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Assessing biotic response to anthropogenic forcing using mollusc assemblages from the Po-Adriatic System (Italy)

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Abstract

Preserving adaptive capacities of coastal ecosystems in the Anthropocene requires an understanding of their natural variability prior to modern times. We quantified responses of nearshore molluscs assemblages to past environmental changes using 101 samples (~57300 specimens) retrieved from the subsurface Holocene succession and present-day seabed of the Po-Adriatic System (Italy). Present-day assemblages shifted in their faunal composition with respect to their mid-late Holocene counterparts. Major differences are observed in lower nearshore settings, where present-day samples show higher heterogeneity, reduced standardised

richness, reduced relative abundance of *Lentidium mediterraneum*, and increased relative abundance of *Varicorbula gibba*, scavengers (genus *Tritia*), and deposit feeders (nuculid bivalves). A dominance of infaunal opportunistic species and shifts towards detritus-feeding and scavenging are often associated with disturbed benthic habitats. Our results suggest that the ongoing anthropogenic stressors (mainly bottom trawling and non-native species) are currently shifting benthic communities into novel states outside the range of natural variability archived in the fossil record.

Keywords: Conservation Palaeobiology, Mediterranean, Holocene, Anthropocene, Ecosystem services.

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Introduction

In the last centuries, humans have been impacting the natural dynamics of the Earth system (Steffen et al., 2020), changing the rates and magnitudes of environmental processes and, by means of direct and indirect cascading effects (e.g., Heithaus et al., 2008), altering the distribution of organisms and structure of ecosystems across the globe. It has been estimated that more than half of the terrestrial biotas have been directly and strongly impacted by human activities (e.g., Mittermeier et al., 2003) such as urbanization, overexploitation of natural resources, and introduction of non-native species either for sustenance purposes or accidentally (IUCN, 2000). These processes, in turn, have led to habitat degradation, affecting the structure and functioning of ecosystems, and thus the overall biodiversity of the Earth. For continental biotas early warnings on the undesired effects of globalization and industrialization were documented since the last century (e.g., d'Arge and Kneese, 1972; Wilson, 1987) and were more readily observable than in the ocean (Dirzo et al., 2014). In the marine realm, researchers have started to document human-induced changes in marine and coastal ecosystems only more recently (Lenhan and Peterson, 1998; Newell and Ott, 1999; Kowalewski et al., 2000; Jackson et al., 2001; Kidwell, 2007; Lotze et al., 2006; Edelist et al., 2013; McCauley et al., 2015; Tomašových et al., 2019; Jouffray et al., 2020; Steiger et al., 2022). These studies documented that the long history of intensive human utilisation of ecosystem services in some areas (e.g., Adriatic Sea) exceeded the adaptive capacity of local biotas, with a potential risk of pushing modern ecosystems toward different ecological states and driving the decline of economically important species (Burgess et al., 2013; McCauley et al., 2015; Bargione et al., 2021). But, to what extent are present-day ecosystems or key species already being affected by human impacts?

Will continuing anthropogenic pressures result in sustained ecosystem regime shifts or extinctions of key species in the near future?

To narrow the uncertainty in answering these questions, it is necessary to understand the variability of ecosystems or individual species under natural conditions, with no, or at most limited, human interference. Documenting the magnitude of past changes is essential for defining marine ecosystem baselines, which can be used to evaluate present-day ecosystem status, set realistic conservation goals, assess efficacy of restoration efforts, and mitigate future human impacts (e.g., Kowalewski et al., 2000; Jackson et al., 2001; Dietl et al., 2015). However, ecological studies provide a relatively short record by which to measure ecosystem changes, and disentangling present-day natural factors from anthropogenic forcing is often a challenging, if not impossible, task (e.g., Pitacco et al., 2019). Geohistorical data, including the youngest fossil record, are thus needed to understand the status and variability of marine ecosystems prior to major phases of human impact (Kowalewski et al., 2000; Jackson et al., 2001; Lotze et al., 2006, 2011; Dietl and Flessa, 2011; Kidwell and Tomašových, 2013; Kidwell, 2015).

Here, we focused on the Adriatic Sea, which is part of the Mediterranean basin—a global hotspot of marine biodiversity due to its exceptional rates of endemism combined with a relatively large spatial extent (Myers et al., 2000; Coll et al., 2010; CEPF, 2022). At the same time the Adriatic Sea is being affected by multiple anthropogenic stressors and has already been highly impacted by human activities (e.g., Furlan et al., 2019 and references therein). Habitat loss and degradation, pollution, eutrophication, overfishing, and invasive species are major causes of changes in the Adriatic coastal ecosystems, with many of these pressures operating for decades or centuries (e.g., Coll et al., 2010; Lotze et al., 2011).

In this study, aimed at providing a deeper historical perspective, we compared mid-late Holocene assemblages preserved in the subsurface stratigraphic record of the Po coastal plain (Northern Italy; Fig. 1) with surficial assemblages that accumulated along the Po Delta and Emilia Romagna coastline during the Anthropocene (*sensu* Crutzen, 2002 and references therein). To ensure environmental comparability through time, the study focused on aggrading-to-prograding shallow marine and coarse-grained successions of the Po-Adriatic System. Specifically, we evaluated changes in the composition of mollusc assemblages between the present-day fluvial influenced coastal shoreface and delta front settings with sustained sedimentary inputs (hereafter referred to as “nearshore”) and their mid-late Holocene counterparts representing a time interval when anthropogenic pressure were notably less significant (between ~6 and 0.5 kyr cal BP i.e., prior to the early modern period). This study contributes to the area of near-time Conservation Palaeobiology that provides the framework against which to evaluate extant biotic dynamics (Dietl et al., 2015).

Background

Near-time Conservation Palaeobiology in its role of synthetic discipline helping the conservation of ecosystem functions uses fossil archives to define the reference condition (baseline) of an ecosystem (or its components) against which to compare modern ecological structure of the same ecosystem (Flessa, 2002). Detected changes should aid in predicting future states of ecosystems and populations in a scenario of increasing global warming and anthropogenic impacts (Kowalewski, 2001; Currano et al., 2008, 2016; Dietl and Flessa, 2017; Tyler and Schneider, 2018; Slater et al., 2022). This role is especially needed in highly anthropized areas, like

the Adriatic, one of the most impacted basins of the Mediterranean Sea (e.g., Furlan et al., 2019). In this region, Conservation Palaeobiology approach has been used extensively to document both biotic changes through time, and to disentangle natural vs. anthropogenic drivers of these changes (Barmawidjaja et al., 1995; Scarponi et al., 2017a; Schnedl et al., 2018; Gallmetzer et al., 2019; Tomašových et al., 2021; Barbieri et al., 2021; Cheli et al., 2021).

Our work builds directly on previous studies by Kowalewski et al. (2015) and Scarponi et al. (2022). The first study, using macrobenthic fossil assemblages from the subsurface marine succession of the Po coastal plain evaluated quantitatively ecosystem changes at the coarse spatial scale (multiple depositional systems) across the Late Pleistocene and Holocene interglacials and contrasted such changes against the data available for present-day assemblages of the Northern Adriatic Sea. Specifically, the study focused on two stratigraphic units, dominated by a large suite of coastal, shallow-marine, and deltaic deposits, documenting the present (pre-Anthropocene) and last interglacial conditions of the Po-Adriatic System. Quantitative comparisons were conducted at very coarse spatial and environmental scales by merging data from all marine depositional systems recorded within each time-period. Kowalewski et al. (2015) observed high congruence of mollusc fossil assemblages from the penultimate and the current interglacial time intervals, and attributed this concordant pattern to either a resilient or persistent response of the Adriatic benthic communities. The recurrence of the same community composition in two distinct stratigraphic units separated by ~100.000 years (i.e., from the Late Pleistocene and Holocene) can indicate either ecological persistence, if associations continue through the perturbation, or strong resilience, if

the community shifts to a novel state upon perturbation, but then rebounds to its previous state with the return of pre-disturbance environmental conditions.

To distinguish between these two scenarios, Scarponi et al. (2022) conducted a new study based on a more constrained paleoenvironmental framework (only nearshore settings considered) and incorporating data from the lowstand nearshore deposits of the Po-Adriatic System, accumulated during the last late glacial phase and preserved in the sedimentary record of the Central Adriatic Sea (see Pellegrini et al., 2018; Azzarone et al., 2020). The fossil record recovered from sediment cores in the Po-Adriatic System indicated that nearshore assemblages of the penultimate and the current (pre-Anthropocene) interglacial were indistinguishable statistically from one another despite notably different assemblage composition during the intervening glacial conditions. These results suggested that the nearshore mollusc associations of the northwestern Adriatic Sea should be resilient to the limited rise of sea surface temperatures predicted for the near future but stand in stark contrast to benthic community responses to recent anthropogenic impacts in this region (Kowalewski et al., 2015). The latter study, however, did not evaluate if those anthropogenic changes affected the entire onshore-offshore gradient or were only limited to specific bathymetric zones. Nevertheless, recent conservation palaeobiology studies conducted in the northeastern Adriatic Sea documented a strong shift in the faunal composition of mollusc assemblages that occurred during the last centuries in more offshore settings (20-40 m e.g., Mautner et al., 2018; Gallmetzer et al., 2019). In contrast, the Holocene-to-present-day changes along the nearshore settings in the western part of the basin directly influenced by Po river discharge have remained underexplored.

Study area

The Northern Adriatic is an epicontinental, semi-enclosed, shallow sea (average depth 35 m), which is characterised by a wide shelf with a low topographic gradient of 0.02° (Poulain et al., 2001). The Northern Adriatic Sea extends ~350 km southward from the Gulf of Trieste and is delimited westward by Italy and eastward by the Balkan Peninsula. The Italian coasts of the northwestern Adriatic Sea are mostly sandy and—in the few cases where the landscape has not been modified—separated from the coastal plain by a few-meters-high dune system (Sistilli et al., 2015). The submerged portion of the beach (either shoreface or delta front) is delimited landward by a reduced swash zone (foreshore) and offshore by the depth at which the sediment could be remobilised by waves and currents (i.e., closure depth principle, see Nicholls et al., 1996). Within this bathymetric interval, two sub-environments can be identified. The upper zone (= upper nearshore), where the flux of sediment is nearly constant, is a dynamic environment represented by highly mobile bars and troughs changing their morphology and location at temporal scales of days to years. The lower zone (= lower nearshore) is a depositional setting characterized by a more stable profile, where only storm waves can strongly reshape bottom morphology (at the scale of decades to centuries). Beyond that, a transition zone occurs where morphological changes develop on longer time scales and finer sediments are increasingly common. In other words, beach subdivision is defined here as a function of the local wave energy expected in a predetermined time-window. The longer the time interval considered, the greater probability that a wave able to interact with deeper seabed can occur. Using a time-interval of 100 years as predetermined time window, the submerged beach in this part of the western Adriatic Sea extends down to a 10 m isobath. As for the boundary between

the lower and upper nearshore, this limit is commonly placed approximately at 4 m water depth (Sistilli et al., 2015).

Another important element of the northwestern Adriatic Sea is the Po Delta that represents the most readily observable sub-aerial morphologic feature recording coastal progradation of the last few millennia after the relative sea level stabilization (Amorosi et al., 2016). However, the past sea-level dynamics are recorded below the Po coastal plain, where a sequence of wedge-shaped marine sedimentary bodies records the waxing and waning of the Northern Adriatic Sea during the most recent glacial-interglacial cycles (e.g., Amorosi et al., 1999; Scarponi and Kowalewski, 2004; Amorosi et al., 2016, Campo et al., 2020). The uppermost wedge-shape unit, mainly Holocene in age, has been studied in detail during the last decades (e.g., Amorosi et al., 1999; Scarponi et al., 2013; Bruno et al., 2017; Cheli et al., 2021; Rossi et al., 2021). The lowermost boundary of this unit is the transgressive surface (TS), a boundary of regional extent, that can be readily recognized in cores using lithologic and palaeontological data (Bruno et al., 2017). Above the TS, estuarine to shallow marine deposits of variable thickness (e.g., Scarponi et al., 2017b) document the late phase of post-glacial sea-level rise and the maximum marine ingressions (dated around 7.0 kyr; Rossi et al., 2021 and references therein). This overall retrogradational set of units is overlain by an aggradational-to-increasingly-progradational succession of silty-mud to coarser grained coastal and deltaic facies (e.g., Amorosi et al., 2019). When considered jointly, these geological lines of evidence indicate that during the middle Holocene the physiography of the study area transitioned from barrier-lagoon-estuary systems to wave-dominated coastal and deltaic systems (Amorosi et al., 2019). Subsequently, during the late Holocene, (2.0 kyr cal. BP till mid-20th century), the deltaic and coastal systems of Emilia-

Romagna experienced a period of increased river discharge that promoted a strong progradation phase and the transition from wave-dominated to river-dominated deltaic systems shifting laterally due to multiple episodes of river avulsion (e.g., Amorosi et al., 2019). During the last decades coastal progradation in the Northern Adriatic Sea seems to have stopped or slowed down due to anthropogenic subsidence and sea-level rise (see Cencini 1998; Gambolati et al., 1999; Da Lio and Tosi, 2018; Ninfo et al., 2018; Meli et al., 2021).

Methods

The analyses compared two specific time intervals: (1) the mid-late Holocene (between ~6 and ~0.5 kyr cal. BP) documented in subsurface cores, and (2) the present day represented by the surficial assemblages accumulating along the Po Delta and Emilia Romagna coastlines, mainly during the last 100 years (Scarponi et al., 2013). The age of the samples was based on direct radiocarbon dating of the fossil material and timing of the parasequence development in the study area, see Appendix S1; Amorosi et al., 2017). The samples of fossiliferous deposits preserved in the subsurface of the Po coastal plain (Fig. 1) were acquired from previously investigated cores, whereas the data on the surficial assemblages derive from new sampling efforts combined with previously collected samples recorded in the Italian Mollusc Database of the Santa Teresa research center—National Agency for New Technologies, Energy and Sustainable Economic Development (ENEA) (Bedulli et al., 1984).

Data selection criteria

To limit possible biases due to different taphonomic conditions and to ensure environmental comparability, the analyses were restricted to samples from

nearshore settings, sampled along the Emilia Romagna and the Po Delta coastline (Fig. 1). Samples from backshore deposits were not considered. Samples from ENEA database that recorded only the live assemblage counts were also excluded.

Mid-late Holocene samples were derived from cores and ranged in volume between ~ 110 and ~ 375 cm³ each, whereas surficial assemblages from present-day settings were collected by different methods, mainly Van Veen Grab (8000 cm³) and short cores (400 cm³) (Appendix S1). Core samples were treated following a standard procedure reported in Wittmer et al. (2014). For the ENEA samples only the taxonomic list, specimen counts, and sampling method (i.e., SCUBA diving, dredge, grab, and fishing net) were reported (Appendixes S1-S2). We restricted our analyses to molluscs (bivalves, gastropods and scaphopods), which dominated the studied macrobenthic assemblages. Analyses were conducted at species level. Because the great majority of bivalve specimens were represented by individual valves, their final counts were divided by two to account for disarticulation (Scarponi and Kowalewski, 2004).

The assignment of mid-late Holocene samples to nearshore setting was based on stratigraphic, sedimentological and micropalaeontological lines of evidence reported in literature (see Appendix S1 columns “facies associations”). Samples were then included in either upper or lower nearshore based on their estimated water depth following procedure reported in Wittmer et al. (2014), summarized here briefly. For each species retrieved in a sample and present in the ENEA database (Santa Teresa research center; Bedulli et al., 1984), its preferred bathymetry was estimated, as the present-day abundance-weighted average preferred depth (PD). Then a water depth estimate for each sample was obtained by computing the mean PD of all the species retrieved in a sample weighted by their abundances.

Quantitative analyses

The molluscan assemblages in the two time intervals were examined by comparing sample-standardised diversity (richness and evenness), changes in relative abundance of dominant species, trophic structure, and substrate relationship. Taxonomic composition and diversity were analysed at environmental (nearshore) and sub-environmental levels (upper and lower nearshore).

Bivariate and multivariate methods along with network analyses were used to compare assemblage composition representing the investigated environmental units. Finally, trophic structure and substrate relationships in both time intervals were investigated by assessing the relative abundances of various feeding and substrate preference groups among the 10 most abundant species.

Multivariate analyses. The compositional variation in mollusc assemblages was first assessed by means of ordination analyses. The dataset for ordination analyses was restricted to samples with at least 20 specimens, and singletons (species occurring in only one sample) were removed (Wittmer et al., 2014). To check for volatility and sensitivity of the results, a more restrictive dataset was employed, consisting of samples with at least 60 specimens (singletons removed as well) (Scarponi et al., 2022). The sample-by-species matrices have been standardised (Wisconsin double relativisation) or transformed (4-root-transformed relative abundances) to reduce the effect of hyper-abundant taxa. The indirect ordination was performed by non-metric multidimensional scaling (NMDS) using Bray-Curtis (BC) distance measure (k = 3 dimensions) on both the standardised and transformed matrices. In addition, permutation-based multivariate analysis of variance (PERMANOVA) was employed to evaluate differences in centroids of the multivariate groups of samples between the two time intervals. Here sub-environments represent groups, so that

permutations occur across the two time intervals within sub-environment only. Average BC dissimilarity of nearshore samples from their group centroid, as well as pairwise BC dissimilarity between the samples were used as measure of compositional heterogeneity (beta diversity) within each environment and time interval (Anderson et al., 2006).

Network analyses. We created multilayer network representations of the mid-late Holocene and present-day records by using the same dataset employed for the NMDS. Here we conceptualised those records as complex systems with a two-layered structure in which one layer described taxonomic composition and the other quantified sedimentologically defined relationships (Fig. S1). Nodes in those networks represent samples, taxa, and environmental zones—based on sedimentological attributions (Appendixes S3-S4). This multilayer framework has been used in palaeobiological research to create temporal networks in which layers represent ordered time intervals, such as consecutive geological stages (Rojas et al., 2021) or equal time bins (Pilotto et al., 2022). However, in this study, the layers in the assembled networks did not represent time intervals but biological and sedimentological constraints in the underlying geohistorical data. We used the Infomap framework, a higher-order approach that operates on multilayer networks (Edler et al., 2017), to reveal the network's modular structure. Because the underlying data were sparse, the assembled networks were small, and the optimized solutions did not exhibit a hierarchical organization. Indeed, standard network clustering provides limited information on the large-scale organization of the studied systems. To overcome this limitation, we used varying Markov time models (Rojas et al., 2022) that allowed us to explore the larger-scale modular patterns of the mid-late Holocene succession and present-day nearshore seabed of the Adriatic Sea at

different resolutions. In the Map Equation framework, the parameter Markov time sets the scale of the modules (Kheirkhahzadeh et al., 2016). We obtained the optimised partitions of the assembled networks for a range of Markov time values using the following Infomap arguments: $N = 500$, $i = \text{multilayer}$, $\text{flow-model} = \text{undirected}$, markov-time , $\text{multilayer-relax-rate} = 0.8$. The multilayer-relax rate (r) is the probability to relax the constraint of a random walker visiting a sample in one layer for moving towards the same sample in the other layer as described in Rojas et al. (2021). We used an alluvial diagram to visualize changes in the modular structure across the different Markov time models. Each column in the alluvial diagram represents the network partition obtained at the given Markov time. For each partition, nodes (i.e., samples, taxa, and depositional features) grouped into modules are represented as vertically aligned rectangles, with height proportional to their flow volume (i.e., long-term visit rates of nodes describing the behaviour of the random walk). Horizontal streamlines connect sets of nodes in adjacent networks, with height proportional to the node's flow (Rojas et al. 2022). The alluvial diagrams provided here represent 98% of the network flow and were created using the Alluvial diagram app available on <https://www.mapequation.org>.

Bivariate analyses. Spearman's coefficient was used to measure the strength of the rank correlation between selected bio-environmental descriptors that are thought to be relevant for the sampled nearshore assemblages: sample depth, standardised richness, relative abundance of economically valuable species, and relative abundance of non-native species. NMDS sample scores were correlated with these bio-environmental descriptors to shed light on the potential drivers of variation in assemblage composition captured by the ordination patterns. In addition, comparison of the rank abundance distribution of species (i.e., proportion of

individuals representing each species) was employed to evaluate changes in structure of the regional species pool across the two time intervals.

Quantitative analyses were performed in R (R Development Team, 2018, v 3.6). Codes and data are provided in the supporting information. The Infomap software package (Edler et al., 2017) was used for clustering the assembled networks. Results can be reproduced using the Infomap Online freely available at <https://www.mapequation.org>.

Results

The dataset examined (i.e., samples with at least 20 specimens and singletons excluded) consisted of 30 assemblages (28,949 specimens representing 67 species in total) from present-day nearshore settings and 71 samples (28,332 specimens and 58 species) from the comparable settings of the mid-late Holocene (Appendix S1). Present-day samples cover the entire bathymetric gradient of the nearshore setting (i.e., 0-10 m water depth, see Methods), whereas the mid-late Holocene samples do not extend beyond 8 m water depth. The NMDS ordinations, regardless of the matrix transformation or sample size threshold applied (Figs. 2; S2-S4), showed only partial overlap between present-day and mid-late Holocene nearshore assemblages, with samples from the lower nearshore grouping separately according to their age. In addition, the upper and lower nearshore are well separated from each other in both time intervals (Figs. 2; S2-S4). Similar patterns are revealed by the network analysis. The higher-order Markov dynamics on the assembled networks captured the large-scale structure of the dataset by explicitly delineating two modules (representing 98% of the network flow) comprised of strongly connected sets of species, samples, and sedimentological features, that can be directly interpreted as lower and upper nearshore sub-environments (Fig. 3). Furthermore,

the Holocene nearshore sub-environments show a higher mixing at the boundary. That is, the modules representing upper and lower settings overlap or share a few samples due to the uncertainty inherent to the sedimentological descriptions in the fossil data or reflecting Holocene to present-day changes in the Po-Adriatic System. Rarefied diversity, water depth and per-sample relative abundance of edible taxa (Figs. 2, S2-S3) are significantly correlated with NMDS1 ($\rho = 0.63\text{--}0.69$ and $p\text{-values} \ll 0.001$ in all cases), whereas correlation between NMDS2 and sample-standardised diversity or abundance of economically relevant taxa depends on the matrix treatment (Wisconsin standardisation vs. 4th-root transformation, respectively; Figs. 2, S2-S3). PERMANOVA based on species abundance data reported consistently different assemblage composition between nearshore samples of the two time-intervals (Table 1).

Comparison of BC pairwise dissimilarities between the samples provides evidence of higher heterogeneity within present-day nearshore settings (mean BC dissimilarity = 0.72), than within the mid-late Holocene nearshore settings (mean BC dissimilarity = 0.33; Table 2). The lower heterogeneity in mid-late Holocene nearshore was likely driven by lower turnover (i.e., higher congruence of sample taxonomic composition) among the upper nearshore samples (mean BC dissimilarity = 0.15), while in present-day assemblages heterogeneity was comparable in both sub-environments (mean BC dissimilarities = 0.60 and 0.65; Table 2). Differences in heterogeneity within nearshore deposits of the two-time intervals were also supported by multivariate dispersion of the two sample groups around their centroids (Fig. S5), and by the higher-order Markov dynamics that revealed non-trivial modules at higher Markov times on the network representing present-day nearshore seabeds (Fig. 3). The nearshore settings of the two time intervals are also distinct from one another

due to the occurrence of non-native species, here defined as those taxa that were initially distributed outside the central-eastern Mediterranean Sea. While the presence of non-native species is widespread in the investigated area (i.e., 87% of present-day samples record at least one non-native species; Appendix S1), they are more common in the deeper nearshore settings (Fig. S6c), but their relative abundance is generally limited (always <10% of per-sample abundance).

Mid-late Holocene assemblages display an expected monotonic increase of the standardised diversity and relative abundance of economically relevant species moving from upper to lower nearshore settings (Fig. 4), with shallower samples characterized by their lower abundance (median relative abundance <10%) compared to deeper settings (median relative abundance of 35%, but rarely exceeding 50% of the specimens per sample; Figs. 2, 4; S6). This pattern is more complex in present-day nearshore settings, which are characterized by a lack of monotonic relationship between rarefied species richness and economically valuable taxa, which commonly attain relative abundances >50% in both upper and lower nearshore samples (Fig. 4). In present-day settings, when the economically relevant species are dominant (i.e., abundance >50%), rarefied species richness usually decreases considerably (Fig. 4).

A very similar set of species dominates nearshore environments in both time intervals, with eight out of the top ten most abundant species shared between them, and more than 90% of the specimens retrieved in both time intervals is represented by infaunal, filter feeders (Table S1). However, in present-day assemblages the accidentally introduced non-native bivalve *Anadara* gr. *kagoshimensis* is recorded among the top species (Table 3) and the dominance of *Lentidium mediterraneum* is less pronounced than in mid-late Holocene samples. Although *L. mediterraneum* in

the network analysis is the highest ranked species in both modules representing upper nearshore settings of the investigated time-intervals, the contribution of the individual taxa to the modules delineated in both networks (Tables S2; S3), as measured in terms of the flow (see Pilotto et al., 2022), highlights the mid-late Holocene to present-day shift in their relative importance (Fig. 5; Table 3). Apart from the non-native species *A. gr. kagoshimensis* present along the entire gradient, the lower nearshore assemblages appear to have undergone more notable changes since the late Holocene compared with the upper nearshore assemblages. These changes involved the exclusion of *L. mediterraneum* from the 10 most abundant species and the increase in opportunistic, scavenger, and deposit feeder taxa such as *Varicorbula gibba*, *Tritia varicosa*, and *Nucula nitidosa*, respectively.

Discussion

Our study provides an evaluation of assemblage dynamics in the nearshore settings of the Northern Adriatic Sea over the last several thousand years, based on the analysis of fossil mollusc remains. Thus, it provides a palaeoecological baseline against which it is possible to assess recent shifts in mollusc assemblages from the present-day nearshore settings.

Biotic response in the Anthropocene: Nearshore

NMDS and network analyses both provide evidence supporting a modularity within nearshore environments corresponding to two groups of samples with distinct species composition (Figs. 2-3, 5). This modularity parallels the morphodynamic zonation of the Adriatic nearshore zone (Sistilli et al., 2015). The observed patterns in relative species abundance and dominance of infaunal filter feeders in both time intervals (Tables 3, S1; Appendix S1), suggest that the identity of the most abundant

species populating nearshore settings has not changed notably over the last several thousand years, except for the addition of non-native taxa (e.g., the accidentally introduced *A. gr. kagoshimensis*) or aquaculture-related molluscs such as *Mytilus edulis* and *Ruditapes philippinarum* (Appendix S1). Thus, the present-day nearshore mollusc assemblages retain the basic structure of the assemblages that thrived in comparable environments during the mid-late Holocene. This finding is encouraging. However, strong impacts are observed in deeper (~10-40 m water depth) soft-bottom settings of the Northern Adriatic Sea, where the composition of molluscs assemblages shifted markedly during the 20th century compared to the late Holocene baseline (Vidovic et al., 2016; Galltmezter et al., 2017; 2019; Mautner et al., 2018; Tomasovych et al., 2020; Haselmair et al., 2021). This profound ecological change reduced species richness and led to a decline in abundance of grazers and deposit feeders, and increase of stress-related species (e.g., *V. gibba*; Fuksi et al., 2018; Tomašových et al., 2020). Thus, the offshore benthic communities in the Northern Adriatic Sea are substantially different from those of a few thousand years ago and do not show the high geographic heterogeneity in faunal composition that characterized the late Holocene (Galltmezter et al., 2019; Haselmair et al., 2021). Similar compositional shifts in benthic communities were also observed over the last century in ecological surveys of living assemblages (e.g., Crema et al., 1991; Chiantore et al., 2001).

In contrast to these more offshore habitats, our data suggest that while the present-day northwestern Adriatic nearshore seabed is directly impacted by a number of human stressors (see below), those stressors have not significantly reshaped (so far) the taxonomic and functional compositions of the shallow-water benthic assemblages. The presence of non-native species in targeted nearshore settings is

widespread but they are still largely limited in terms of their relative abundance (Fig. S4; Table 3). When the upper and lower nearshore samples are examined separately, the mid-late Holocene and present-day assemblages diverge in terms of species abundances and diversity structure (Figs. 2, 5; S6; Table 3). Multivariate analyses indicate that water depth, rarefied species richness and relative abundance of economically relevant edible species are the main factors responsible for the variation in assemblage composition captured by the NMDS1 axis. Bathymetry drives the shift of nearshore samples toward lower axis 1 values. As noted above the present-day samples cover the entire bathymetric gradient of the nearshore setting (i.e., 0-10 m water depth, see Methods), whereas the mid-late Holocene samples do not extend beyond ~8 m water depth. However, the shift of the present-day upper nearshore samples toward lower NMDS1 values (Fig. 2; S2-S4) is determined by the other two correlates (diversity and relative abundance of economically relevant edible species; Figs. 2; S6). Overall, species thriving in shallower settings seem to be more resilient than those thriving in the deeper part of the investigated gradient (i.e., lower nearshore). Finally, samples found in lower nearshore settings, despite containing the same set of taxa show completely different diversity and dominance structure in the two time intervals (Figs. 2, 5; S2-S6, Table 3). Although we posit here that anthropogenic factors are the primary drivers of the shifts in the structure of mollusc assemblages, natural climatic changes during the Holocene (e.g., Marriner et al. 2022) might have also played a role. The lack of regional sea surface palaeotemperature records from the Northern Adriatic Sea precludes direct assessment of the extent to which the climatic fluctuations might have contributed to late Holocene shifts in community composition. However, the fact that there is a higher congruence in the taxonomic composition of nearshore assemblages from

samples (Fig. S5) that encompass an overall multimillennial cooling trend (even if limited) in the Mediterranean during the mid-late Holocene (pre-Anthropocene, Jalali et al., 2016), indicates that changes in seawater temperatures are unlikely to have been a primary causative explanation for detected patterns.

Upper nearshore. NMDS and correlation analyses (Figs. 2; S5; Table 1) document a moderate shift toward reduced dominance of *L. mediterraneum* and a modest increase in hard-substrate (e.g., *Mytilus*) and non-native species (e.g., *A. gr. kagoshimensis*), which led to an increase in standardised diversity (Figs. 2; S4, S6) and shift toward lower NMDS1 scores. This change is supported by the multilayer network analysis showing that a limited number of taxa are clustered into the module depicting upper nearshore settings in the mid-late Holocene network. In contrast to the present-day counterpart, this module does not include hard-substrate or non-native species. These patterns could be explained by the intense development of coastal infrastructure (e.g., groins and breakwaters, piers) over the last century. The infrastructure development impacted more than half of the sampled shoreline (Cencini, 1998; Dafforn et al., 2015) and provided artificial hard-substrates further facilitating spread of non-native species (Airoldi et al., 2015). Shallow marine infrastructure increases heterogeneity of coastal habitats, which in turn can increase species diversity (habitat heterogeneity hypothesis, MacArthur and MacArthur 1961; Almond et al., 2021) by favoring hard-substrate species. These effects are especially relevant in the study areas, which during the Holocene was characterized by a very limited extent of natural hard-substrate habitats.

Another factor driving diversity in present-day upper nearshore settings is the decreasing dominance of *L. mediterraneum* (75% in present-day assemblages vs. 95% during the mid-late Holocene; Table 3). Although the shift is noticeable, *L.*

mediterraneum abundance tends to be variable both spatially and temporally (e.g., Occhipinti-Ambrogi et al., 2002). Due to our limited sampling effort (i.e., small number of samples) of present-day upper nearshore settings, make it difficult to evaluate if the drop in abundance mostly reflects a sampling artifact or an anthropogenic signal linked to higher habitat heterogeneity recently developed along the Adriatic coastline. The ongoing land-use changes like wetland draining, expansion of agriculture, urbanization, road construction, and waterway regulation affected the area since late Roman times, but with the highest intensity during the last two centuries. Indeed, the Greek geographer Strabo reported, around 2000 years ago, that the Po Delta and surrounding coastal areas were a continuous almost uninterrupted series of wetlands and rivers (Horace, 1923). It is noteworthy that *L. mediterraneum* thrives in euryhaline shallow marine settings, especially at the mouth of rivers (Massé, 1972), and can withstand eutrophic waters and high sedimentation rates (Ambrogi and Bedulli, 1981). Since the 17th century (but on a large scale during the late 19th-20th centuries) hydraulic works of river diversions and merging, as well as wetland drainage took place. Along the Po Delta and Emilia Romagna coastlines less than 5% of freshwater marshes and <30% of salt marshes that existed in the area during the Roman times are still present, and the coastline is now dominated by recreational facilities, harbors, and other infrastructures (Cencini, 1998). In the second half of the 20th century the Emilia-Romagna coastal plain became one of the popular tourist destinations of the Mediterranean Sea. However, in protected areas with limited anthropogenic stressors like the Po Delta Biosphere Reserve, *L. mediterraneum* is found with an overwhelming abundance (but see also Occhipinti-Ambrogi et al., 2002). In this area *L. mediterraneum* is widely dominant in water depth <2.5 m, with a mean population density of 130,000 ind/m² and reaching

relative abundances of 95% in macrobenthic communities (Ambrogi and Bedulli, 1981; see Table 3 for comparison with mid-late Holocene upper nearshore settings).

Finally, the increase in non-native species due to aquaculture activities (mainly *R. philippinarum* and *Magallana gigas*) and accidental introductions (e.g., *Rapana venosa* and *Anadara* gr. *kagoshimensis*; Appendix S1) appears to have played a minor role in the region. As for *R. philippinarum*, while not very abundant in high-energy nearshore habitats, the taxon is one of the most successful non-native species in brackish settings along the entire northwestern Adriatic coastline. Introduced in the region during the early 1980s for farming purposes (Cesari and Pelizzato, 1985), it expanded along the coast colonising a variety of brackish settings and replacing the native *R. decussatus*. Expansion of the *R. philippinarum* aquaculture is also responsible for the introduction of other non-native species such as the seaweed *Gracilaria vermiculophylla* (Sfriso et al., 2012; Airoldi et al., 2016).

In summary, the separation of present-day and mid-late Holocene assemblages observed in our multivariate analyses (Figs. 2; S2-S5; Table 1) is driven by the reduced dominance of *L. mediterraneum* along the heavily urbanized settings of the northwestern Adriatic, as well as, to a lesser degree, by the increase in species richness (Fig. S6d) possibly due to coastal development and appearance of non-native species that were accidentally or intentionally introduced to the region (Fig. S6c).

Lower nearshore. In such settings, present-day assemblages show a higher magnitude of changes with respect to their mid-late Holocene counterparts (Fig. 2; S2-S3; Table 3; S2). First, *L. mediterraneum* is no longer present among the 10 most abundant species in this sub-environment, being replaced by the other

Mediterranean corbulid—*V. gibba* (Table 3). *L. mediterraneum* is not even grouped into the network module representing the present-day lower nearshore settings (Table S3). *V. gibba* dominance is often related to environmental instability driven by oxygen depletion, turbidity or sustained sediment fluxes both in benthic communities (e.g., Pérès and Picard, 1964; Hrs-Brenko, 2006) and Pliocene-Quaternary Mediterranean fossil assemblages (e.g., Dominici, 2001; Amorosi et al., 2002). According to Ambrogi and Bedulli (1981), *L. mediterraneum* is still one of the most abundant species in lower nearshore settings of the Po Delta (especially between 5 m and 8 m water depth), whereas in deeper settings *V. gibba* is more abundant and sometimes dominant (see also Occhipinti-Ambrogi et al., 2002). The shift in dominance between *L. mediterraneum* and *V. gibba* from the mid-late Holocene toward present-day observed in our data, however, needs further investigation, as the two-time intervals are not uniformly sampled along the bathymetric gradient (Fig. 2d). This bias in sampling coverage could explain at least in part the switch in dominance of the two corbulids (Table 3). The pattern, however, may also reflect an ecological signal related to anthropogenic disturbances, already documented in other parts of the Adriatic Sea. In fact, previous studies focused on soft-bottom habitats of the Northern Adriatic Sea attributed the 20th century dominance of *V. gibba* (= *Corbula gibba*) and *Tritia varicosa* (= *Nassarius pygmaeus*) to trawling-enhanced remobilization of the Adriatic seabed and to increase in frequency of anoxia events driven by eutrophication (e.g., Crema et al., 1991; Giani et al., 2012; Gallmetzer et al., 2017; Tomašových et al., 2020). Such repeated stressors tend to reduce ecosystem complexity and keep macrobenthic communities permanently at an early stage of recovery with moderate diversity and high abundance of opportunistic, resistant species such as *V. gibba* and scavenger taxa (e.g., *T. varicosa*) (Table 3;

Occhipinti-Ambrogi et al., 2005; Tomašových et al., 2018), while epifauna is more patchily distributed (Riedel et al., 2012). Our findings are concordant with these previous studies. However, improved sampling coverage of the entire nearshore bathymetric gradient in the mid-late Holocene record is necessary to limit the effects of potential sampling biases.

It is noteworthy that the present-day lower nearshore assemblages characterised by the reduced standardised diversity (Fig. S6a), tend to be dominated by the economically relevant *Chamelea gallina*, an edible infaunal bivalve. This species contributed the most to the network delineation of the lower nearshore settings in the present-day network (Table S3). While hypoxic events in the Northern Adriatic Sea are becoming less common comparing to the 1970s and 1980s (Rinaldi et al., 1991), the seabed is still intensively trawled along almost its entire bathymetric profile (Russo et al., 2020 and references therein). A fleet of hydraulic dredgers (ca. 450 vessels) operates on the sandy coastal bottoms (3-15 m water depth) in the Northern Adriatic Sea (Romanelli et al., 2009) exploiting *C. gallina*. The areas hosting commercially exploitable densities of this species are swept around 2.0 times each year on average, with peaks of 20 times a year (Morello et al., 2005). Our data reinforce the ongoing concerns regarding impact of trawling on the lower nearshore seabed, especially on benthic biodiversity. When standardised richness per sample is plotted as a function of the relative abundance of economically relevant edible species, the lower nearshore assemblages show a strong drop in median sample-level diversity (Fig. 4). The increase in abundance of such species, that is a peculiar feature of the studied present-day assemblages, is probably related to the 20th century expansion of marine invertebrate fisheries and aquaculture. Opportunistic species like *C. gallina* or *V. gibba* benefit most from novel environmental conditions

provided by urban seas like the Adriatic. These taxa, given their ecological requirements, can thrive best in human-impacted areas. In addition, the “law of large numbers” may apply in this context. The “law” states that the most abundant species remain most abundant because they tend to produce more offspring than the less abundant species (Di Michele et al., 2004). Both features confer to this species a strong adaptive potential to face the environmental perturbations to which it is continuously subjected. However, even in the case of *C. gallina*, human impacts exert negative effects on its populations. According to Bargione et al. (2021 and references therein), forty years ago *C. gallina* annual yield in the Adriatic Sea was 4-to-5 times higher than it is today (15,000–20,000 tons/year). Nevertheless, while human exploitation of molluscs as a food source has significantly altered community compositions, populations of exploited species like *C. gallina* are still able to persist given responsible management. However, species less tolerant to anthropogenic stressors that decreased in abundance from the mid-late Holocene (e.g., species of *Bittium* and *Spisula*; Table 1), would require the establishment of larger protected areas that should allow them to survive and to sustain populations in other parts of the basin via larval dispersal.

Perspectives

We used sample-level metrics of community composition and diversity to evaluate nearshore habitats over the last few millennia and assess long-term changes in Adriatic coastal mollusc assemblages. Adriatic geohistorical records highlight a marked shift between nearshore assemblages from the two investigated time intervals. Compared to the mid-late Holocene baseline, present-day molluscan assemblages show an increase in standardised diversity in upper nearshore settings

due to increase in habitat heterogeneity and introduction of non-native species. The increase in standardised species diversity of surficial assemblages reflects local mixing of dead organisms by physical processes across upper nearshore communities that are more heterogenous today than they were in the past. The elevated spatial heterogeneity of mollusc assemblages is likely attributable to transformation and fragmentation of coastal habitats driven by human activities in the most recent centuries. In lower nearshore settings, on the other hand the decrease in standardised diversity and the rise of opportunistic taxa signal a strong anthropogenic transformation of these habitats related to eutrophication, increased frequency of hypoxic events and intense bottom trawling. Given the economic and socio-cultural importance of shellfish fisheries in the Mediterranean basin, it will be difficult to set the Holocene baseline for lower nearshore environments as an achievable (or desirable) restoration goal. Conservation strategies in such settings need to accept and incorporate human societies as part of the ecosystem (urban sea, Dafforn et al., 2015) and consider them as one of the major stakeholders that should be involved in the sustainable management of coastal ecosystems. The historical perspective provided in this study should allow us to establish better conservation strategies.

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Figure Captions

Figure 1. Map of the study area. Blue squares represent the georeferenced sediment core locations along the Po coastal plain of Emilia Romagna. The red dots indicate locations of the present-day surficial samples. Numbers next to the symbols indicate the nearshore samples retrieved in each location.

Figure 2. Nonmetric multidimensional scaling (NMDS) and rank correlation analyses. A) NMDS 3-D ordination (axes 1 and 2, see figure S4 for axes 1 and 3) of nearshore samples with at least 20 specimens (singletons excluded). Samples are symbol- and colour-coded according to the time interval and sub-environment. The size of each symbol corresponds to the log transformed sample size. Convex hulls delimit the ordination space occupied by each nearshore group of samples: brown = present day, blue = mid-late Holocene. B) Correlation between NMDS axis 1 sample scores (NMDS1) and species diversity rarefied to 20 specimens. C) Correlation between NMDS1 and relative abundance of economically relevant edible species recovered in each sample (see Appendix S2 for details). D) Correlation between NMDS1 and the water depth assigned to each sample (see Methods for details). In each panel samples are symbol- and colour-coded according to the time interval and sub-environments: U-shore_H = mid-late Holocene upper nearshore; L-shore_H = mid-late Holocene lower nearshore; U-shore_P = present-day upper nearshore; L-shore_P = present-day lower nearshore. In b–d panels, Spearman's correlation coefficient (ρ) is reported also for NMDS axis 2 sample scores. Correlation between sample NMDS scores and key community parameters is statistically significant ($p < 0.001$) in all comparisons except for NMDS2 vs % edible species and sample water depth ($p > 0.7$).

Figure 3. Varying Markov time models of the networks representing the mid-late Holocene succession (A) and present-day nearshore seabed (B) of the Po-Adriatic system. This alluvial diagram highlights changes in module assignments of nodes between network partitions obtained at different Markov times (Kheirkhazadeh et al., 2016). The partition capturing the two-step dynamics on the links (Markov time = 2) is highlighted and its modular structure is used to colour nodes in other partitions.

Figure 4. Relationship between economically relevant edible species (relative abundance per sample) and standardised diversity in targeted nearshore settings. Lines are Lowess functions based on samples pooled at nearshore level (blue circles = mid-late Holocene, brown triangles = present day). Standardised richness shows different behaviours in the analysed time intervals: Holocene assemblages show a moderate increase in both economically relevant taxa and standardised diversity between the upper and lower nearshore settings. The pattern is much less clear in present-day settings, with standardised diversity much more variable in lower nearshore samples. Economically relevant species tend to reach dominance more frequently only in the present-day assemblages. U-shore_H = mid-late Holocene upper nearshore; L-shore_H = mid-late Holocene lower nearshore; U-shore_P = present-day upper nearshore; L-shore_P = present-day lower nearshore.

Figure 5. Modular patterns of the networks representing the mid-late Holocene succession and present-day nearshore seabed of the Northern Adriatic Sea (reference partitions). This alluvial diagram highlights changes in assignment of the taxa to nearshore sub-environments between the two time intervals. Although both networks show a similar modular structure, some taxa clustered into the module representing the Holocene lower nearshore belong to the module representing the present-day upper nearshore.

Table Captions

Table 1. Permutational analysis of variance (PERMANOVA). Results (based on 999 permutations), indicate statistically significant differences between the nearshore units of the two-time intervals. Within our nested design, nearshore is a factor whereas upper and lower nearshore are considered as levels (i.e., strata) of our factor, so that permutations occur only within each level and not across all levels. Given the strong differences in the number of samples from the compared units (see Table 2), we apply PERMANOVA comparatively and not as a formal statistical test. PERMANOVA is based on the same dataset utilised for NMDS analyses (i.e., samples with ≥ 20 specimens and to species occurring in more than one sample excluded).

Table 2. Pairwise comparisons of samples ($n \geq 20$) using Bray-Curtis dissimilarity. Compositional heterogeneity within targeted environments and sub-environments during Holocene (H) and present-day (P) samples, estimated by pairwise Bray-Curtis dissimilarity between the samples. Abbreviations: IQR = interquartile range; 0.25Q = first quartile; 0.75Q = third quartile; n = number of pairwise comparisons computed following the formula: $n = 0.5 * (n-1)$.

Table 3. Ten most abundant taxa in Holocene and present-day nearshore settings. The ten most abundant species (relative abundance) in Holocene and present-day settings and their ranking at nearshore and sub-environmental level. Bivalves counts were divided by two, due to disarticulation. Taxonomic notes: *Anadara* gr. *kagoshimensis* includes also *A. transversa* (Say, 1822), which both are non-native species from southern Asia. The reports of *A. inaequalvis* (Bruguière, 1789), in the ENEA dataset are treated as misidentifications of *A. gr. kagoshimensis*. Based on Philip Bouchet communication *A. inaequalvis* is a valid species that does not occur in the Mediterranean as an introduced species (Molluscabase eds., 2022).

<i>Pairs</i>	<i>F.Model</i>	<i>R2</i>	<i>p.value</i>
Present day vs Holocene	19.710	0.166	0.001

ACCEPTED MANUSCRIPT

Table 1

<i>Subenvironmental level (n samples)</i>	<i>median</i>	<i>mean</i>	<i>IQR</i>	<i>0.25Q</i>	<i>0.75Q</i>	<i>n</i>
L_shore-H (16)	0.505	0.480	0.257	0.363	0.620	120
U_shore-H (55)	0.119	0.154	0.124	0.077	0.201	1485
L_shore-P (13)	0.721	0.648	0.600	0.347	0.947	78
U_shore-P (17)	0.652	0.599	0.440	0.384	0.824	136

<i>Nearshore level (n samples)</i>	<i>median</i>	<i>mean</i>	<i>IQR</i>	<i>0.25Q</i>	<i>0.75Q</i>	<i>n</i>
Holocene (71)	0.227	0.330	0.395	0.101	0.496	2485
Present day (33)	0.818	0.722	0.414	0.540	0.954	435

ACCEPTED MANUSCRIPT

Table 2

Species	Present day		Holocene	
	% ab	rank	% ab	rank
Nearshore				
<i>Lentidium mediterraneum</i>	0.56	1	0.89	1
<i>Chamelea gallina</i>	0.12	2	0.03	2
<i>Varicorbula gibba</i>	0.11	3	0.01	6
<i>Donax semistriatus</i>	0.06	4	0.02	3
<i>Spisula subtruncata</i>	0.02	5	0.01	4
<i>Bittium reticulatum</i>	0.02	6	0.01	5
<i>Tritia varicosa</i>	0.02	7	0.00	10
<i>Anadara gr. kagoshimensis</i>	0.01	8	/	0
<i>Peronidia albicans</i>	0.01	9	0.00	9
<i>Tritia neritea</i>	0.01	10	0.00	27
Upper nearshore				
<i>Lentidium mediterraneum</i>	0.75	1	0.95	1
<i>Donax semistriatus</i>	0.08	2	0.01	2
<i>Chamelea gallina</i>	0.07	3	0.01	3
<i>Varicorbula gibba</i>	0.02	4	0.00	6
<i>Bittium reticulatum</i>	0.02	5	0.01	4
<i>Tritia neritea</i>	0.01	6	0.00	16
<i>Lucinella divaricata</i>	0.01	7	0.00	12
<i>Spisula subtruncata</i>	0.01	8	0.00	7
<i>Anadara gr. kagoshimensis</i>	0.00	9	/	0
<i>Tritia nitida</i>	0.00	10	0.00	41
Lower nearshore				
<i>Varicorbula gibba</i>	0.37	1	0.07	4
<i>Chamelea gallina</i>	0.26	2	0.27	2
<i>Tritia varicosa</i>	0.06	3	0.02	7
<i>Spisula subtruncata</i>	0.04	4	0.11	3
<i>Antalis inaequicostata</i>	0.03	5	/	0
<i>Peronidia albicans</i>	0.03	6	0.02	9
<i>Anadara gr. kagoshimensis</i>	0.03	7	/	0
<i>Nucula nitidosa</i>	0.02	8	0.00	26
<i>Donax semistriatus</i>	0.02	9	0.06	5
<i>Abra alba</i>	0.02	10	0.00	29

Table 3

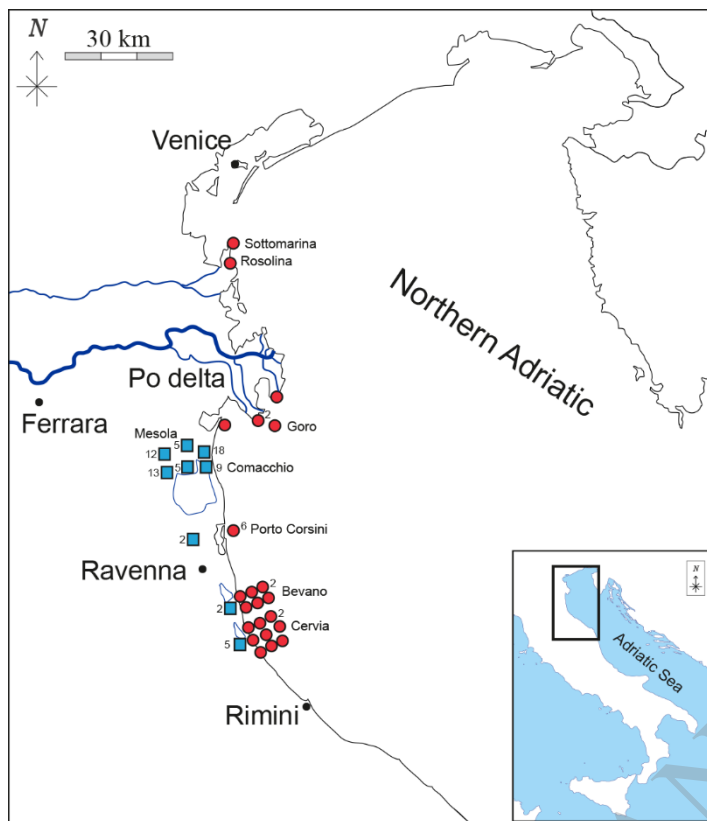


Figure 1

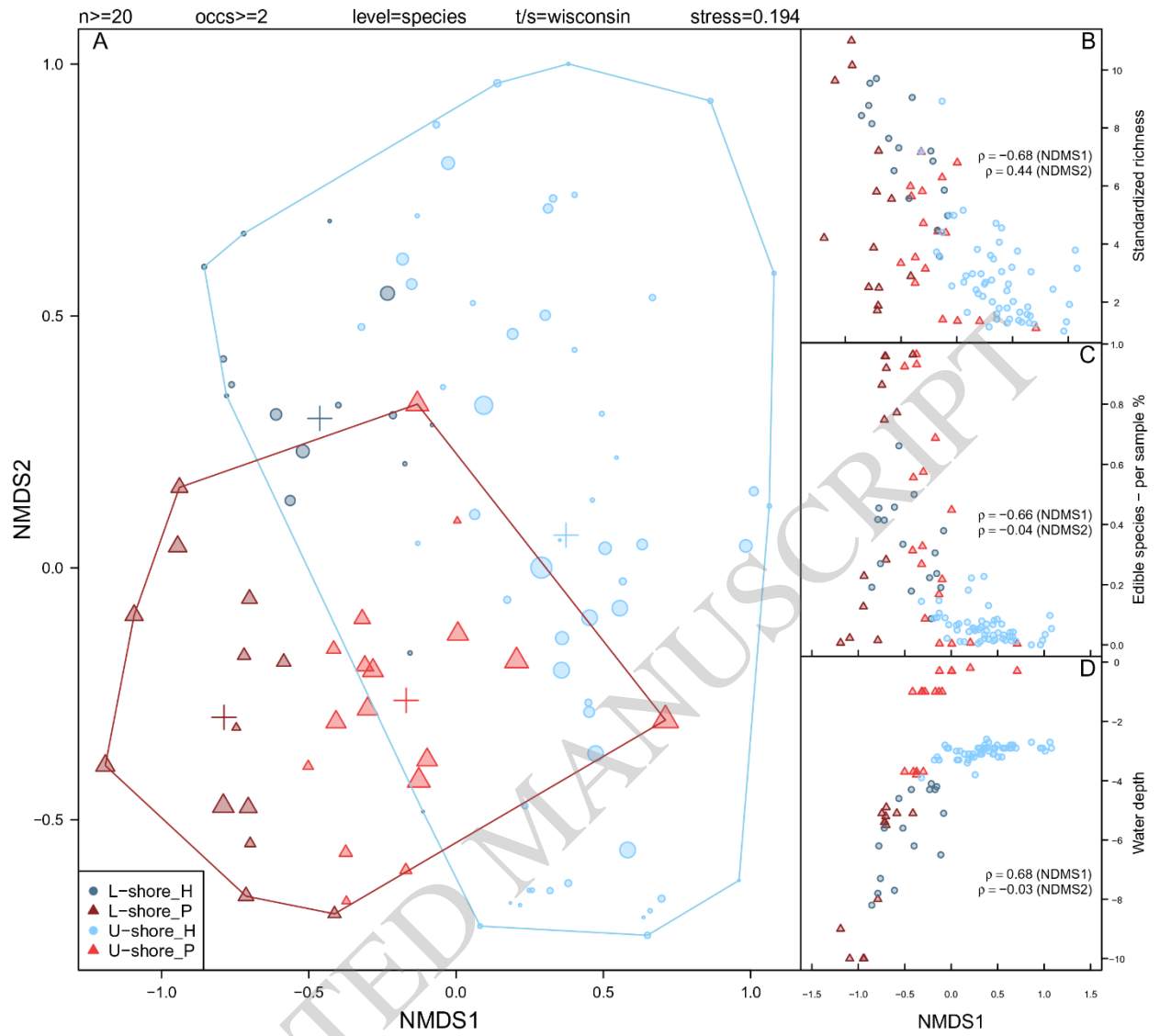


Figure 2

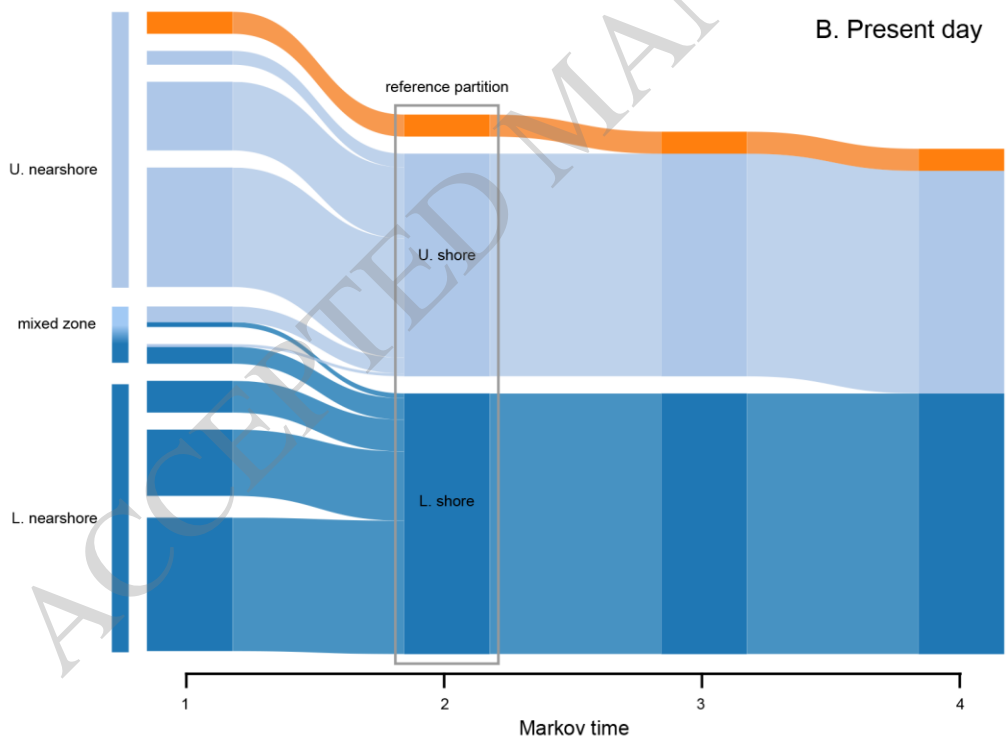
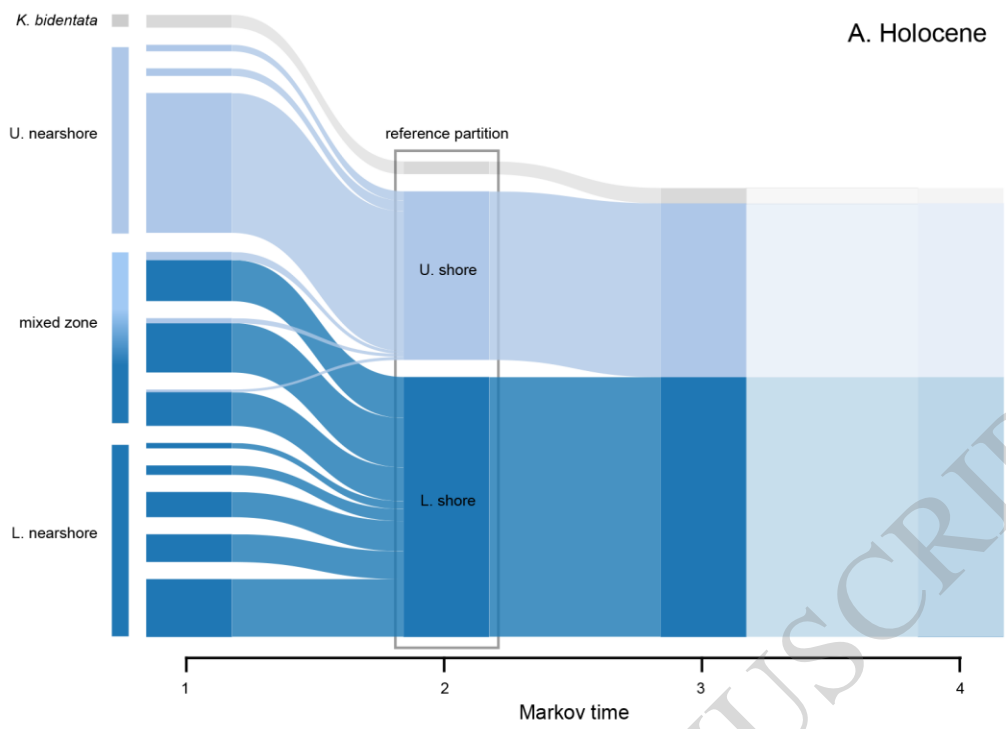


Figure 3

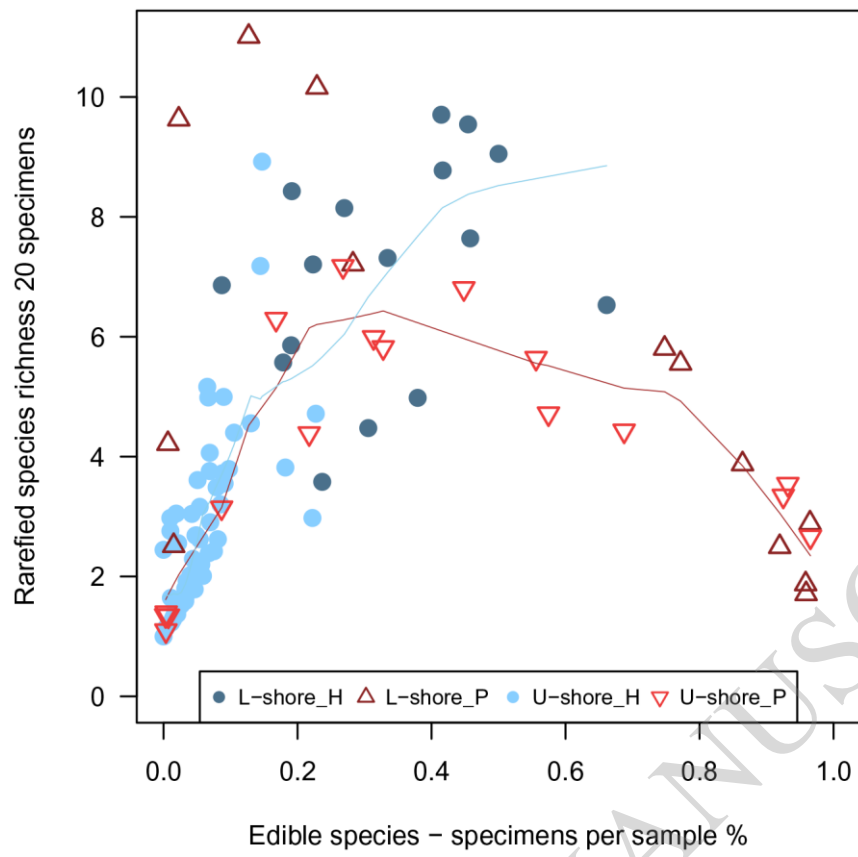


Figure 4

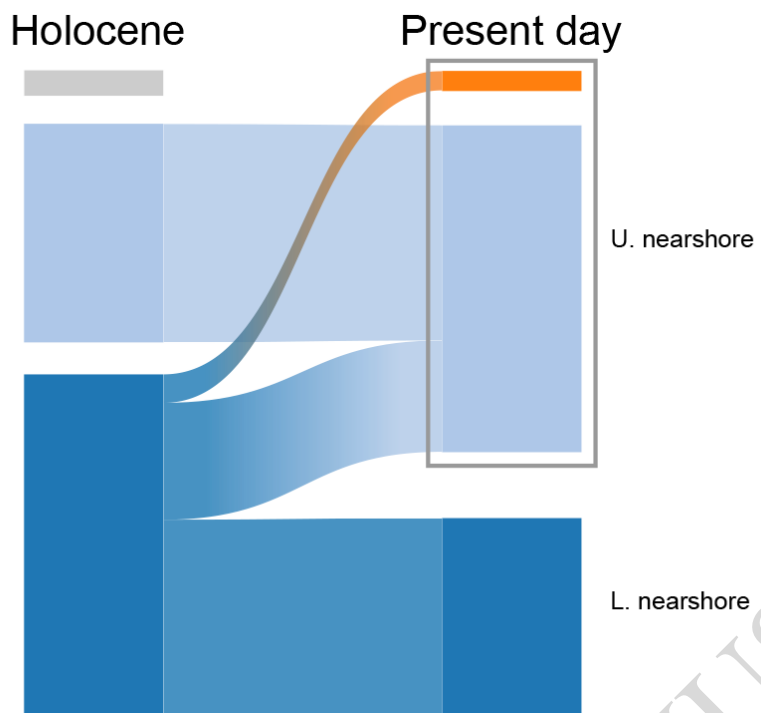


Figure 5