1984, 1991; Crema et al., 1991). Altogether these ever-increasing human influences caused significant changes and degradation in the marine habitats of the northern Adriatic Sea in the 20th century (e.g. Justić, 1991; Coll et al., 2008; Vidovic et al., 2016; Gallmetzer et al., 2019; Tomašových et al., 2020). These effects are evident in the fossil record not only in terms of shifts in relative abundances and community composition (Vidovic et al., 2016; Gallmetzer et al., 2017, 2019; Mautner et al., 2018; Schnedl et al., 2018; Tomašovych et al., 2018; Haselmair et al., 2021) but also in changes in the body size of individual species (Fuksi et al., 2018; Tomašových et al., 2020). Fuksi et al. (2018)

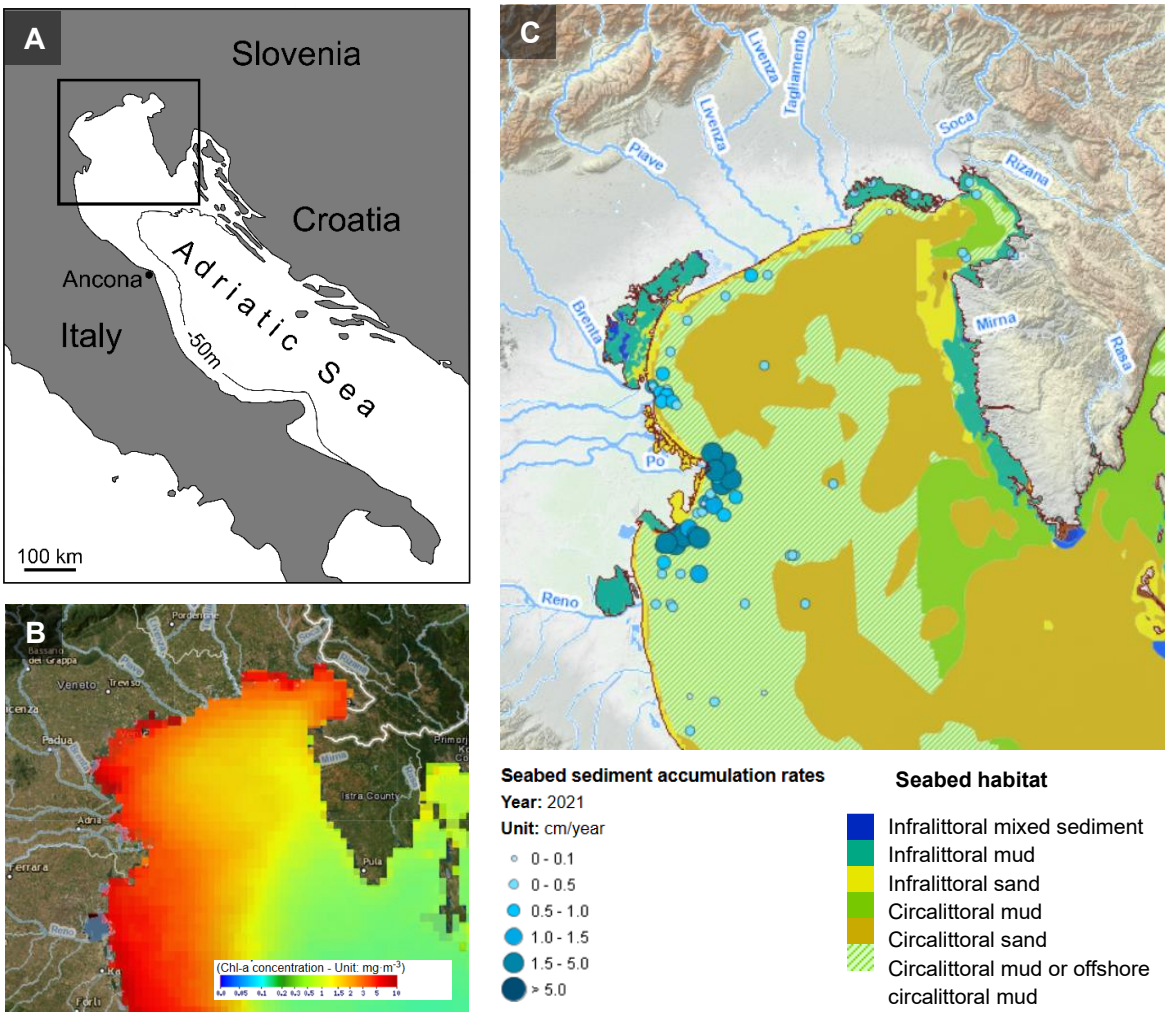

Figure 2 – Overview of the environmental factors in the northern Adriatic Sea. (A) Location of the study area. (B) The surface ocean chlorophyll-a concentration (monthly mean in September 2023) derived from satellite sensors, which can serve as proxy for nutrient availability. (C) The seabed sediment accumulation rates (the rates were determined by dating of the sediment or estimated from acoustic-seismic and sediment core data) and seabed habitats (predictive seabed habitat map classifies habitat descriptors following the Marine Strategy Framework Directive. The conditions are strongly influenced by the Po River, especially on the western margin, where sediment and nutrient input is the highest. Image credit: European Marine Observation and Data Network (EMODnet).

studied the opportunistic bivalve *Varicorbula gibba* in death assemblages preserved in sediment cores spanning several centuries to a few millennia. They established a correlation between the increase in body size during the 20th century and organic enrichment, likely resulting from expanded algal production and, indirectly, hypoxic conditions. In contrast, populations prior to the human impacts of the 20th century exhibited relatively consistent, smaller sizes during the late highstand phase in the northern Adriatic Sea. Moreover, the increased occurrence of hypoxic events was accompanied by a

decline in the degree of sediment mixing caused by burrowing benthic organisms, resulting in a substantial improvement of the stratigraphic resolution of the youngest fossil record, thus enabling detection of sub-centennial ecological shifts in sediment cores (Tomašových et al., 2020). Taken together, these investigations have demonstrated that benthic death assemblages in the northern Adriatic Sea can be used to distinguish population states before and after human-induced environmental changes.

2.2 Sampling

This master thesis is part of the research project “Historical Ecology of the Northern Adriatic Sea”, funded by the Austrian Science Fund FWF (project P24901). The four

Figure 3 – Location of the four sampling stations Brijuni, Venice, Piran 1 and Piran 2 in the northern Adriatic Sea. The satellite image of the northern Adriatic Sea depicts a pronounced westward increase in the influence of the Po River and lower water turbidity on the eastern margins (after Gallmetzer et al. (2019), image credit: Jacques Descloitres, MODIS Land Rapid Response Team, NASA/GSFC).

sampling stations “Brijuni”, “Venice”, “Piran 1” and “Piran 2” (Fig. 3) are characterized by different sediment types and degrees of protection from bottom trawling.

In summer of 2013, at each station, three sediment cores (Tab. 1) were taken using the Slovenian research vessel *Manta Bianca* and extracted with an UWITEC piston corer with hammer action (Gallmetzer et al., 2016). One of the cores from each station was used for palaeoecological analyses of the molluscan assemblages (Gallmetzer et al., 2019) and the remaining ones were used for granulometric and geochemical analyses. As described in Gallmetzer et al. (2019), the topmost 20 cm of the cores were sliced into 2-cm thick increments to achieve a higher resolution, while the remaining portion of the cores were divided into 5-cm thick sections. All increments of the sediment cores were sieved using a 1 mm mesh and the dried death assemblages were examined in the present study.

Table 1 - Overview of core and grab material used for this study. DM = diameter of the core, BP = before present.

Station locality/ID	Material description	Core dimensions	Core chronology (lower age limit)	*References*
Brijuni	Core M44 Grab sample 4	1.6 m long piston core 9 cm DM	~ 11,000 years BP	*Schnedl et al., 2018; Gallmetzer et al., 2019; Tomašových et al., 2022*
Piran 1	Core M1, M23 Grab sample 1	1.5 m long piston cores 16 cm DM	~ 10,000 years BP	*Fuksi et al., 2018; Mautner et al., 2018; Gallmetzer et al., 2019*
Piran 2	Core M53 Grab sample 8			
Venice	Core M38 Grab sample 4	1.4 m long piston core 9 cm DM	~ 9,000 years BP	*Gallmetzer et al., 2019; Tomašových et al., 2020*

The trends in composition of molluscan assemblages within the sediment cores from stations Brijuni (Schnedl et al., 2018), Piran 1 and Piran 2 (Mautner et al., 2018; Tomašových et al., 2019), and Venice (Gallmetzer et al., 2019) were documented by previous studies. Grab samples were collected in summer 2014 using a Van Veen grab

with a ground area of 0.125 m^2 and a penetration depth of ~ 15 cm (Haselmair et al., 2021). Each sample was sieved through a 1 mm mesh on the day of sampling and all living organisms were collected and preserved separately in 70% ethanol. The dried death assemblages from the grab samples and sediment cores were picked out in the lab using a stereomicroscope.

2.3 Sediment analysis

2.3.1 Granulometry

One 9-cm-diameter core from each sampling station was used for granulometric analysis and for ^{210}Pb sediment dating (Gallmetzer et al., 2019). The core used for these analyses at the Venice station was only 85 cm long, due to the differences in the paleorelief between the spots where cores for the sediment analyses and for palaeoecological analysis were taken. Core slicing procedures were consistent with those used for the molluscan core. Within each core increment, a subsample (10-20 g) was extracted and sieved through five mesh sizes (1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm). These fractions were dried and weighed, and the 0.063 mm fraction underwent further analysis using a SediGraph III 5120 Particle Size Analyzer, following established protocols. The sediment grain size was categorized into four classes: clay (<0.002 mm), silt (0.002–0.063 mm), sand (0.063–2 mm), and gravel (2–63 mm).

2.3.2 Geochronology

The chronology of the sediment cores (Tab. 2) was established using two methods: sediment dating through the analysis of ^{210}Pb and dating of mollusc shells (Mautner et al., 2018; Schnedl et al., 2018; Gallmetzer et al., 2019; Tomašových et al., 2019). The most common bivalve species in the cores, *Timoclea ovata* for station Brijuni, *Gouldia minima* for stations Piran 1 and Piran 2, and *Lucinella divaricata* for station Venice, were dated with ^{14}C-calibrated amino acid racemization (Gallmetzer et al., 2017, 2019; Mautner et al., 2018; Schnedl et al., 2018; Tomašovych et al., 2018). Based on the geochronological data and changes in the sediment composition in the cores at each station, the increments

were grouped and classified into four sea-level phases of the Holocene transgression using the sequence-stratigraphic terminology of model III from Catuneanu et al. (2009): 1) a transgressive phase (TST) ranging from the onset of the marine transgression ~ 11,500 years BP at the locations currently at 40 m water depth and ~ 9,000 years BP at 20 m depth (Colantoni et al., 1979; Storms et al., 2008; Schnedl et al., 2018), 2) a maximum flooding zone (MFZ) marking the maximum ingression (~ 7,000-5,500 years ago; Trincardi et al. 2011; Amorosi et al. 2017), 3) an early highstand phase (eHST) lasting until the onset of the sea-level stillstand ~ 2,000 years BP, and 3) a late highstand phase (lHST), which marks the era of pronounced marine ecosystem changes that were induced by human activities in the recent past (Tab. 2).

Table 2 – Core depths and age ranges of stratigraphic units (systems tracts): late highstand (lHST), early highstand (eHST), maximum flooding zone (MFZ) and late and early transgressive systems tract (lTST and eTST) at the four sampling stations. The median ages represent the estimates for 4-5 cm-thick increments that are based on dating of bivalve shells. Modified after Gallmetzer et al. (2019).

	Core	Stratigraphic unit	Median ages of increments per unit (yrs)
Brijuni			
	0-10 cm	lHST 2	*< 200*
	10-20 cm	lHST 1	*300-600*
	20-50 cm	eHST 2	*2,100-2,600*
	50-90 cm	eHST 1	*3,200-4,300*
	90-120 cm	MFZ	*4,900-5,200*
	120-160 cm	TST	*5,000-6,100*
Venice			
	0-8 cm	lHST 2	*< 620*
	8-30 cm	lHST 1	*870-1,100*
	30-90 cm	eHST	*1,000-2,100*
	90-105 cm	MFZ	*3,500-3,700*
	105-135 cm	TST	*6,300-6,900*
Piran 1			
	0-8 cm	lHST	*< 1,200*
	8-16 cm	eHST	*1,000-3,100*
	16-35 cm	MFZ	*4,700*
	35-65 cm	lTST	*4,700-4,800*
	65-150 cm	eTST	*4,500-6,000*
Piran 2			
	0-8 cm	lHST	*< 1,100*
	8-16 cm	eHST	*1,500-3,500*
	16-35 cm	MFZ	*3,800-5,800*
	35-65 cm	lTST	*4,100-6,400*
	65-150 cm	eTST	*4,500-8,600*

2.3.3 Geochemical analysis

As described in Gallmetzer et al. (2019), a separate 9-cm core from every sampling site was sealed upon retrieval and sent for geochemical analysis at the Institute of Marine Sciences in Venice (ISMAR). Initially, radiographic images were taken of the intact cores to observe down-core density patterns and to determine the core increments best suited for subsample extraction. Then, in every core, 10 increments (just eight in the shorter Venice core) were chosen. Three increments were taken from the uppermost 10 cm (0-2 cm, 4-6 cm, and 8-10 cm) and seven were uniformly dispersed along the remaining core, with depths slightly varying between cores from individual stations. The protocol described in Vidovic et al. (2016) was employed to measure the concentration of nutrients (total carbon, total organic carbon, and total nitrogen in % of dry weight) and heavy metals (Hg, Cu, Cr, Ni, Pb, As, Cd, Zn in mg/kg dry weight) for each selected increment. In this study, the concentration of Hg was chosen as a proxy for heavy metals due to its prevalence as a major pollutant in the area and its biogeochemical reactivity (Faganeli et al., 2003; Vidovic et al., 2016; Gallmetzer et al., 2019).

2.4 Core stratigraphy and sediment composition

Different depositional environments and stratigraphic histories are represented by the sampling sites. Except for Piran 1 and Piran 2, which have similar sedimentary characteristics and stratigraphy, the three locations in the northern Adriatic Sea differ significantly in molluscan community composition, sediment composition, and grain size (Mautner et al., 2018; Schnedl et al., 2018; Gallmetzer et al., 2019; Tomašových et al., 2019). After sea level and circulation had reached their modern state during the eHST in Brijuni and Venice, or during the MFZ in Piran, different benthic communities emerged and persisted for several hundred to thousand years (Gallmetzer et al., 2019). They represent the baseline communities in these areas, which have declined due to intensifying historical or very recent anthropogenic impacts, depending on the sampling station (Gallmetzer et al., 2019). The results of previous analyses of the core stratigraphy and sediment composition are summarized in the following sections.

2.4.1 Brijuni

Station Brijuni is situated within the Brijuni Islands National Park in Croatia ~ 400 m offshore. This area has largely been spared from extensive commercial and public use since the late 20th century, as fishing activities are banned in this location since 1983 (Fatović-Ferenčić, 2006). The current water depth is ~ 44 m, the seabed consists of muddy sand and signs of mucilage cover were present at the time of sampling (Gallmetzer et al., 2019). The sand and gravel within this core are largely of biogenic origin and consist mainly of fragments of mollusc shells, crustacean exoskeletons, and bryozoan colonies.

The core can be stratigraphically subdivided into six units (Tab. 2). In the lower part of the core, the TST unit is characterised by a transition from a terrestrial to a marine setting, with a shallow water environment established in the early TST (Gallmetzer et al., 2019). The MFZ unit comprises a shell-bed featuring large, strongly bored shells covered by encrusting bryozoans, serpulids and coralline algae, and at the end of the MFZ bryozoans start to increase in abundance. The eHST consists of coarser sediment in the lower part and finer sediment in the upper part. The lHST unit represents the anthropogenically impacted phase and an increase in total organic carbon among other pollutants in the uppermost 10 cm. The strong up-core change in grain size composition is overall characterized by a fining-upward trend, featuring a considerable amount of molluscan gravel at the base, bryozoan-molluscan sand at the upper part, and a higher proportion of coralline algae at the uppermost part where silt and clay compose ~ 80% of the sediment.

Time averaging, estimated as the interquartile age ranges (adjusted for age error) for *T. ovata* in the 5-cm increments, predominantly fall within the range of 500 to 1,000 years (Gallmetzer et al., 2019; Tomašových et al., 2022). Based on ^{210}Pb sediment dating, the sedimentation rate has been ~ 0.15 cm/year during the deposition of the lHST unit. This exceeds the sedimentation rate estimates based on down-core changes in median ages of *T. ovata*, which range between ~ 0.01-0.04 cm/year (Gallmetzer et al., 2019).

2.4.2 Piran 1 and Piran 2

Station Piran 1 is located 2.3 km off the Slovenian coast within the protected zone of an oceanographic buoy from the Marine Biology Station Piran, and station Piran 2 is located ~ 2 km further offshore in unprotected waters. Both are located at a water depth of ~ 22 m

and are characterized by similar grain size composition and stratigraphy, exhibiting a coarsening-upward trend (Gallmetzer et al., 2019). At the time of sampling, the sediment surface consisted of muddy sand with a high content of shell debris and patches of various epifaunal species, mainly sponges and ascidians and an abundant vagile fauna of ophiuroids, crustaceans and molluscs (Gallmetzer et al., 2019).

The cores cover the last ~ 10,000 years and can be divided into five stratigraphic units. In contrast to the other stations, the TST unit is considerably more expanded and the HST unit is condensed (Gallmetzer et al., 2019). The mud content decreased to 20% in the top 25 cm of the core while sand and gravel fractions increased, consisting of mollusc shells, fragments of echinoderms and crustaceans, and foraminifera. In both cores, a thick shell bed formed throughout the MFZ and remained active during the HST phase, in contrast to station Brijuni (Gallmetzer et al., 2019). This is most likely related to increased water energy and decreased sedimentation rates at the Piran stations throughout the Holocene (Gallmetzer et al., 2019).

The ^{210}Pb dating of the sediments shows that the sedimentation rate in the HST unit is about 0.29 cm/year at station Piran 1 and 0.16 cm/year at Piran 2 (Gallmetzer et al., 2019). The interquartile age ranges of dated shells vary mainly between 1,000-2,000 years (Tomašových et al., 2019).

2.4.3 Venice

The station Venice is located most offshore, about 18 km south-east of Venice Lagoon at a water depth of 21 m, and the sediment in this core is almost pure, well-sorted siliciclastic sands. At the time of sampling, the seabed was covered with large amounts of shell debris mixed with rhodolites and sporadic sessile and vagile epifauna (Gallmetzer et al., 2019).

The bottom of the core reaches back ~ 9,000 years BP and can be subdivided based on changes in the composition of biogenic components of the sediments (Gallmetzer et al., 2019). During the time of deposition of the lower part of the core, seagrass meadows were established at the site but already receded during the eHST and had largely disappeared in the lHST phase (Gallmetzer et al., 2019). As published in Gallmetzer et al. (2019), the similarity of the median ages of *L. divaricata* shells from the 5-cm intervals within the five stratigraphic units suggests considerable sediment mixing.

Fitting the ^{210}Pb excess values against sediment depth at 10-50 cm indicates that apparent sedimentation rates are 0.88 cm/year. This value is much higher than estimates based on down-core changes in median ages of *L. divaricata* over the same stratigraphic interval, which indicate net sedimentation rates of ~ 0.01-0.05 cm/year throughout the Holocene (Gallmetzer et al., 2019). This implies that the ^{210}Pb profiles are steepened by incomplete mixing to 50 cm at Venice, below the base of the fully mixed surface layer (Gallmetzer et al., 2019). Thus, a major hiatus in sediment accumulation is indicated by an abrupt shift in median age from 3,700 to 6,300 years between the 100-105 cm (MFZ) and 110-115 cm (TST) increments (Gallmetzer et al., 2019).

2.5 Data collection and analysis

2.5.1 Data collection

All *E. pusillus* tests and fragments were sorted from the > 1 mm sediment fraction of the five sediment cores using a stereomicroscope. One sediment core per sampling station was assessed, except for Piran 1 where two cores were investigated. Additionally, one grab samples per station was examined. Every whole and incomplete test with > 50 % preservation, and fragments with an intact periproct were counted as an individual for the abundance analysis. For the test size analysis, only whole tests and fragmented specimens, for which either length or width could be measured were included (Tab. 3).

The data from two cores (M1 and M23) from station Piran 1 were combined to increase the sample size of *E. pusillus* tests for size analysis. The maximum dimension along the anterior-posterior (length) and lateral (width) axis was measured using the Microscope ZEISS SteREO Discovery V20 and ZEN software.

Table 3 – Overview of the total number of E. pusillus individuals and number of tests used for size analysis in all cores and grab samples.

Station locality	Core/ Grab sample	Number of individuals	Number of tests for size analysis
Brijuni	M44	2,599	2,246
	Grab 4	55	28
Piran 1	M1	85	51
	M23	103	69
	Grab 1	54	28
Piran 2	M53	145	111
	Grab 8	47	26
Venice	M38	91	63
	Grab 4	97	59

The 2-cm increments in the uppermost 20 cm of the sediment cores were combined into 4-cm increments for the analyses for better comparison with the 5-cm increments below. Owing to the different diameters of the sediment cores, and in order to allow a more accurate comparison of abundance between the sampling stations, the counted number of *E. pusillus* specimens per increment was converted to density calculated as the number of individuals per 100 cm^3 (ind/100 cm^3). The mean of the number of tests in each corresponding increment of the two Piran 1 cores was utilised here. The proportion of fragmented tests is calculated as the percentage of tests with both dimensions measured relative to the total number of specimens, which include fragments and tests where only length or width were measured.

To increase sample size for the test size analysis all measurable tests from the grab samples were included in the IHST unit of each of the sampling stations. To analyse the spatial and temporal changes in the size-frequency distribution all increments of the cores were grouped according to the stratigraphic units.

2.5.2 Statistical analyses

In most incomplete *E. pusillus* specimens, the posterior region of the test is preserved, and consequently only their width could be measured. Therefore, to estimate the length of fragmented specimens based on their measured width, an ordinary least squares (OLS)

regression model was fitted to the size data from complete specimens (Fig. 4). The OLS regression suggests that the model is a good fit for the data (R^2= 0.99, F = 22.86, p < 0.001).

The size of *E. pusillus* tests was calculated as the geometric mean of the length and width. Because size-frequency distributions of test size are right-skewed, and to assess changes throughout the Holocene, the median test size per stratigraphic unit was compared using the non-parametric Kruskal-Wallis test to detect significant differences and post-hoc pairwise Wilcoxon test if applicable. The Kruskal-Wallis test is often used for data with non-equal variances and significant differences can indicate differences in median and dispersion.

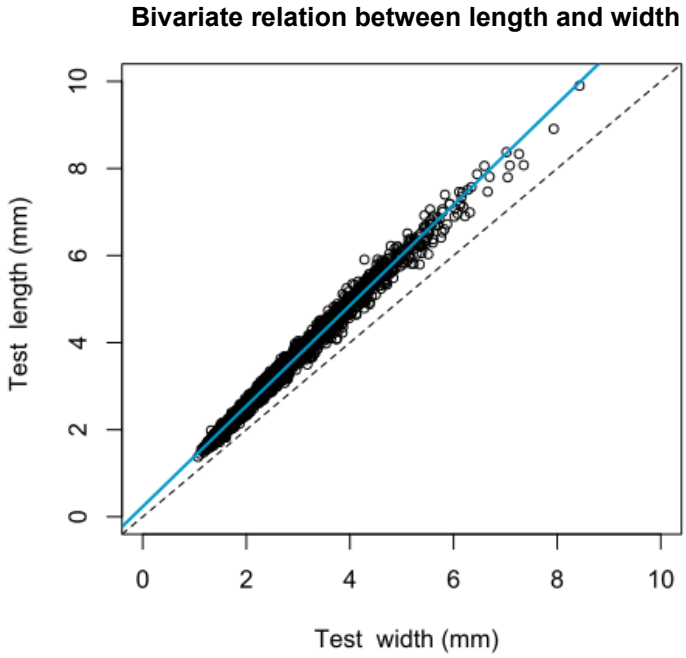

*Figure 4 – Relationship between test length and width (blue line). The dashed line shows the best fit regression line. Length = 0.23 + 1.16 * width.*

Non-metric multidimensional scaling (NMDS) ordination was used to visualize the general pattern of changes in test size across sampling stations and stratigraphic units in an approach similar to the one used by De Baets et al. (2022). Dissimilarity between the size-frequency distributions representing different stations and stratigraphic units is based on the Kolgomorov-Smirnov (KS) distance. The KS distance ranges from 0 to 1 and quantifies how dissimilar the empirical distributions are from each other. Lower values indicate that

the distributions are more similar in a non-parametric way. Samples with <15 measured specimens per station and stratigraphic unit were excluded from this analysis.

All data analyses were carried out in R version 4.3.1 (R Core Team, 2023).

2.5.3 Radiocarbon dating of *E. pusillus* specimens

Eighty tests of *E. pusillus* were dated by ^{14}C accelerator mass spectrometry (AMS) using the MIni CArbon DAting System (MICADAS) with direct CO_2 gas input (Synal et al., 2007) at the Arizona Climate and Ecosystems Isotope Laboratory, Northern Arizona University.

From the lHST unit of each station, 20 specimens were randomly selected, each with at least 40% of the test preserved and weighing at least 0.5 mg. Depending on the number of available tests the material from either the uppermost core increments or from the grab samples was used. All designated tests were cleaned by sonication for several minutes in distilled water in an ultrasonic bath, until all impurities and infilling sediment were eliminated. Afterwards they were dried, photographed (aboral, oral, and lateral view), measured and weighed before the radiocarbon dating procedures. During the cleaning process, it was observed that several specimens from station Brijuni contained cemented calcite within the test, which could not be removed by sonication. These tests are unsuitable for radiocarbon dating as the presence of theses cements could distort the results and they were therefore not used for dating.

Radiocarbon ages were calibrated to calendar ages using the “rcarbon” R package version 1.4.4 (Crema & Bevan, 2021), Marine20 curve (Heaton et al., 2020) and the regional marine reservoir correction (ΔR) of -152 ± 39 years for the north-eastern Adriatic Sea based on the average of estimates from Siani et al. (2001) and Peharda et al. (2019). The ages are reported as years before present (years BP, relative to the year 1950 AD) and the interquartile age range (IQR) was used to measure the extent of time averaging.

E. pusillus tests from core M53 of the Piran 2 station that were previously dated (Nawrot et al. 2022) were also included in this study. The tests (N = 25) were taken from the 20-30 cm core increment, assigned to the MFZ unit. The calibrated ^{14}C ages suggest millennial time averaging in the MFZ phase (median age = 5,472 years BP, IQR = 1,980 years).

3 RESULTS

A total of 3,023 specimens across all five cores and 253 specimens in the four grab samples were counted. Overall, the abundance of *E. pusillus* tests in northern Adriatic death assemblages shows strong spatial and stratigraphic variation, while median test size remains stable.

The spatial variability of test density across the stations is pronounced (Fig. 5). The highest density of 75 ind/100 cm^3 is recorded in the TST unit at Brijuni, while the highest test densities at the other stations do not exceed 3 ind/100 cm^3. The general trend of *E. pusillus* densities at the Brijuni core is opposite to the one observed at the Piran 1 and Piran 2 stations. Venice records fluctuating density since the increase at the end of the TST unit.

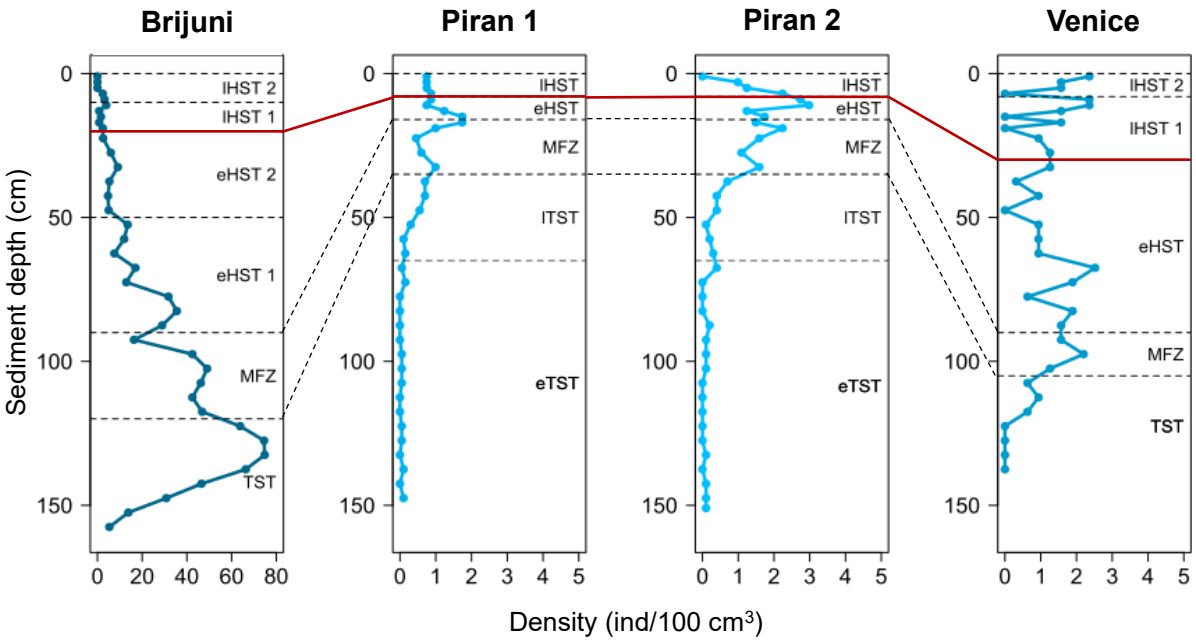

Figure 5 – Density of E. pusillus tests in the sediment cores from the four stations. The red line indicates the lower boundary of the increments of the IHST unit. Note a different scale for station Brijuni, which contains an order of magnitude higher densities compared to the other stations.

The number of specimens in each of the grab samples is similar across all stations. The grab sample from Brijuni contained a total of 55 individuals, 54 individuals were counted in Piran 1 and 47 individuals in Piran 2. The grab sample from Venice contained the highest number of 97 individuals (Tab. 3).

3.1 Stratigraphic trends in abundance

3.1.1 Brijuni

Compared to the other stations, Brijuni stands out due to its substantially higher total abundances (Tab. 3) as well as due to the strong decline at the onset of the lHST phase, with almost no tests present in the upper 20 cm of the sediment core (Fig. 6).

Across the northern Adriatic Sea, *E. pusillus* reaches the highest densities in station Brijuni with a total of 2,599 counted specimens. The peak in the number of tests (~ 75 ind/100 cm^3) occurs in the core increments between 125-135 cm, at the top of the TST unit, and begins to decline during the transition to the MFZ unit. At the beginning of the eHST unit

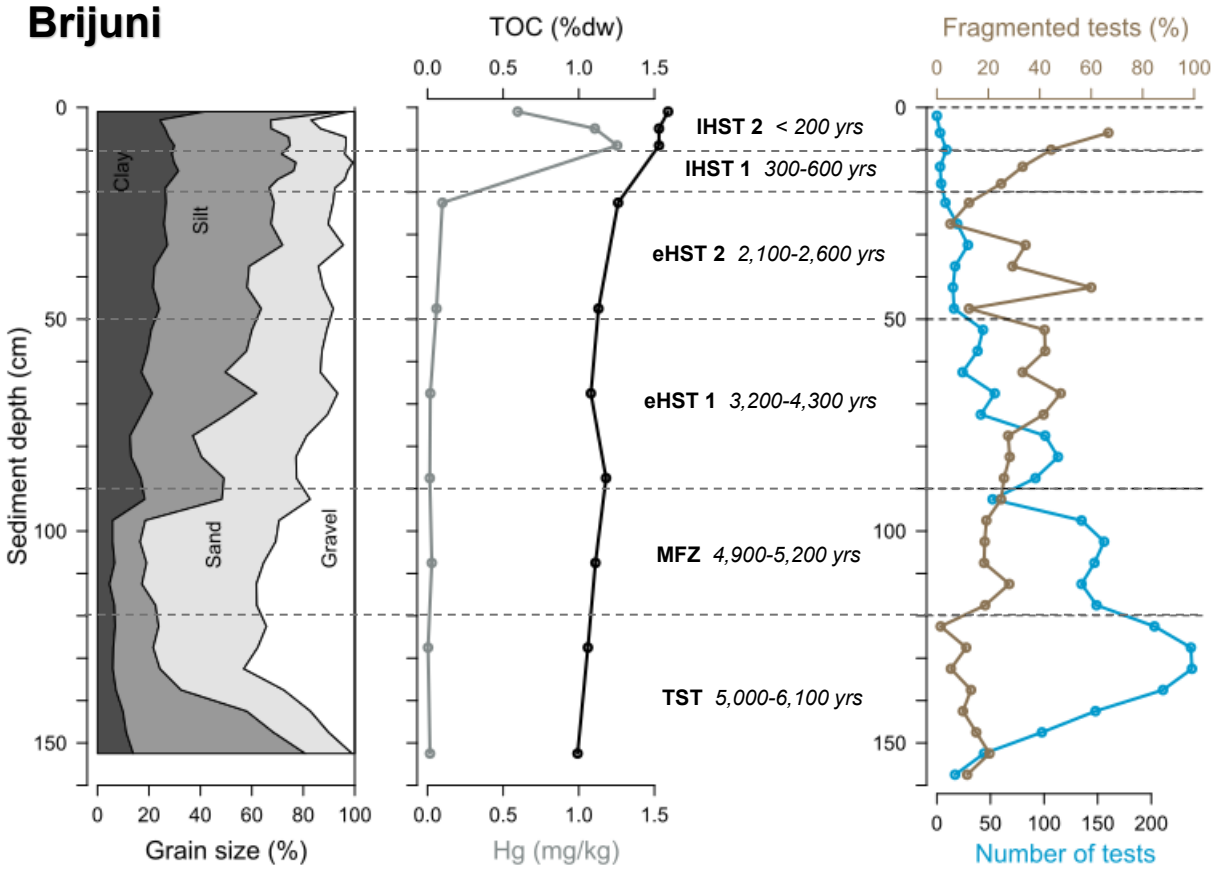

Figure 6 – Grain size composition, concentration of total organic carbon (TOC) and mercury (Hg), the number of E. pusillus tests per core increment and the proportion of fragmentation at station Brijuni. The age ranges (yrs BP) of the stratigraphic units are based on dated bivalve shells. Data from Gallmetzer et al. (2019).

abundance increases again to ~ 34 ind/100 cm^3 between 75-85 cm core depth, but the successive decline continues throughout the eHST unit. Nearly no specimens (only two intact tests) are present in the uppermost 10 cm of the core, covering the last ~ 200 years.

The variation in the abundance of *E. pusillus* is particularly pronounced at this station with only 19 individuals present in the lHST unit in contrast to 1,196 individuals in the TST unit. The percentage of fragmentation follows an opposite trend in relation to total abundance. In this core the proportion of fine sediment particles and concentration of TOC increase upwards, and a pronounced peak of mercury is present in the lHST unit (Fig. 6).

3.1.2 Piran 1 and Piran 2

In contrast to the high number of specimens at station Brijuni, the two sediment cores from station Piran 1 (Fig. 7) only contained a total of 188 specimens and the core from station Piran 2 (Fig. 8) contained 145 specimens. Overall, the two stations show a similar trend of test abundance, and an inverse trend compared to station Brijuni. The proportion of fragmented tests exhibits an opposite trend relative to the total abundance in Piran 1 (Fig. 7), while in Piran 2 it follows a similar course (Fig. 8). The TST in the Piran cores is expanded and represents the stratigraphic unit with the lowest number of individuals. In the lower part of the core the specimen density does not exceed ~ 1 ind/100 cm^3. At the top of the TST unit, the number of *E. pusillus* specimens increases until the onset of the

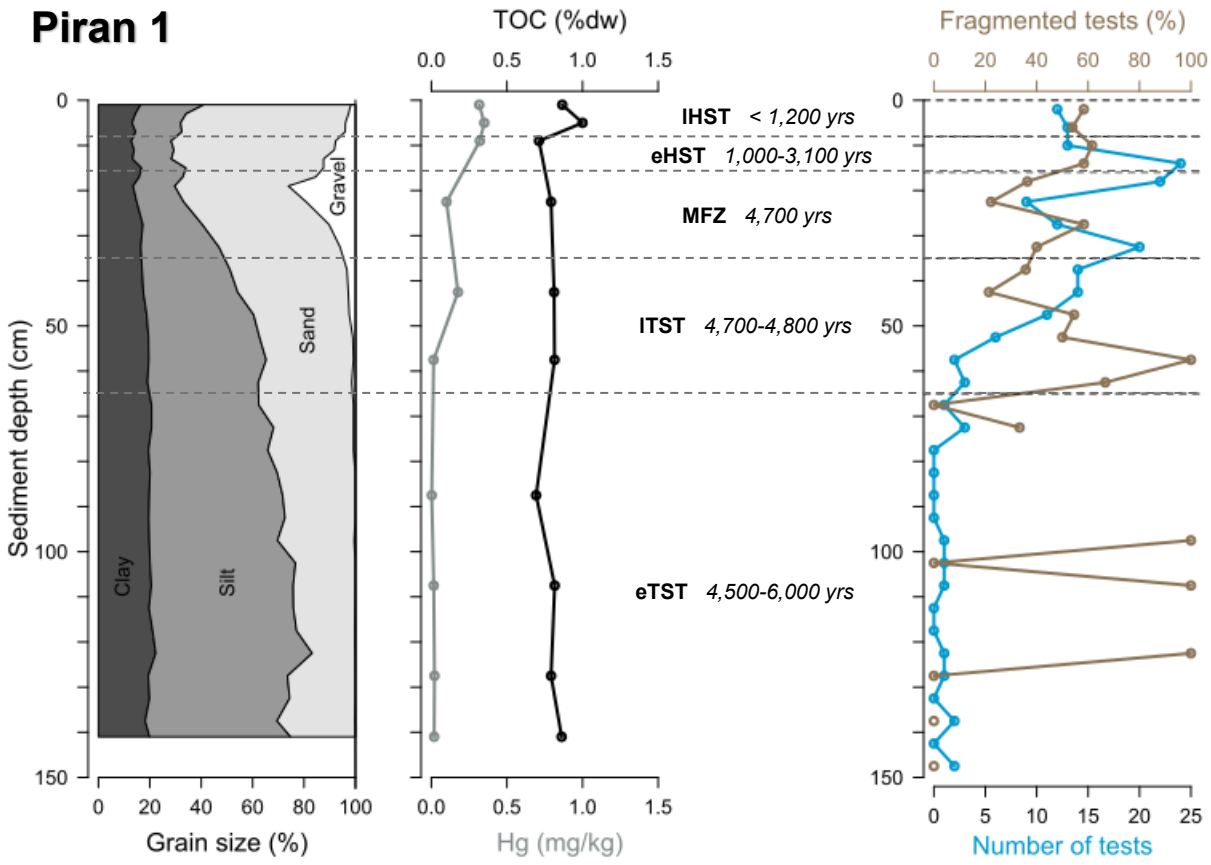

Figure 7 – The variables grain size composition, concentration of total organic carbon (TOC), mercury (Hg) content, and the number of E. pusillus tests in relation to fragmentation throughout the core at station Piran 1. The TST units are significantly expanded, while the lHST and eHST units are strongly condensed. The age ranges (yrs BP) of the stratigraphic units are based on dated bivalve shells. Data from Gallmetzer et al. (2019).

MFZ unit, where it decreases slightly. The abundance reaches its peak in the condensed eHST unit and declines strongly again in the lHST. The highest density of specimens (~ 3 ind/100 cm^3) occurs between 8-12 cm in the eHST unit in station Piran 2 (Fig. 5).

Both sediment cores are characterized by a coarsening-upward trend in grain size (Fig. 7; Fig. 8). At station Piran 1, the TOC content remains relatively stable throughout the core, only with a peak in the lHST unit. At Piran 2, the TOC content remains stable throughout the core. However, mercury concentrations at this station exhibit a strong peak at the boundary between the eHST and lHST units, which is less pronounced at Piran 1.

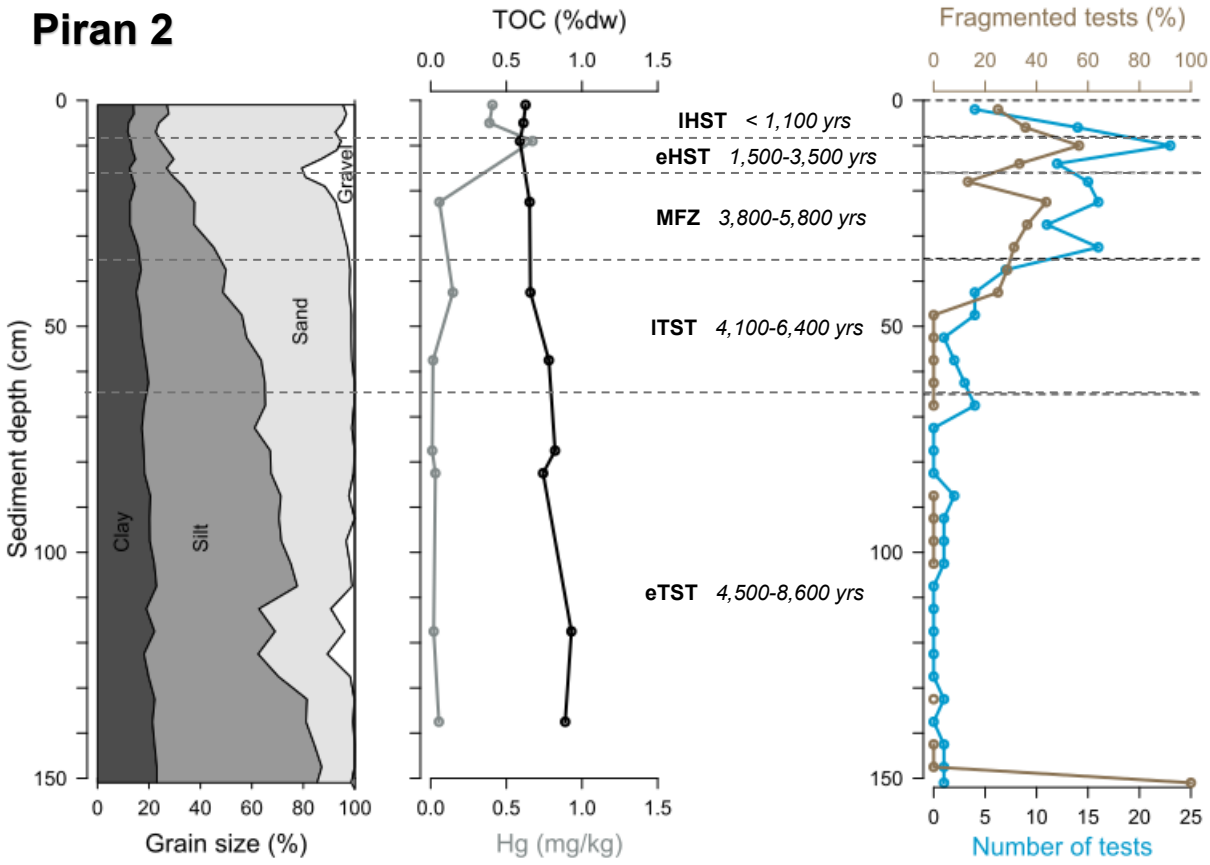

Figure 8 – Stratigraphic changes in grain size, content of total organic carbon (TOC) and mercury (Hg) along with the total abundance of E. pusillus in relation to fragmentation at station Piran 2. The age ranges (yrs BP) of the stratigraphic units are based on dated bivalve shells. Data from Gallmetzer et al. (2019).

3.1.3 Venice

The sediment core from station Venice has only 91 *E. pusillus* tests in total, with the lowest number of specimens counted in the TST unit. The sediment composition at this station consists almost exclusively of sand and the content of TOC and mercury is relatively low throughout the core (Fig. 9). The overall highest number of tests is recorded in the eHST unit, and the maximum density of ~ 3 ind/100 cm^3 occurs in the 65-70 cm increment (Fig. 5). The density in the lHST unit is more stable compared to the eHST and ranges between 1-2 ind/100 cm^3. However, there is no consistent trend in abundance and the proportion of fragmented tests is relatively high along the sediment core (Fig. 9). Venice is the only sampling station, where live *E. pusillus* specimens were found in the grab samples. A total of four living individuals were recovered in three out of the eight grab samples.

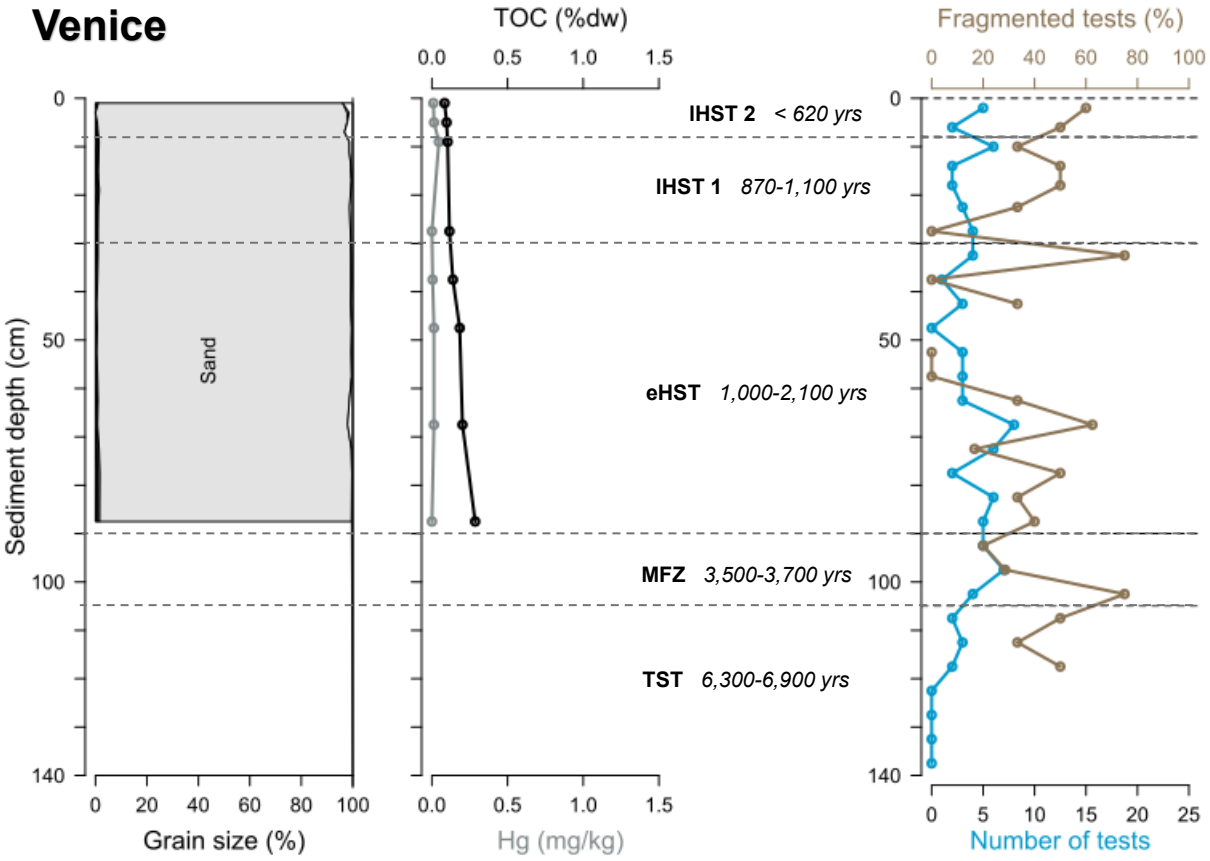

Figure 9 – Grain size composition, concentration of total organic carbon (TOC) and mercury (Hg), the number of E. pusillus tests per core increment and the proportion of fragmentation at station Venice. The age ranges (yrs BP) of the stratigraphic units are based on dated bivalve shells. Data from Gallmetzer et al. (2019).

3.2 Temporal and spatial trends in test size

A total of 2,681 *E. pusillus* tests were measured in all five sediment cores and four grab samples. Both the smallest (1.38 mm) and the largest test length (9.90 mm) was recorded in the TST unit at station Brijuni. The largest median test size and the highest number of measured specimens per stratigraphic unit were also observed in this station (in the lHST and TST units respectively; Tab. 4). Based on the observed size classes, with median test lengths across all stations and stratigraphic units of 2.34-3.37 mm, it can be assumed that the death assemblages are dominated by adult specimens (Warwick & Pearce, 2020).

Table 4 – Median test sizes in mm per stratigraphic unit. The 95th quantile in mm in the brackets. N denotes the number of measured tests per unit. The two cores from station Piran 1 are combined and the grab samples are included in the lHST unit.

	N	**Brijuni**	***N***	**Piran 1**	***N***	**Piran 2**	***N***	**Venice**
lHST	*43*	3.26 (6.53)	*41*	2.36 (3.48)	*40*	2.49 (3.97)	*74*	2.68 (4.04)
eHST	*462*	3.07 (5.66)	*21*	2.45 (3.66)	*20*	2.45 (3.53)	*33*	2.58 (4.31)
MFZ	*655*	3.02 (5.35)	*44*	2.27 (3.49)	*45*	2.11 (3.57)	*11*	2.28 (4.06)
TST	*1,117*	3.02 (5.29)	*42*	2.29 (3.18)	*31*	2.23 (3.03)	*4*	2.41 (3.33)

Figure 10 shows the size-frequency distribution grouped according to the sampling station (Fig. 10A) and according to stratigraphic unit (Fig. 10B). When data are combined within each core, the highest median and 95th percentile test size occur in Brijuni (Fig. 10A). The Kruskal-Wallis test results indicate that median test sizes differ significantly between Brijuni and the other stations (χ^2 = 181.79, *df* = 3, $p < 0.001$). The median test sizes at station Venice are also significantly larger than those at the Piran 1 and Piran 2 stations. Station Piran 1 and Piran 2 are the only stations without significant differences in median test sizes (Tab. 5).

Across all stations combined, the four stratigraphic units are characterized by similar median test sizes, with only a slight decrease in the lHST unit (Fig. 10B). This unit shows significantly lower median test sizes compared to all other stratigraphic units (Kruskal-Wallis test: $\chi^2 = 22.12$, $df = 3$, $p < 0.001$; Tab. 5).

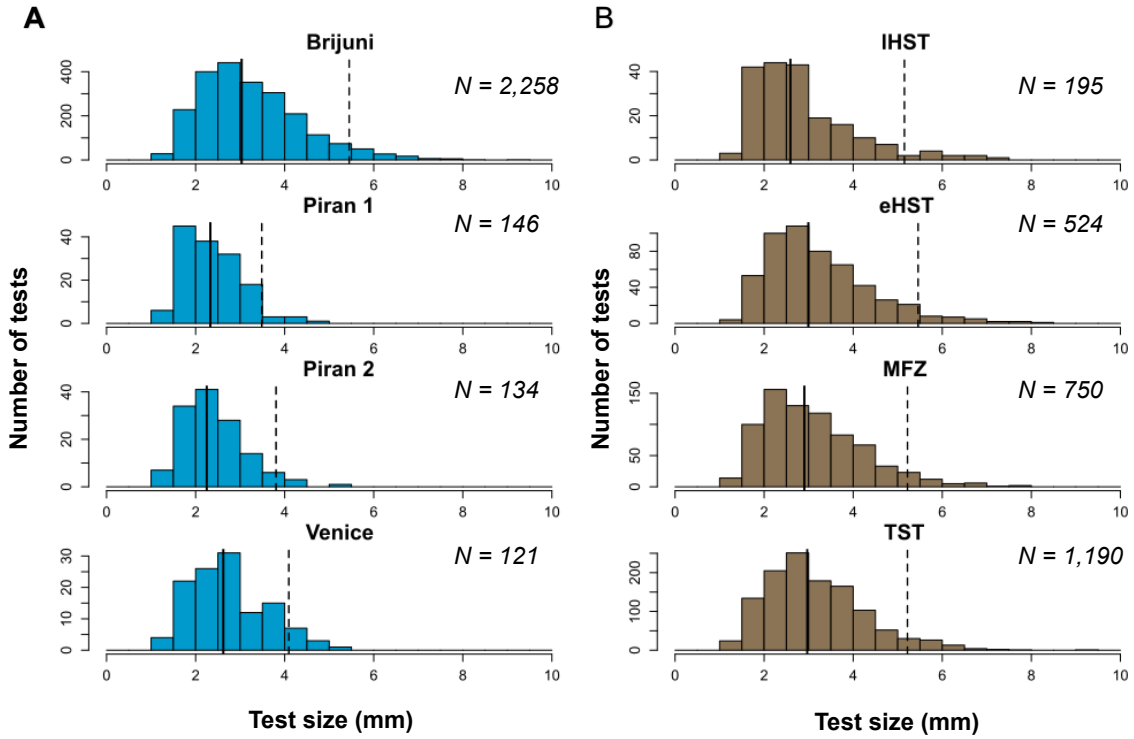

Figure 10 – Size-frequency distribution based on data grouped according to sampling station (A) and according to stratigraphic unit (B). The black line represents the median test size and the dashed line the 95th quantile.

Station Brijuni records the largest sample size and median test size which is reflected in the size-frequency distribution across the stratigraphic units. But this station is also the only station that records a strong decrease in the number of specimens in the uppermost lHST unit relative to the lower units (Fig. 11).

Table 5 – The post-hoc pairwise Wilcoxon test results with Holm's correction indicate significant differences in median test size between all sampling stations except Piran 1 and Piran 2 (A) and between the lHST unit and all other stratigraphic units (B). Significant differences are marked by (*).

A	Brijuni	Piran 1	Piran 2
Piran 1	*<0.001**		
Piran 2	*<0.001**	*0.905*	
Venice	*<0.001**	*0.002**	*0.003**

B	TST	MFZ	eHST
MFZ	*0.341*		
eHST	*0.421*	*0.175*	
lHST	*<0.001**	*0.005**	*<0.001**

When viewed at a finer resolution, the median test size within the sampling stations shows overall stability with no significant differences between the stratigraphic units (Fig. 11; Tab. 6). The frequency of smaller test sizes in the stratigraphic units at Piran is higher than in Brijuni and Venice.

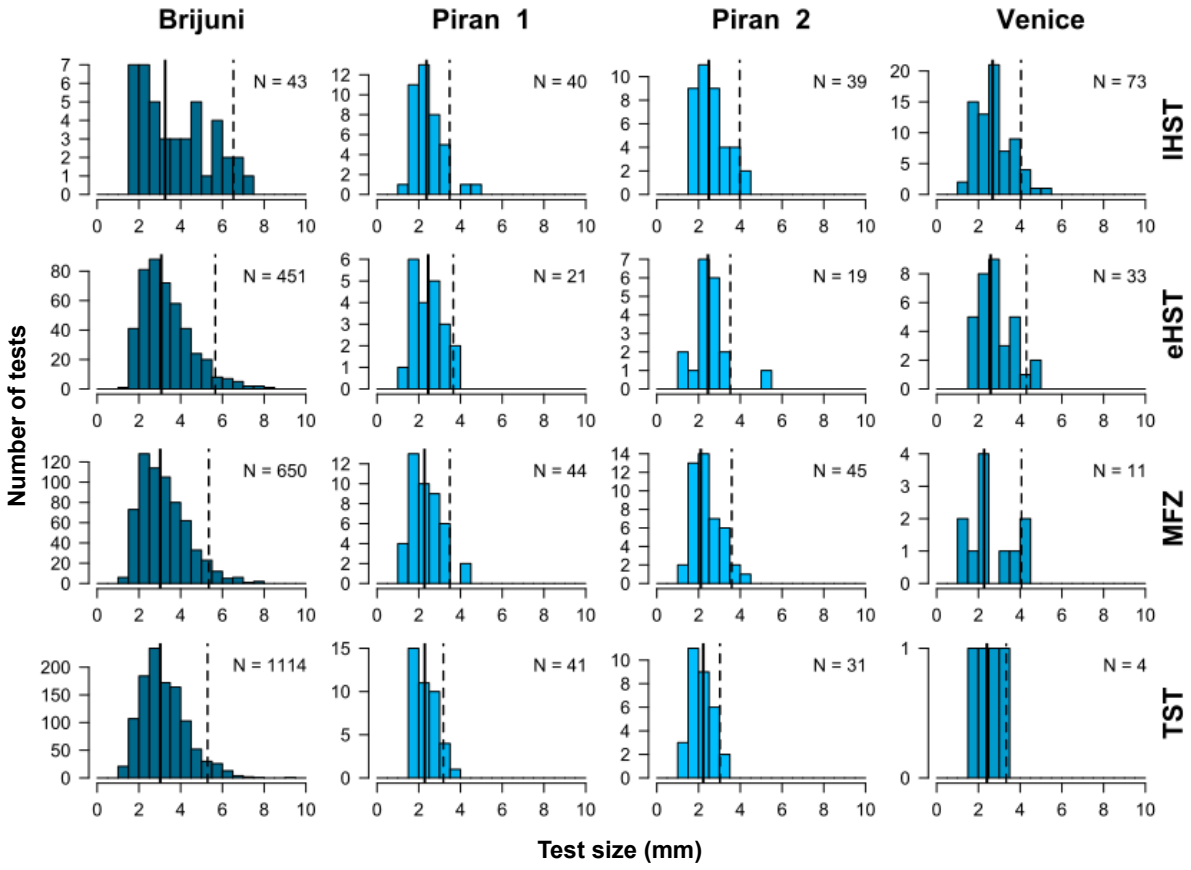

Figure 11 – Size-frequency distribution across all stations and stratigraphic units. The black line represents the median test size and the dashed line the 95th quantile.

At station Brijuni, test sizes remain stable and slightly shift towards larger sizes in the lHST unit. This unit exhibits a different, heavy-tailed, almost bimodal distribution compared to the other stratigraphic units at this station, which show a right-skewed unimodal distribution. The median test size in the lHST unit at station Brijuni is the largest (3.26 mm) across all stations and stratigraphic units and the smallest is present at station Piran 2 in the MFZ unit (2.11 mm; Tab. 4).

Table 6 – The Kruskal-Wallis test results indicate no significant changes in median test sizes between the stratigraphic units in each station.

	N	**χ^2**	***df***	***p*-value**
Brijuni	2,277	4.08	3	*0.253*
Piran 1	148	0.73	3	*0.866*
Piran 2	136	6.77	3	*0.080*
Venice	122	0.56	3	*0.906*

These differences are also apparent when the data is visualized as NMDS (Fig. 12), where the sample from the lHST unit in Brijuni plots further away from the other stations and stratigraphic units. Although there are no statistically significant differences in median test sizes across all stratigraphic units and stations (Tab. 6), it is worth noting that the median test size in Brijuni is 3.26 mm, which is larger than in the older units at this station (3.02 mm) and more than 1 mm larger compared to the other stations, even though the sample sizes are comparable (Tab. 4).

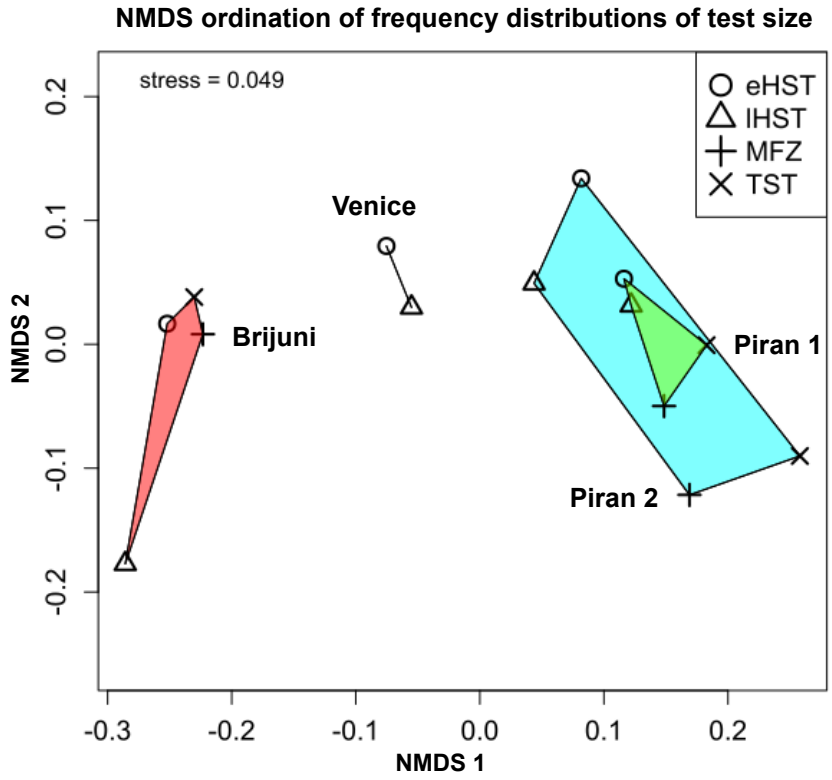

Figure 12 – NMDS ordination of the four sampling stations according to frequency distributions of test size within stratigraphic units. Samples with <15 measured specimens per stratigraphic unit and sampling station were excluded.

3.3 Time averaging of *E. pusillus* assemblages

Based on the calibrated radiocarbon dating results, the median post-mortem age of the eighty analysed specimens from the surface mixed layer is 894 years BP and ages range from 43 to 6,554 years BP (IQR = 373 years) (Table 7).

Table 7 – Median ages in years BP, interquartile range (IQR), range in years and sample size (N) in each station.

	Brijuni	Piran 1	Piran 2	Venice
Median age	3,390	834	875	446
IQR	658	614	306	247
Range	112-6,074	43-6,230	114-6,554	98-1,199
N	*20*	*20*	*20*	*20*

The frequency of post-mortem ages shows a right-skewed and long-tailed distribution dominated by specimens younger than 2,000 years BP (Fig. 13A). When considering the last millennia in more detail, most specimens were dated to the late 18th and early 19th centuries (Fig. 13B). The age-frequency distribution shows a long tail of moderately frequent older tests. Remarkably, however, there is a complete absence of tests with post-bomb age (i.e. younger than 1950 AD).

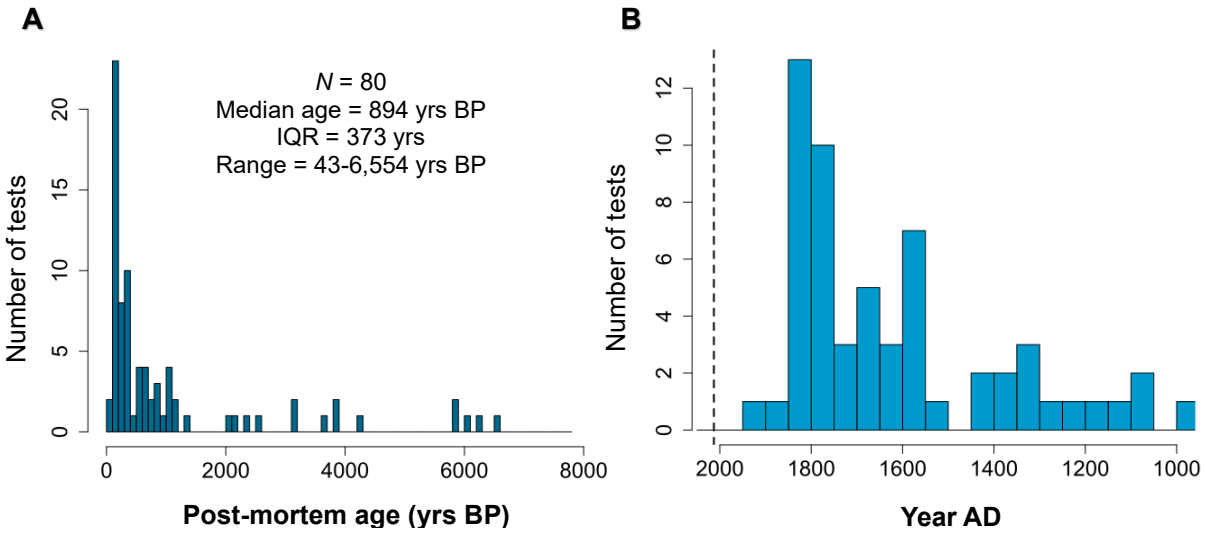

Figure 13 – The frequency of post-mortem ages of all radiocarbon-dated specimens from the surface mixed layer including the first 8-10 cm of the sediment cores and grab samples (A). The last 1,000 years magnified, with the dashed line marking the year 2013, when the sediment cores were collected (B).

Brijuni is the most time-averaged station with a median age of 3,390 years BP and shows a heavy-tailed right-skewed distribution and most tests were dated to the late 16th century. In contrast, at station Venice the median age is 446 years BP, the youngest among the four stations, with the range of 98 to 1,199 years (Fig. 14A; Tab. 7). Here, most tests originate from around the late 18th and early 19th century and no tests older than the past millennia are present (Fig. 14B).

Table 8 – The p-values of the pairwise Wilcoxon test with a-posteriori Holm's correction were used to compare the post-mortem age-frequency distributions in the four stations. Significant differences in median age are marked by (*).

	Brijuni	**Piran 1**	**Piran 2**
Piran 1	0.414		
Piran 2	0.220	0.028*	
Venice	0.025*	0.210	<0.001*

When comparing the frequency of median ages, a Kruskal-Wallis test indicated significant differences between the four stations ($\chi^2 = 20.25$, $df = 3$, $p < 0.001$). The post-mortem age-frequency distributions show significant differences in median age between station Venice and samples from Brijuni and Piran 2, and between Piran 1 and Piran 2 as summarized in Table 8. IQR, quantifying the scale of time averaging, is lowest at station Venice and highest at station Brijuni. The specimen with the youngest post-mortem age (calibrated age: 43 yrs BP; 2σ error: 121 to 0 BP) corresponding to the earliest 20th century, was recorded at station Piran 1 (Fig. 14B). A complete absence of specimens that died after the mid-19th century is evident at the Brijuni and Piran 2 stations, while at the Venice station there is only one specimen that died after the mid-19th century. The age-frequency distributions at the Piran stations are similar, although Piran 2 shows a more thin-tailed distribution, and when considering the last millennia in detail, Piran 1 shows a bimodal distribution around the early 19th and mid-14th centuries, while Piran 2 has one peak around the end of the 18th century.

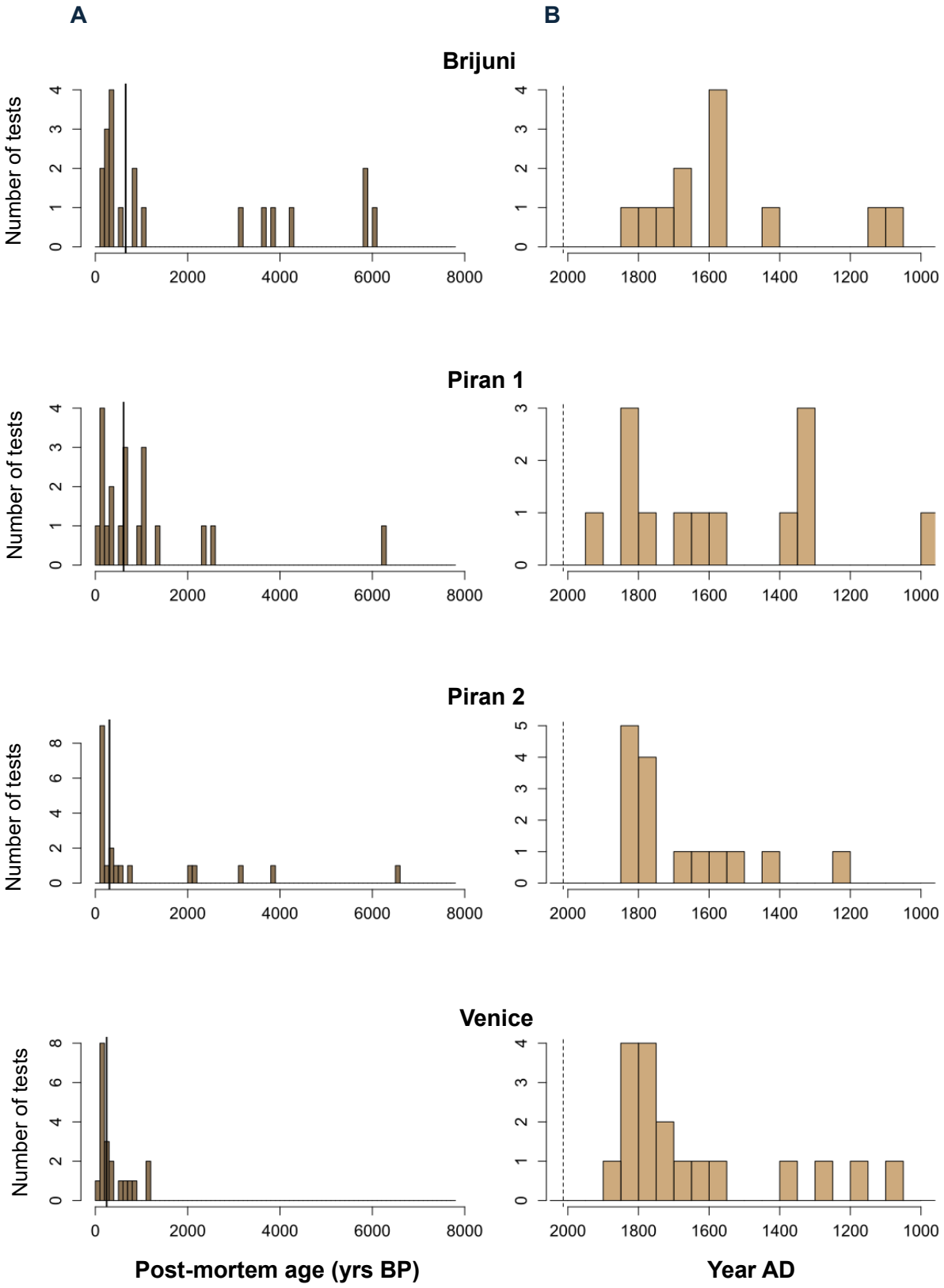

Figure 14 – Radiocarbon dating results corresponding to the surface mixed layer plotted per station (A) and higher resolution of the last 1,000 years (B). The black line marks the median age, and the dashed line marks the year 2013.

Figure 15 shows the test size in relation to the calibrated post-mortem age of the dated specimens indicating that there is no clear temporal trend towards larger or smaller test sizes, although station Brijuni is recording slightly larger test sizes in younger specimens. The post-mortem ages of samples from the mixed surface layer in Venice show similar ages and are all younger than ~1,200 years. Piran 2 is the only station where tests from the MFZ unit were additionally dated and analyzed by Nawrot et al. (2022) and are here compared to the tests from the top IHST unit. The distribution also suggests no change in test size over time when these data are included.

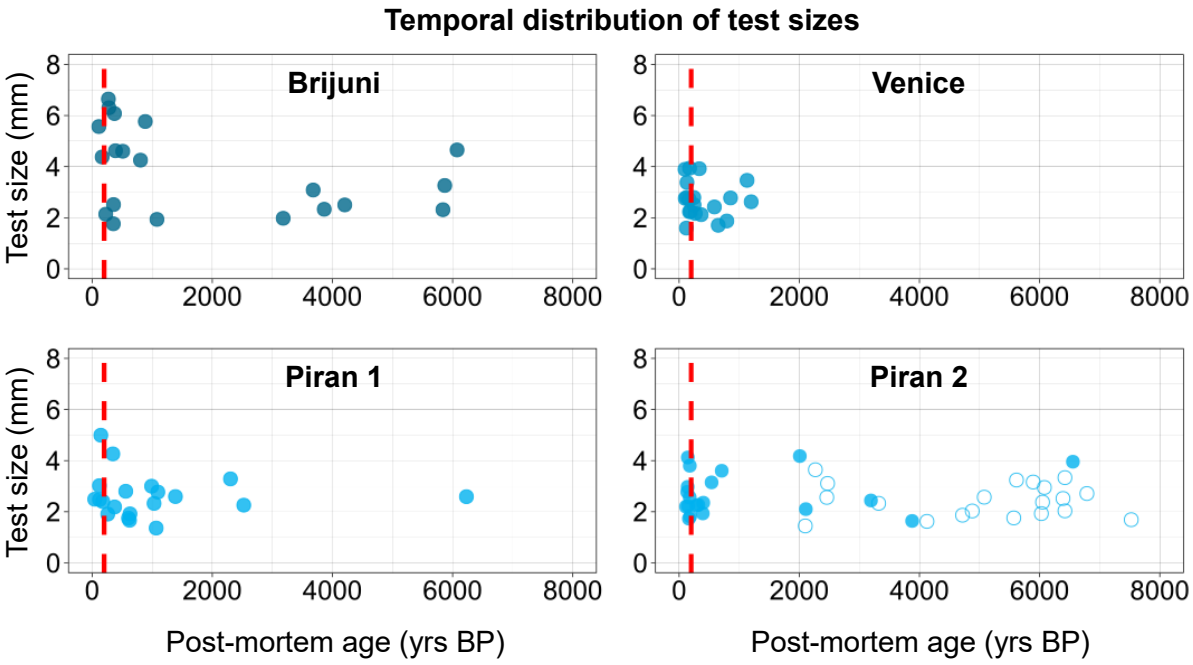

Figure 15 – Test size in comparison to calibrated radiocarbon-dated age (BP) at each station. The red line marks the last ~ 200 years. The filled circles represent specimens from the surface mixed layer. The non-filled circles in Piran 2 symbolize the previously dated specimens from the shell-bed in the MFZ unit (data from Nawrot et al., 2022).

4 DISCUSSION

Marine benthic organisms, owing to their limited mobility, are highly dependent on the conditions of their surroundings and vary in their tolerance to environmental stress, thus reflecting the abiotic factors that alter and shape the environment (Dauer, 1993). The northern Adriatic Sea has been subject to human alteration since early in its history, peaking already during the time of the Roman Empire and in the late Middle Ages due to extensive deforestation, land use and fishing activities (Beug, 1977; Oldfield et al., 2003; Kaligarič et al., 2006; Kranjc, 2009; Lotze et al., 2011). The impact on the ecosystem has increased substantially over the last ~ 200 years (e.g. Justić, 1991; Airoldi & Beck, 2007; Coll et al., 2012), far longer than the records of ecological monitoring. This makes long-term datasets necessary to disentangle natural variability from anthropogenic impacts. The approach of collecting and analysing sediment cores and grab samples enables us to compare the characteristics of benthic populations over time and in the framework of biotic and abiotic drivers, capturing population successions before, during and after severe anthropogenic impacts. Until now, most research using this approach has focused on molluscs, and the results indicate significant changes in community structure in response to human impacts (Gallmetzer et al., 2017, 2019; Tomašových & Kidwell, 2017; Fuksi et al., 2018; Mautner et al., 2018; Schnedl et al., 2018; Tomašovych et al., 2018, 2019, 2020; Haselmair et al., 2021). Specifically, some organisms adapt to eutrophication and degradation in the area by changing their body size, such as the opportunistic bivalve *Varicorbula gibba* (Fuksi et al., 2018). Size-frequency distributions of *V. gibba* in death assemblages across the northern Adriatic Sea reveal a strong shift towards higher abundances and larger body sizes. This shift is due to an abrupt ecological change affecting benthic communities during the twentieth century that can differentiate between Holocene and Anthropocene death assemblages (Tomašových et al., 2020).

The purpose of this study is to answer the question of whether we can observe similar trends in other groups of organisms, such as echinoids, and to provide new insights into the spatial and temporal distribution of an infaunal irregular sea urchin over the last ~ 10,000 years. The data presented in this study shows significant fluctuations in *E. pusillus* abundances coinciding with environmental changes over this period and across sampling stations, but notably stable test sizes, which will be discussed in more detail in the following chapters.

4.1 Spatial and temporal patterns in abundance of *E. pusillus*

Sediment composition controls the structure of benthic assemblages (e.g. Zuschin & Stachowitsch, 2009), and is especially important for echinoderms. The four sediment cores capture the ecological history on the regional scale and cover a wide range of low-sedimentation settings with different soft-bottom habitats, which is also reflected in the heterogeneous distribution of *E. pusillus* (Fig. 6).

Apart from strong stratigraphic differences between the sampling stations, the recent death assemblages obtained from the grab samples suggest a more homogeneous occurrence, except for Venice where almost twice as many specimens (N = 97) were counted, despite of the lowest test densities in the sediment core. No identifiable temporal trend is evident in Venice over the last millennia. This possibly reflects the properties of the sediment at this station, which show almost exclusively well-sorted sands throughout the core. In this context, it is worth noting that Venice is also the only station where living *E. pusillus* were collected.

Although the Brijuni station records the highest densities during the earlier phases of the Holocene transgression of the northern Adriatic basin, the number of tests in the grab sample (N = 55) is comparable to those from the Piran 1 (N = 54) and Piran 2 (N = 47) stations. This observation might imply a more uniform distribution across the northern Adriatic Sea and overlook the historical patterns in abundance of this species prior to anthropogenically induced environmental changes. This is particularly evident when considering the stratigraphic distribution at station Brijuni, where this species reached the highest sampled densities, but declined drastically during the last millennia (Fig. 6). Petović & Krpo-Ćetkovic (2016) studied the effects of depth and substrate type on the diversity and distribution patterns of echinoderms in the south-eastern Adriatic, and their results indicated that substrate type was the most important factor influencing the composition of echinoderm assemblages in the upper infralittoral zone. Considering these results, sediment properties become the most apparent driver of abundance. In fact, *E. pusillus* is known for its preference for coarse sediments, particularly shell hash, due to their high organic content and the increased oxygen flow between the particle interspaces of the uncompacted sediment (Ghiold, 1982). The historical success of this species in Brijuni can be explained by this observation since the record also shows different sediment

compositions during the stratigraphic phases of the flooding of the basin (Fig. 7). During the transgressive phase, higher water energy and coarser sediments provided well-oxygenated substrates, which were well-suited to this species. Subsequently, increasing water depth and siltation processes caused by soil erosion due to land use and deforestation in the early history (e.g. Poulos & Collins, 2002; Oldfield et al., 2003) contributed to the successive decline. Finally, increased anthropogenic pressures and their effects contributed to the pronounced decline of the population in Brijuni.

As summarized in Gallmetzer et al. (2019) epifaunal communities dominated by large bivalves at Brijuni were preserved in the core as a shell bed. However, different oceanographic regimes and increasing siltation facilitated the development of epifaunal assemblages mainly composed of bryozoans. As seen in this core, the siltation caused by human activity, through soil erosion due to deforestation and land use, can go back several millennia and is reflected in the molluscan community. The degradation by bottom trawling and hypoxia, on the other hand, has only become critical in the last century. These observations by Gallmetzer et al. (2019) are consistent with the overall pattern of test abundances in Brijuni. Consequently, this may explain the different signal in Venice located farther offshore compared to other stations. Here, in contrast, the highest numbers are recorded in the lHST unit, while finer sediment particles do not increase in the upper part of the core. This further supports the assumption that siltation, due to increased sediment supply following land-use changes, was the main driver for the decline of *E. pusillus*.

At Piran, however, sediment properties developed in the opposite direction along the stratigraphic phases. Abundances of *E. pusillus* increased and reached a maximum in the eHST phase after sea level and water circulation had reached their modern character (Fig. 8). Water energy increased and sedimentation rate declined, leading to the formation of coarser sediments. The sediment core shows a near absence of tests during the transgressive unit, with an increase in abundances at the end of this phase when the proportion of silt declines. Despite the opposite granulometric trend and well-suited substrate, *E. pusillus* abundances are also reduced in the uppermost lHST unit, indicating unfavorable environmental conditions for successful establishment in this area. This is most likely a consequence of increased human pressure on the ecosystem.

In the northern Adriatic Sea, the population dynamics in the transgressive and maximum flooding phases also correspond to natural environmental changes such as the deepening of sites due to sea-level rise and the associated establishment of the modern circulation

system in the northern Adriatic (Cattaneo & Trincardi, 1999), which led to a decrease in hydrodynamic energy at Brijuni, but an increase in current activity at Piran and Venice (Gallmetzer et al., 2019). The oceanographic changes caused by the increase in water depth are associated with a decrease in water energy and higher sedimentation rates, leading to sediment siltation and increased water turbidity at station Brijuni (Gallmetzer et al., 2019), which further intensified the impacts of siltation processes caused by land-use changes. This contrasts with the stations at Piran, where water energy has increased, and sedimentation rate has decreased over time.

With the establishment of the modern circulation system at the end of the TST (~ 7,000-6,000 years ago; Asioli et al., 1996), stronger bottom currents led to increased sorting of finer particles and reduced sedimentation rates. This allowed the *Arca* and oyster shell bed that had formed during the MFZ to remain active during the highstand phase at the Piran stations. In contrast, at station Brijuni increasing siltation led to the changes in epifaunal assemblages dominated by bryozoans (Gallmetzer et al., 2019). After sea level stabilization in the eHST, the established populations started to decline markedly with the intensification of human impacts in the lHST, that can be directly or indirectly related to this trend.

Similarly, in Belize's atoll lagoons, sediment cores from the Holocene period showed signs of potential mass mortalities of sea urchins like *Diadema antillarum* and *Echinometra* sp. (Gischler, 2010). This might have been due to shifts in local environmental conditions affecting lagoon circulation, along with temperature and precipitation changes in that specific area during the Holocene period (Gischler, 2010). However, the significant and widespread recent die-off of sea urchins in the Caribbean during the early years of the 1980s was unparalleled in its impact and was unprecedented compared to the Holocene (Gischler, 2010).

This human-induced degradation is also reflected in the overall molluscan assemblages in the northern Adriatic, as a decline in density and species richness at Brijuni and at both Piran stations, but not at Venice, and at the functional level, leading to infauna-dominated communities (Gallmetzer et al., 2019). Compared to infaunal molluscs, such as *V. gibba*, which are opportunistic and resistant, *E. pusillus* might be less competitive, especially given the fact that additional stressors in the northern Adriatic, such as hypoxic or anoxic events, increased drastically in the second half of the twentieth century (Justić, 1991; Stachowitsch, 1991; Tomašových & Kidwell, 2017), and echinoderms are generally known

to be more sensitive to hypoxia, with lower oxygen thresholds than other organisms (Diaz & Rosenberg, 1995; Gray et al., 2002; Riedel et al., 2012). This is also confirmed by the assignment of *E. pusillus* to species that are highly sensitive to organic enrichment and disturbance, as proposed by Borja et al. (2000) for the purpose of assessing ecological quality of soft-bottom benthos.

The *E. pusillus* occurrence in long-term sediment records suggests that the critical requirements for its successful establishment in benthic assemblages are not met anymore. This is also supported by other recent ecological studies from the eastern Adriatic Sea, which reported only six live specimens among numerous tests in Mljet National Park (Zavodnik, 2003) or 12 live versus 280 dead tests in grab samples from the Rijeka Bay in Croatia (Zavodnik & Kovačić, 2000) despite of intensive sampling efforts. In contrast, populations of *E. pusillus* on the Atlantic coast of Belgium can reach densities of hundreds of individuals per m^2 (Degraer et al., 2006). Although this species seems to be more aggregated than others, they can flourish almost to the exclusion of other forms and dominate in certain areas of the North Sea (Ursin, 1960).

However, it is important to point out the limitations of this study, namely the distinction between ecological and taphonomic effects. Time-averaging in particular can represent the first-order driver of the observed fossil abundance, since on the one hand high sedimentation rates can potentially cause dilution of fossil concentrations by the sediment, and on the other hand, low sedimentation rates can lead to stratigraphic condensation (Kidwell, 1985), causing a higher accumulation of tests in a given core increment. The application of absolute dating methods can aid in this aspect and offers another argument for the lack of adequate conditions for successful population establishment due to the absence of specimens from the last decades (Fig. 12). The calibrated radiocarbon age of the youngest specimen across all stations (from the grab sample from Piran 1) is ~ 43 years BP, while the median age of all dated specimens is 894 years BP (IQR = 373 years). This can indicate that the sediment is highly time-averaged but also that there are no, or at least rare recent occurrences of *E. pusillus* in the sampling area. The rarity of tests younger than early 19^{th} century and the lack of dated tests younger than ~ 1950 AD (i.e. those with post-bomb radiocarbon age) can only be explained by lower production of tests, and thus lower population densities during the last century compared to the historical baseline (Tomašových & Kidwell, 2017).

4.2 Test size dynamics

Changes in bottom water oxygen concentrations, temperature or food availability can often affect the size of benthic species, and analysing size-frequency distributions can therefore provide information on the functioning of modern ecosystems affected by anthropogenic impacts (Angilletta et al., 2004; Queirós et al., 2006; Reizopoulou & Nicolaidou, 2007; Beukema et al., 2014). In response to environmental stress, such as food limitation and cooling, echinoids reduce their body size (Salamon et al., 2016), while growth and mortality are affected by oxygen concentrations (Gray et al., 2002). Remarkably, the size-frequency distributions suggest a stable size structure of *E. pusillus* populations through time, despite significant environmental changes and fluctuations in its abundance (Fig. 10). It is important to note, however, that station Brijuni deviates from the other stations not only in terms of much higher abundances but also in larger test sizes (Fig. 9A), and consequently has the strongest effect on the overall distribution in each stratigraphic unit (Fig. 9B). Therefore, the slight decrease in test size in the lHST when all stations are analysed together can be explained predominantly by the low numbers of tests found in that unit in Brijuni, which may mute a possible increase in size occurring at individual stations. An additional factor is that low sedimentation rates result in multi-decadal or millennial time averaging, which strongly diminishes the temporal variance in body size and biases abrupt shifts towards gradual trends (Tomašových et al., 2020). However, the data of this study suggests that the lack of change in test size cannot be explained by temporal mixing alone, as all sampling stations, except Brijuni, show no significant differences in test size.

While changes in substrate characteristics and water energy summarized above could explain the spatial and temporal distribution of *E. pusillus*, the next question is whether these factors also influenced body size. The test size of the dated specimens does not change through time (Fig. 14), but there are differences between the stations, especially between Brijuni and Venice. Test sizes are slightly increased in the lHST unit at Brijuni, while sizes at Venice show a more uniform distribution.

There are two potential explanations of the observed patterns in *E. pusillus* test size. Firstly, the lack of a clear stratigraphic trend in size could be explained by time averaging which diminishes the signal. Although the dating results show a right-skewed distribution such that the youngest specimens are the most frequent, the centennial-scale time

averaging (IQR 250-650 yrs) suggests that this may be a driver for the lack of change. More strikingly, the results reveal that the youngest specimens are decades to a few centuries old, indicating that the last time when tests were produced in abundance was around 1800 AD. Lack of younger tests during the last century may suggest very low population densities or an inability to establish a sustainable population, since test production in the second half of the 20th century had dropped too low for sampling them from the death assemblages. Whether the population decline observed in the late 19th century was the consequence of a single or multiple mass mortality events, or a more gradual but still relatively rapid decline in population densities, cannot be easily distinguished. Secondly, this species may not be able to adapt to environmental changes by adjusting its body size. This could be due to an inability to adapt quickly enough to increased frequency of disturbances, and instead reacting with high mortality, or it may simply maintain the same body size regardless of environmental changes, which is more unlikely.

Though there is research on many aspects of *E. pusillus* biology and ecology, a number of possible factors that may confound interpretation of patterns in test size has not been studied yet. However, this species has various sand dollar characteristics, and yet resembles spatangoids and regular sea urchins in other aspects, allowing these taxa to be compared (Ghiold, 1982). For example, several studies revealed that growth rates of the irregular and infaunal *Echinocardium cordatum* were higher in organic-poor sandy substrates than in organic-rich silty sands (Buchanan, 1966; Wieking & Kröncke, 2003). This apparent paradox has been attributed to the higher quality of organic material typically found in sands (Jennes & Duineveld, 1985; Wieking & Kröncke, 2003) and a greater accessibility to it, which not only affects the growth of sea urchins but could also lead to a more selective feeding behaviour, which affects their body size (Steger et al., 2019). The selective feeding of *E. cordatum*, the preferential uptake of certain fractions of the sediment organic matter pool, has been confirmed by the highly enriched organic content in its digestive tract (De Ridder et al., 1984; Boon & Duineveld, 2012) and the adaptation of its degree of selectivity by increasing the preference for particular food compounds in habitats with low food concentrations (De Ridder et al., 1985; Boon & Duineveld, 2012). Studies on the feeding behaviour of *E. pusillus* suggest that this species should be considered a selective deposit-feeder (Nichols, 1959; Ghiold, 1982) due to the usage of suckered podia to select and transport substrate particles with attached organisms to the mouth.

The higher amount of organic matter due to eutrophication observed in the northern Adriatic would bring more food into the system, which could theoretically lead to an increase in body size as a result of increased growth rates, but the autecology of this species and its requirements for suitable oxic conditions could limit this process due to lower oxygen concentrations that go together with eutrophication. *E. pusillus* burrows several centimetres into the sediment, without a direct connection to the sediment surface and its mobility is limited. This could explain their sensitivity to hypoxic conditions and their preference for coarse, well-ventilated sediments. Without sufficient oxygen, they cannot utilise these nutrients, especially in pelitic sediments caused by siltation. Furthermore, Warwick & Pearce (2020) observed that as the size of this species increases, the mortality rate also increases, presumably because of predation by demersal fish. In addition to its small size, slow-growing characteristics and long lifespan (Warwick & Pearce, 2020), the species also has a planktotrophic larval stage, which could make *E. pusillus* even more sensitive to disturbances in the supply of nutrients and oxygen.

In summary, the echinoid in question is well-suited for analysis of size and abundance, as demonstrated by its preservation within sediment cores that capture the Holocene period. The study can fill a gap in its still relatively unknown demographics and autecology, and thus demonstrate the consequences of anthropogenic impacts on often overlooked members of benthic communities.

CONCLUSIONS

To gain insights into the ecological response of *E. pusillus* in benthic ecosystems, a comprehensive analysis was conducted on multiple grab samples and sediment cores, spanning the past ~ 10,000 years, and capturing environmental and ecological changes during the Holocene. This long-time approach allowed for the investigation of whether anthropogenic signals can be detected in the abundance and body size of echinoids over the past millennia. Moreover, it enabled the examination of the potential drivers responsible for the observed trends in their spatial and temporal dynamics in the northern Adriatic Sea. Station Brijuni recorded the highest densities, especially during the transgressive phase, but after the maximum flooding zone and the early highstand phase, the densities decreased substantially and reached a minimum during the late highstand phase, paralleling the up-core decrease in sediment grain size. In contrast, the stations in Piran showed an opposite pattern both in grain size and *E. pusillus* abundance with coarser sediments and higher test densities after the transgressive phase. The sediment at Station Venice consists only of sands, shows fluctuating densities of tests and represents the only station with relatively high abundances during the late highstand. Fine-grained sediment input may be the main driver of decrease in abundance since anthropogenic land-use shifts increased sediment supply and subsequently increased siltation in addition to oceanographic changes. *E. pusillus* is known for its preference for coarse sediments, particularly shell hash, due to their high organic content and the increased oxygen flow between the particle interspaces. Furthermore, there is a paucity of dead tests originating from the late 19th and 20th centuries in the surface mixed layer. Radiocarbon ages suggest a strong decrease in test production and therefore population densities over the past ~ 200 years. The impact of eutrophication, hypoxia, and bottom trawling on the populations may have reached a critical level during that time. Although abundance has fluctuated substantially over the past millennia and across the northern Adriatic Sea, test sizes have remained remarkably stable. The rapid decline of populations combined with temporal mixing of fossil assemblages may explain the overall lack of body size shifts. These findings establish a framework for assessing temporal and spatial variation in *E. pusillus* in the northern Adriatic, providing a basis for comparing data across regions and distinguishing natural variability from recent human impacts.

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