



Basin-wide infaunalisation of benthic soft-bottom communities driven by anthropogenic habitat degradation in the northern Adriatic Sea

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ABSTRACT: Shallow coastal seas play an important role in the economy of many countries by sustaining fisheries, tourism, aquaculture and other economic activities. Their exploitation has large-scale ecosystem effects that are easily overlooked, as they often built up over decades or centuries, and historical ecological reference data are rarely available. Here, we assess these effects by comparing live and surface death assemblages (recording historical community states) of soft-bottom molluscs across a range of habitats in the northern Adriatic Sea, using the degree of mismatch between the 2 assemblages as a proxy for ecological change. We found a consistent live–dead mismatch at all stations. Although the degree of mismatch varied between stations with low and high time-averaging (i.e. the range of post-mortem shell ages), the community change followed the same trend over the entire Adriatic basin regardless of the type of sedimentary environment, with a loss of epifaunal species and the reduction of grazers, carnivores, and herbivores. In turn, the abundance of infaunal and opportunistic species feeding on plankton or detritus strongly increased in the living communities. Directionality and magnitude of these changes cannot be explained by time-averaging or by differences in species durability, but reflect a true ecological shift in response to multiple, long-lasting anthropogenic pressures, mainly bottom trawling, eutrophication and hypoxia. The original heterogeneous assemblages characteristic of different sedimentary habitats are thus replaced by a more infaunal, functionally impoverished and less diverse benthic community representing a new ecological baseline shaped by human impact.

KEY WORDS: Ecological shift · Benthic molluscs · Anthropogenic impact · Live–dead mismatch · Living assemblages · Adriatic Sea · Holocene

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1. INTRODUCTION

Soft-sediment seafloors and their biota, which account for the largest part of shelf sea habitats, are directly impacted by bottom trawling (BT), pollution, eutrophication, hypoxia, siltation, and sediment extraction and dumping (Jackson et al. 2001, Halpern et al. 2008, Tomašových & Kidwell 2017, Breitbart et al. 2018). Marine basins characterised by dense coastal settlements and high productivity in the catchment basin are particularly affected (Rabalais et

al. 2010). The northern Adriatic Sea (NAS), in this regard, is a prime example. It is surrounded by touristic and industrial hotspots, and its southwestern part is strongly influenced by the Po River, whose catchment area encompasses Italy's largest agricultural and industrial production area (Degobbis et al. 2000, Spillman et al. 2007, Marini et al. 2008, Correggiari et al. 2014, Huntley & Scarponi 2015). The exploitation of marine resources here reaches far back into historical times (Lotze et al. 2006, 2011, Fortibuoni et al. 2017).

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Although time series recording the composition of living communities are usually limited to a few decades at most (Stachowitsch 1991, Chiantore et al. 2001, Nerlović et al. 2011), palaeoecological data increasingly document the nature of benthic changes over decades and centuries (e.g. Aronson et al. 2005, Dietl et al. 2016, Tyler & Kowalewski 2017, Gilad et al. 2018, Agiadi & Albano 2020, Powell et al. 2020). Ecological monitoring surveys suggested that the original benthic zonation mapped by Vatova (1949) in the earliest 20th century did not match communities observed in the late 20th century in the NAS (Crema et al. 1991, Scardi et al. 1999, Chiantore et al. 2001), indicating major effects of eutrophication and other anthropogenic impacts, although these comparisons were affected by differences in sampling gear and methods. Subsequently, several core-based studies demonstrated that many locations in the NAS were affected by anthropogenic impacts that exceeded the range of natural variability in community composition during the past millennia (Kowalewski et al. 2015, Gallmetzer et al. 2017, Tomašových et al. 2018, 2019), with a major shift in composition of soft-bottom communities in the mid-20th century (Simonini et al. 2004, Occhipinti-Ambrogi et al. 2005, Mavric et al. 2010, Tomašových et al. 2020). However, the spatial heterogeneity of benthic communities in the NAS is high, owing to a steep eastward decline in primary productivity and sediment accumulation rates (Zuschin & Stachowitsch 2009, Mozetič et al. 2012, Alvisi & Cozzi 2016), and it remains unclear whether anthropogenically induced changes are homogeneous over the entire basin or unique to each location.

To expand the spatial scale of analyses, we compare surface living (LAs) and death assemblages (DAs) of molluscs collected with Van Veen grabs across distinct habitats in the NAS. DAs are a mixture of multiple generations of shells in the upper 10–15 cm of the sedimentary column (mixed layer), and are hence time-averaged, i.e. they combine shells of highly variable post-mortem age (Olszewski 1999, Kowalewski 2009). On continental shelves, time-averaging of DAs typically attains several centuries and even millennia as sediment-accumulation rates are slow and the mixing depth by burrowing organisms exceeds 10 cm (Kidwell & Tomašových 2013). DAs are rather inert to recent compositional changes, as recently dead shells tend to be swamped by older shells (Kidwell 2008). Thus, they primarily archive community states prior to anthropogenic impacts that intensified in the 20th century. If a DA diverges strongly in structure and taxonomic composition from the LA collected from the same site, and other

sources of mismatch such as interspecific differences in preservation, post-mortem transport, or time-averaging effects can be discounted, this suggests that ecological conditions have changed over time and now support a different type of community (Alin & Cohen 2004, Albano & Sabelli 2011, Weber & Zuschin 2013, García-Ramos et al. 2016, Cronin et al. 2018). Conversely, low mismatch between LA and DA may indicate similar conditions in the past and at present and thus a pristine setting with long-lasting ecological stability (Kidwell 2007, 2009).

Live–dead (LD) comparisons represent a powerful method for detecting anthropogenic ecosystem modification, particularly related to eutrophication, pollution, deoxygenation and BT (Kidwell 2009, Weber & Zuschin 2013, Albano et al. 2016, Bürkli & Wilson 2017, Tomašových & Kidwell 2017). By considering additional aspects of community transition between DA and LA, such as shifts within subsets of species or on the functional level, LD comparisons provide insights into the contribution of individual anthropogenic drivers, as well as the extent and the direction of ecological turnover (Kidwell 2009). LD studies can be combined with analyses of biotic indices such as the AZTI Marine Biotic Index (AMBI), Multivariate AMBI (M-AMBI) and Bentix to trace ecological status changes over time in anthropogenically impacted habitats to better assess baseline conditions for adequate restoration and management planning activities (Dietl et al. 2016, Leshno et al. 2016, Tveitmann & Dietl 2018, Caswell et al. 2019). However, several studies from the NAS showed that these indices can generate inconsistent results (Simonini et al. 2009, Munari & Mistri 2010, Nerlović et al. 2011) because they require a robust assignment of species to sensitivity groups based on the existence of pristine reference conditions at least somewhere in the study area. Analyses of LD mismatch can better inform such assignments by identifying species sensitivity by their under- or overrepresentation in DAs. At sites affected by high sedimentation rates, as in the case of the Po Delta system (Trincardi et al. 2020) and/or high disintegration of skeletal remains, however, DAs can be dominated by recent cohorts, and the signal of historical baselines can be dampened in LD analyses (Tomašových et al. 2018). This makes inferences based on LD mismatch alone challenging. Therefore, an independent assessment of ecological history derived from core analysis and age dating can validate the LD approach. In the present paper, we use results from our previous studies (Gallmetzer et al. 2017, 2019, Tomašových et al. 2018, 2019) to relate LD mismatch to time-averaging and to geo-

graphic gradients in grain size composition, sedimentation rate, and sediment organic content. We assess (1) whether the degree of mismatch between LAs and DAs serves as a proxy for the magnitude of change experienced by mollusc communities in different regions of the NAS; (2) whether the direction of change on the compositional and functional level identifies winners and losers of ecological shifts; and (3) whether the anthropogenic drivers responsible for the mismatch between LAs and DAs can be detected. Due to the long history of human impact in the NAS, we expect to find LD mismatch at all sampling stations, but to a varying degree and with different characteristics depending on the type of habitat and on the amount of time covered by the DA. Furthermore, we hypothesise that stations protected from BT display a lower level of LD mismatch than their unprotected counterparts, as documented in studies where LD mismatch was strongly determined by trawling (Kidwell 2007). Our study is one of the few with a basin-wide approach and with the advantage of transcending the limited temporal scope of most ecological investigations focusing on recent assemblages. Thus, it provides a new, geographically and temporally comprehensive perspective on the ecological dynamics shaping benthic soft-bottom communities impacted by long-lasting anthropogenic pressures.

2. MATERIALS AND METHODS

2.1. Setting

The NAS, with an average depth of ~35 m (Fig. 1), is characterised by a high freshwater input in the western sector, mainly via the Po River and other smaller Italian rivers such as Adige and Isonzo (Marini et al. 2008). Because the Po River drains the entire north Italian plain which harbours Italy's most productive industrial and agricultural areas, its waters discharge large amounts of nutrients and sediments into the basin, making it one of the most productive regions of the entire Mediterranean Sea (Zavatarelli et al. 1998). The prevalent circulation pattern is cyclonic, thus large portions of the riverine sediment load are deposited in the form of a sediment belt along the Italian coastline (Palinkas & Nittrouer 2007, Zuschin & Stachowitsch 2009, Tesi et al. 2011). Sedimentation rates vary from $<1 \text{ mm yr}^{-1}$ in sediment-starved central and eastern areas, to $10\text{--}20 \text{ mm yr}^{-1}$ off the Po Delta (Palinkas et al. 2005, Tomašových et al. 2018, Gallmetzer et al. 2019) and $\sim 10 \text{ mm yr}^{-1}$ in the north-

ern parts of the Gulf of Trieste (Covelli et al. 2006, 2012). The NAS ranks among the marine regions with the highest anthropogenic impact worldwide that reaches back beyond Roman times (Jackson et al. 2001, Lotze et al. 2011). Eutrophication, pollution and anoxic events peaked during the 1980s and 1990s, and fisheries, particularly BT, experienced exponential growth rates in the second half of the 20th century (Justić 1991, Degobbi et al. 2000, Danovaro et al. 2009, Fortibuoni 2009, Djakovac et al. 2015).

2.2. Sampling

Sampling was carried out in summer 2014 using a Van Veen grab with a ground area of 0.125 m^2 (length 36 cm \times width 34 cm) and a penetration depth of ~15 cm. The 8 sampling stations cover various sediment types, depths, sedimentation regimes, sediment nutrient concentrations and degrees of exposure to BT (Fig. 1, Table 1; Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m671p045_supp1.pdf). Stns Po 4 and Piran 1 are located within the perimeter of oceanographic buoys, and Stn Brijuni is

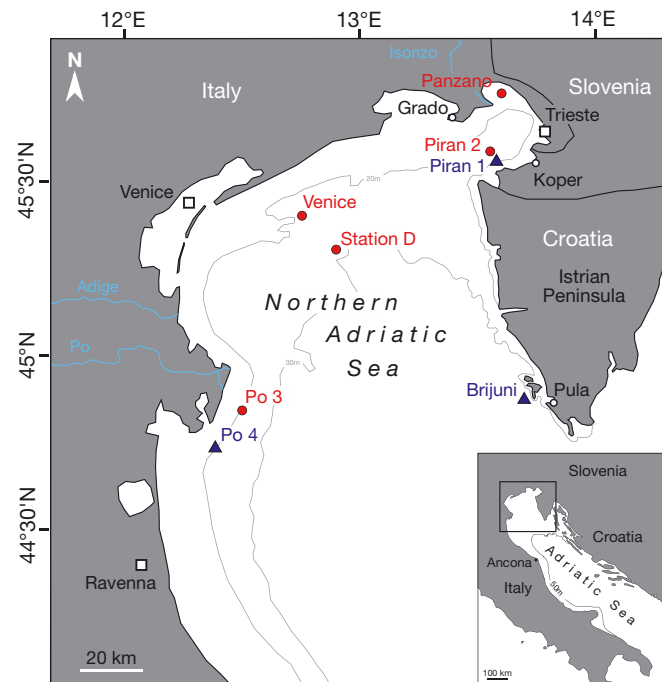


Fig. 1. The 8 sampling stations in the northern Adriatic Sea. Blue triangles: stations protected from bottom trawling (Stns Piran 1 and Po 4 within the perimeter of an oceanographic buoy, Stn Brijuni within the boundaries of a marine protected area); red dots: stations not protected from bottom trawling. Map created using © OpenSeaMap and OpenStreetMap community resources

Table 1. Sediment type (percentage of silt), sediment nutrient concentration (percentage of dry weight) of total organic carbon (TOC) and total nitrogen (TN), their standard deviation (SD) as proxy for changes of these parameters within uppermost 15 cm of sediment column, and interquartile range (IQR) of shell ages as proxy for time-averaging for all sampling stations except Stn D (values not available). Q1: 25th percentile; Q3: 75th percentile of shell ages

Stn	Mean % silt	Mean TOC (% dw)	Mean TN (% dw)	SD (% silt)	SD (TOC)	SD (TN)	Q1 (yr)	Q3 (yr)	IQR (yr)	No. of dated shells	Species dated
Po 3	60.9	1.66	0.138	0.93	0.11	0.008	5	15	10	49	<i>Varicorbula gibba</i>
Po 4	55.0	1.73	0.14	2.59	0.06	0.004	3	7	4	57	<i>V. gibba</i>
Panzano	51.3	1.57	0.14	1.10	0.05	0.004	15	53	38	107	<i>V. gibba</i>
Brijuni	44.2	1.48	0.12	3.48	0.15	0.017	118	1578	1460	57	<i>Timoclea ovata</i>
Piran 1	17.8	0.86	0.084	2.84	0.14	0.018	826	2550	1724	88	<i>Gouldia minima</i>
Piran 2	13.9	0.61	0.044	2.36	0.02	0.013	752	2713	1961	87	<i>G. minima</i>
Venice	0.5	0.13	0.01	0.18	0.05	0.002	88	2257	2169	129	<i>Lucinella divaricata</i>

within the boundaries of a marine protected area (MPA). At each sampling station, 8 replicates were taken, thus covering ~1 m² of seafloor. Except for Stn D, 1.5 m long sediment cores were collected and within-core trends in molluscan composition analysed for Stn Panzano (Gallmetzer et al. 2017, Tomašových et al. 2017), Stn Brijuni (Schnedl et al. 2018), Stns Piran 1 and Piran 2 (Mautner et al. 2018, Tomašových et al. 2019), Stns Po 3 and Po 4 (Tomašových et al. 2018), and Stn Venice (Gallmetzer et al. 2019). Shells of the most common bivalve species in cores (*Varicorbula gibba* for the 2 Po stations and for Stn Panzano, *Gouldia minima* for the 2 Piran stations, *Timoclea ovata* for Stn Brijuni, and *Lucinella divaricata* for Stn Venice) were dated with ¹⁴C-calibrated amino acid racemisation (Gallmetzer et al. 2017, 2019, Tomašových et al. 2017, 2018, Mautner et al. 2018, Schnedl et al. 2018). The interquartile (IQR) age range, based on post-mortem ages of dated molluscan shells from the uppermost 15 cm (corresponding to the maximum penetration depth of the grab sampler) characterises the extent of time-averaging of the DA at each station. From core sediments, a grain size analysis was performed and average net sedimentation rates over the last ~100 yr were calculated by means of ²¹⁰Pb sediment dating and based on down-core profiles of ¹⁴C-calibrated shell ages.

To account for changes in sediment composition and organic enrichment over the time span covered by the DA, measurements for total nitrogen (TN), total organic carbon (TOC), and percentage of silt (% silt) were considered down to a core depth whose mean age (derived from the age distribution of shells in this layer) corresponded to the upper limit of the IQR in the surface DA (the mean of an exponential age distribution is similar in magnitude to the IQR of that distribution). Means and SDs of these values were used as indices of sedimentary conditions and

environmental variability, respectively, together with IQR in a principal component analysis (PCA) to reveal the relative influence of these factors on LD fidelity.

Each grab was sieved through a 1 mm mesh on the day of sampling, and all living fauna >1 mm were collected separately and stored in 70% ethanol. The dried molluscan DA was picked out in the lab using stereomicroscopes. At stations with very shell-rich DAs, only part of the grabs was used for DA analysis: 1 grab for Piran 1, Piran 2, Brijuni, and Stn D, 2 grabs for Stn Venice, and 3 for Stn Panzano. For the samples of the 2 Po Delta stations containing fewer dead shells, 6 and 7 grabs, respectively, were included in the analysis. All living specimens and dead mollusc shells were counted and identified to species level. For bivalves, only complete valves and fragments with preserved umbo were considered. Species abundance was calculated by dividing the number of single valves by 2 and adding the count of articulated specimens. In gastropods and scaphopods, the presence of the shell apex was the inclusion criterion. For chitons, the number of dorsal plates was divided by 6, and the higher number of either cephalic or anal plates was added. In order to detect LD mismatch on the functional level, mollusc species were attributed to feeding guilds and categorised according to the type of substrate relation and vegetation association (Gallmetzer et al. 2019). In addition, species were categorised with respect to their sensitivity to BT following Kidwell (2009). This category includes all facultatively or obligately byssate bivalves, and all epifauna. For the complete dataset with species abundances and functional categorisation, together with the list of literature used for ecological species characterisation, see Dataset S1 in Supplement 2 at www.int-res.com/articles/suppl/m671p045_supp2.xls.

2.3. Data analyses

Non-marine mollusc shells and specimens not determined to species level were excluded from analyses. Three metrics were used to quantify differences in composition, richness, and evenness between LAs and DAs: Bray-Curtis dissimilarity (BC), Delta S (ΔS , rarefied to the sample size of the corresponding LA), and the probability of interspecific encounter (ΔPIE). We also assessed LD mismatch with Spearman rank order correlation (Spearman's ρ) and Jaccard-Chao similarity (JC), as these indices have been frequently used in previous LD studies (see Text S1 and Fig. S1 in Supplement 1).

Non-metric multidimensional scaling (NMDS, calculated for 2 dimensions) was used to analyse gradients in taxonomic and functional composition between LAs and DAs. This analysis is performed at 2 spatial scales—on the level of individual and of pooled grabs for each station, using BC dissimilarity based on square root-transformed relative abundances. Although the number of specimens per grab varies considerably, and within-station variability in composition among grabs is inflated by grabs with a low number of specimens, the grab-level analysis still allows us to test for within-station differences between LAs and DAs. SIMPER was used to identify species or functional groups contributing the most to LD mismatch (Clarke 1993). Within-station compositional mismatch between LAs and DAs at the grab scale for stations with multiple grabs (Po, Panzano) was assessed with PERMANOVA and with between-centroid BC dissimilarity (Tomašových & Kidwell 2011). At the station scale, LD mismatch was represented by simple BC dissimilarity subsampled to the smallest sample size per station ($n = 41$). Finally, we used the Mantel test to assess whether spatial variation in composition between LAs is comparable to spatial variation in composition between DAs, i.e. whether BC dissimilarities between LAs and between DAs are correlated. As sample sizes of DAs exceeded those of LAs, DAs were resampled without replacement to the mean sample size of LAs at each station. BC dissimilarities and PERMANOVA test statistics based on resampled DAs were computed 1000 times. The results were quantitatively similar to those based on raw proportional abundances, and we therefore report the results based on raw data.

We assessed the relationship between time-averaging and LD mismatch (expressed as BC, ΔS , and ΔPIE) with a Spearman rank correlation. Dissimilarities between local assemblages are biased downward owing to sample size limitation (Lande 1996).

The magnitude of this bias depends on the rank-abundance distribution of the parent community or metacommunity that represents the source for the local samples (He & Legendre 2002). Pairs of local assemblages drawn from communities with higher evenness will thus show stronger LD mismatch than samples derived from an uneven community (Tomašových & Kidwell 2010). Hence, a natural gradient in evenness can generate a gradient in LD mismatch even when other factors affecting LD mismatch do not vary between stations. Therefore, we computed 2 null models that predict LD mismatch at station scale in the absence of other effects (e.g. recent ecological change owing to anthropogenic impacts, differences in post-mortem biases, or differences in time-averaging). First, we pooled replicates of DAs at the station scale and randomly selected 2 samples that were subsampled to the smallest sample size observed in both LAs and DAs ($n = 41$). The same procedure was applied to LAs at the station scale. In both cases, the mean null-model LD mismatch is represented by the BC dissimilarity averaged across 1000 pairwise comparisons. Statistical analyses were performed in RStudio version 1.2.1335 using the 'vegan' package (Oksanen et al. 2016, RStudio Team 2018).

3. RESULTS

3.1. Environmental characterisation of sampling stations

The 8 stations can be divided into 2 groups. The first group, Stns Po 3, Po 4 and Panzano, is influenced by river deltas (Po River, Isonzo River) and characterised by muddy sediments, moderate to high net sedimentation rates (up to 2.6 cm yr⁻¹ at Po, Table S1), elevated concentrations of TOC and TN, and low time-averaging (IQR from 4 yr at Stn Po 4 to 38 yr at Stn Panzano, Table 1). Living molluscan assemblages at all 3 stations are dominated by the bivalve *Varicorbula gibba*. The remaining stations form a second group and are located either offshore in the Gulf of Venice (Stns D and Venice) or in the eastern part of the NAS. Net sedimentation rates (<0.1 cm yr⁻¹) and concentrations of TOC and TN in sediments are low, and sediments are more coarse-grained than in the first group, ranging from sandy muds with molluscan and bryozoan gravel (Stn Brijuni) to muddy sands (Piran, Stn D) and siliciclastic sand (Stn Venice). Time-averaging is consistently high at Stns Venice, Brijuni and Piran (from ~1500 to 2200 yr, Table 1).

Table 2. Number of mollusc shells found (N), observed number of species (Sobs), and rarefied number of species (Srar), standardised to 41 (smallest living assemblage [LA] at station scale) and 1090 individuals (smallest death assemblage [DA] at station scale) and for DAs to the corresponding LA sample size

Stn	N DA	N LA	Sobs DA	Sobs LA	Srar DA (min. 41)	Srar DA (min. 1090)	Srar DA (LA sample size)
Po 3	1090	111	40	9	6.5	42.0	16.6
Po 4	2854	210	58	15	9.3	44.4	27.1
Panzano	2382	1441	75	22	4.9	63.9	65.6
Station D	4452	232	121	29	13.2	86.9	44.2
Brijuni	2978	41	137	14	14	108.9	22.9
Piran 1	22 168	64	152	22	17.6	86.3	20.6
Piran 2	17 976	166	152	26	13.5	84.2	33.6
Venice	3730	94	128	18	12.8	107.2	34.9
Total community	57 912	2359	245	59	11.4	112.5	130.5

3.2. LD mismatch in richness and evenness

In total, 60 271 mollusc individuals were determined to species level. Of these, 3.9% were living and 96.1% dead specimens (Table 2). The DA consisted of 43% gastropods, 56% bivalves, and 1% scaphopods and chitons. In the LA, bivalves amounted to 92%, while gastropods contributed 7% and scaphopods and chitons 1%. The DAs with the highest number of shells were found at the 2 Piran stations with >18 000 dead shells 0.125 m^{-2} and 152 species each. The live mollusc community was most abundant at Stn Panzano, with 1441 animals m^{-2} , of which ~88% belonged to the bivalve species *V. gibba* (Fig. 2a). The overall, regional-scale DA contained 245 mollusc species, more than 4 times the number of species found in the pooled LA (59 species).

Rarefied species richness of DAs at station scale (standardised to 1090 individuals) is low at the 3 stations with high net sedimentation rate (Stns Po 3, Po 4, and Panzano, 42–64 species) and higher at the other stations (84–109 species). The relationship between rarefied richness of DAs and their time-averaging (IQR) is positive (Spearman $r = 0.71$, $p = 0.08$). The correlations between IQR and the species richness of LAs at the level of observed (Spearman $r = 0.54$, $p = 0.21$) and rarefied numbers (Spearman $r = 0.53$, $p = 0.23$) are positive, but not significant, although this is probably driven by the small number of stations.

At Stns Po 3, Po 4, Panzano and Brijuni, 100% of the species found alive were also found in the DA. This percentage decreased at the other stations and reached the lowest value (83%) at Stn D, where 5 of the 29 live species were restricted to the LA. Four of these species were tellinoid bivalves (*Abra nitida*, *Moerella pulchella*, *Peronaea planata*, *Gari costulata*) characteristic of organic-rich fine-grained sedi-

ments where they live deeply burrowed (up to at least 20 cm) as detritus feeders (Yonge 1946, Wilson 1979, Gofas et al. 2011). The percentage of dead species found alive was highest at the western stations (31% at Stn Po 4) and smallest (10%) at Stn Brijuni.

At 7 out of 8 stations, the DA is more species-rich than the LA based on raw and rarefied data (Tables 2 & 3, Fig. 2c,d). The mean rarefied dead:live richness ratio of the whole mollusc assemblage (all stations pooled) is ~1.8 (Fig. 2d, Table 3). In accordance with this, ΔS is positive at most stations (ranging from 0.11 to 0.48, Table 3) and slightly negative only at Stn Piran 1 ($\Delta S = -0.04$). ΔPIE is positive at 6 stations, close to zero at Stn Po 4, and negative at Stn Piran 1 (Table 3). The high abundance of *Nucula nucleus* in the LA at Stn Brijuni, and the dominance of *V. gibba* and *N. nucleus* in the LA at Stn Po 3 account for the smaller PIE of LAs at these stations (Table 3). Despite the higher species richness in both DAs and LAs at stations with low sedimentation (and, thus, higher IQR), the relationship between IQR on the one hand and ΔPIE and ΔS on the other hand is weakly negative and not significant.

3.3. LD mismatch in species composition and abundance

A comparison of the 5 most abundant species in the DA and LA at each station reveals a major turnover in molluscan abundances (Fig. 3). At the 2 Po stations, *V. gibba* is the dominant species both in the LA (Po 3: 41%, Po 4: 26%) and the DA (Po 3: 33%, Po 4: 39%). *N. nucleus*, a sub-surface detritus feeder (Yonge 1939), reaches high relative abundances only in the LA (Po 3: 32%, Po 4: 31%). Conversely, the invasive bivalve *Anadara transversa* that was introduced in the NAS in the 1970s (Albano et al. 2018) is

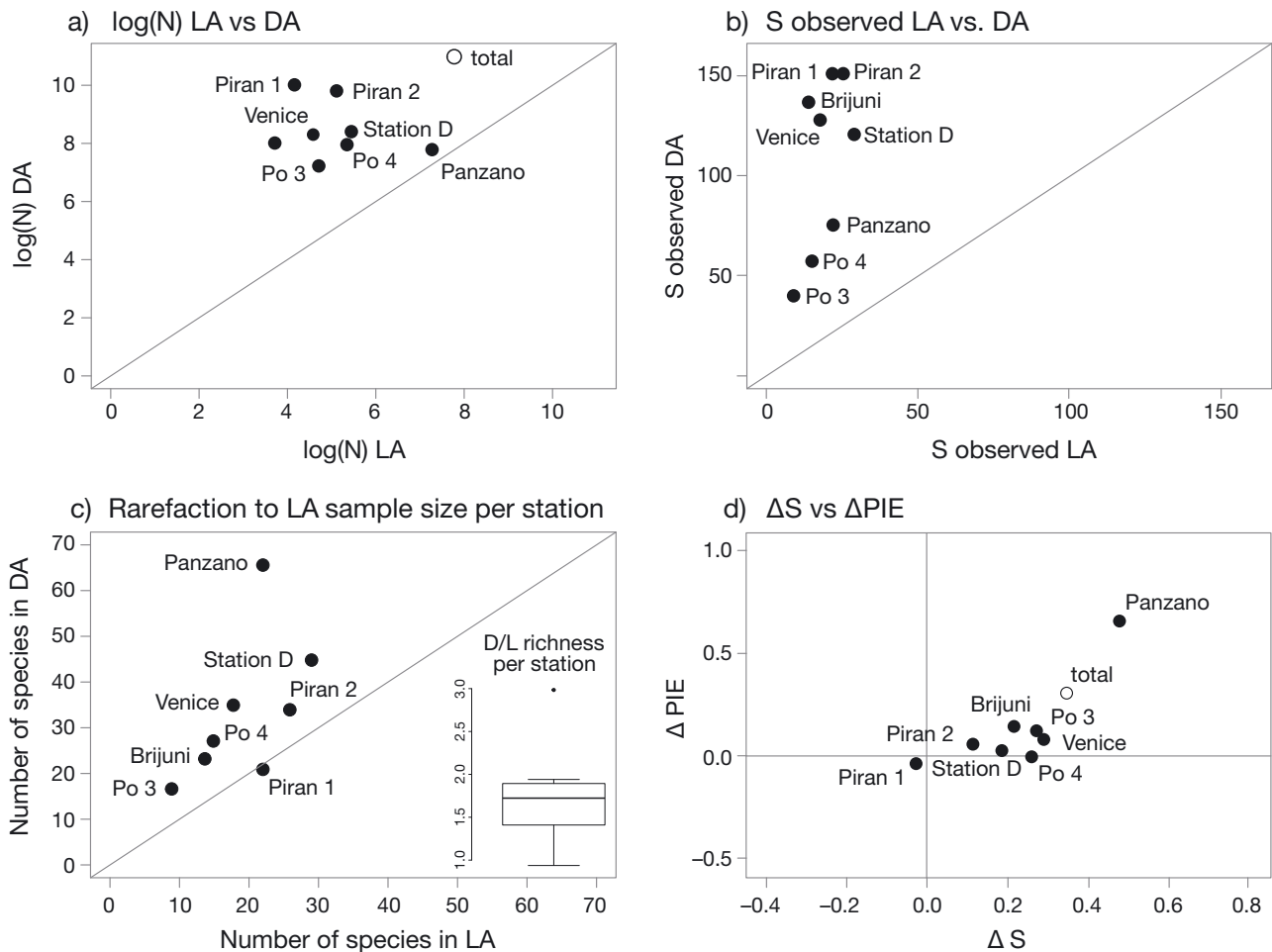


Fig. 2. (a) Abundances of death assemblages (DAs) and living assemblages (LAs) per station and for the total assemblage on a logarithmic scale. (b) Observed number of species (S) in DAs and LAs per station. (c) Rarefaction to LA sample size per station (equivalent to pooled LA sample size per station); boxplot shows distribution of dead:live (D:L) species richness ratio within stations. Median, interquartile range, minimum and maximum values and an outlier (corresponding to Stn Panzano) are shown. (d) Scatterplot of live–dead (LD) differences in evenness (probability of interspecific encounter, Δ PIE) and rarefied species richness (Δ S) between DAs and LAs per station and for the total assemblage. Note distant position of Stn Panzano caused by an individual-rich and highly uneven LA due to the dominance of *Varicorbula gibba*

Table 3. Percentage of living mollusc species also found dead (% L→D), percentage of dead species also found alive (% D→L), ratios of dead to live species richness for observed (Ratio Sobs D:L) and rarefied number of species (Ratio Srar D:L), and fidelity measures used for live–dead (LD) analysis: Delta S (Δ S), probability of interspecific encounter (Δ PIE), Spearman’s ρ , Jaccard-Chao index (JC), and Bray-Curtis dissimilarity (BC)

Stn	% L → D	% D → L	Ratio Sobs D:L	Ratio Srar D:L	Δ S	Δ PIE	Spearman’s ρ	JC	BC
Po 3	100	22.5	4.44	1.85	0.267	0.121	0.574	0.608	0.470
Po 4	100	31.3	3.20	1.81	0.257	-0.004	0.431	0.707	0.513
Panzano	100	29.3	3.41	2.98	0.475	0.659	0.487	0.636	0.569
Station D	82.8	19.8	4.17	1.52	0.183	0.025	0.371	0.807	0.555
Brijuni	100	10.2	9.79	1.63	0.213	0.142	0.293	0.479	0.698
Piran 1	95.5	13.8	6.91	0.94	-0.029	-0.036	0.350	0.699	0.704
Piran 2	88.5	15.1	5.85	1.29	0.112	0.054	0.248	0.380	0.750
Venice	94.4	13.3	7.11	1.94	0.287	0.081	0.315	0.606	0.648

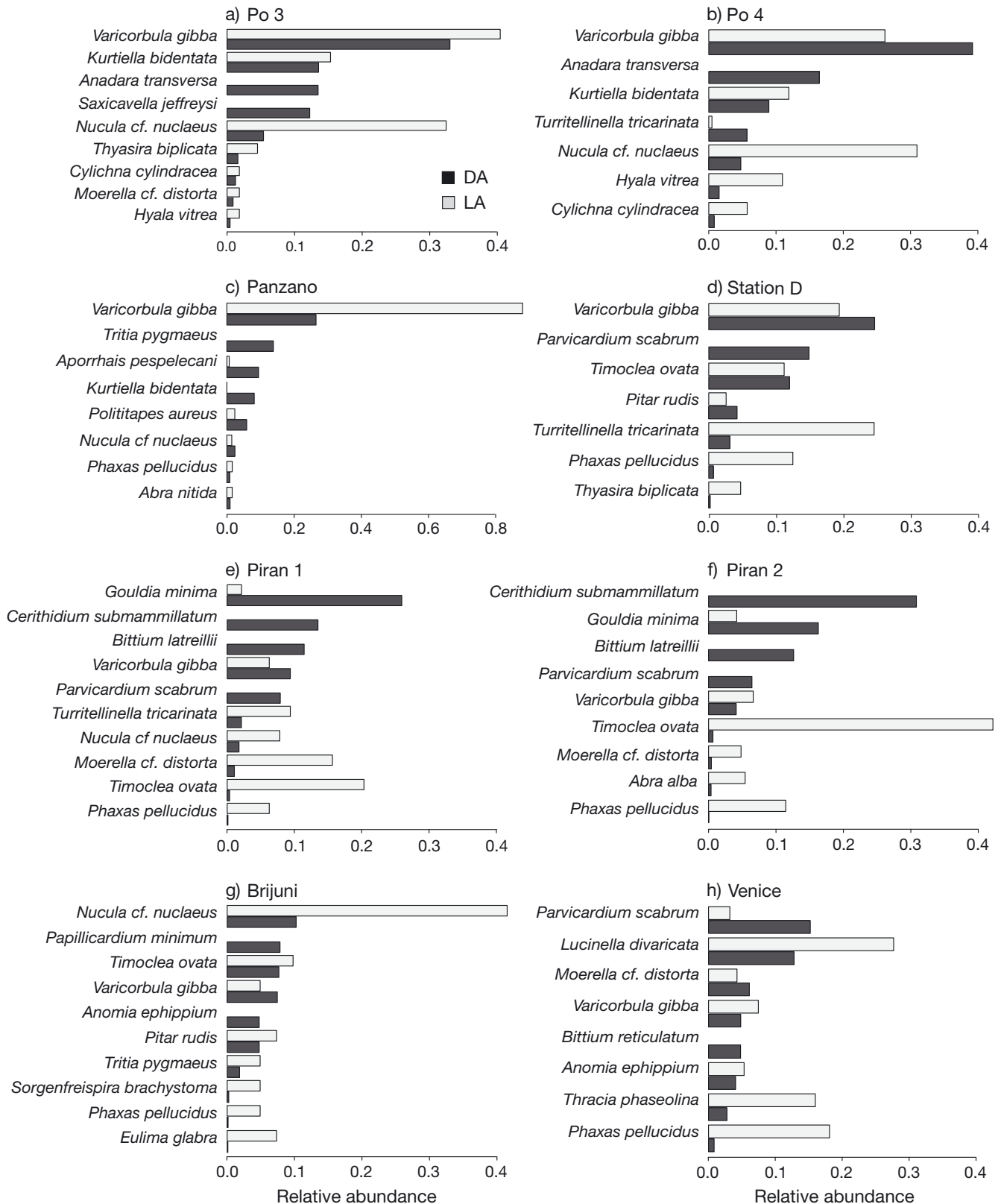


Fig. 3. Relative abundances of the 5 most common species in death assemblages (DAs) and living assemblages (LAs) at Stns (a) Po 3, (b) Po 4, (c) Panzano, (d) D, (e) Piran 1, (f) Piran 2, (g) Brijuni, (h) Venice. In case of overlapping species, the number of species shown is <10. At all stations, infaunal species such as *Varicorbula gibba*, *Nucula cf. nucleus* and *Timoclea ovata* are more abundant in the LAs. DAs are marked by high abundance of dead-only species (e.g. *Cerithidium submammillatum*, *Bittium* spp., *Papillicardium minimum*, *Parvicardium scabrum*, *Tritia pygmaeus*)

found frequently in the DA (Po 3: 14%, Po 4: 16%), but was not found alive. At Stn Panzano, the abundance of *V. gibba* in the LA is exceptionally high (88%), whereas the DA is also dominated by *V. gibba* but with a lower abundance (27%). Other taxa that are abundant in the DA are rare in the LA. The LA and DA at Stns D and Venice share the most abundant species, whose relative abundance, however, differs markedly (Fig. 3). As in other stations, grazing species such as *Bittium reticulatum*, frequent in the DA, do not occur in the LA. The Piran stations stand out because their most abundant dead species (*Gouldia minima*, *Cerithidium submammillatum*, *B. latreilli*) are rare or absent in the LA, whereas mud-associated species such as *Timoclea ovata* or *M. distorta* dominate in the LA. In the LA of Stn Brijuni, *N. nucleus*, a species with preference for fine nutrient-rich sediments, and *T. ovata* increase strongly in their relative abundance compared to the DA. *Papiliocardium minimum* and the epifaunal bivalve *Anomia ephippium*, among the 5 most important members of the DA, are absent in the LA. In summary, the species contributing most to LD mismatch at the station scale are (1) the bivalves *V. gibba*, *N. nucleus*, and *T. ovata*, whose proportional abundance increased strongly in the LA, and (2) several epifaunal gastropods (e.g. *C. submammillatum* and *Bittium* spp.) and bivalves associated with coarser sediments (e.g. *G. minima*, *Parvicardium scabrum*), which are prominent in the DA but absent or reduced in the LA.

Within-station analyses indicate significant differences in species relative abundances when grabs are used as replicates and the number of grabs per DA > 2 (F [Stn Po 3] = 14.1, $p = 0.003$; F [Stn Po 4] = 17, $p = 0.001$; F [Stn Panzano] = 18, $p = 0.01$; F [Stn Venice] = 5.8, $p = 0.046$; F [Stns Piran 1 and 2 pooled] = 6.5, $p = 0.018$), with no overlap in NMDS (Fig. 4a). DAs are clearly separated from each other and from their corresponding LAs, while LAs from stations with high time-averaging (Piran, Brijuni and Venice) overlap and separate from stations with low time-averaging (Po, Panzano). If grabs are pooled to stations, the 8 LAs also do not overlap with their corresponding DAs in the NMDS (Fig. 4b, PERMANOVA $F = 4.1$, $p = 0.01$). The shift from the DA to its corresponding LA follows the same direction in the 2-dimensional space at all stations, and the distance between DAs and corresponding LAs is larger at stations with highly time-averaged DAs than at Po and Panzano.

The first NMDS axis captures the overall gradient in species composition that separates stations with low net sedimentation rate (low content of silt, TOC and TN) from those with high net sedimentation rate

(high content of silt, TOC and TN). NMDS axis 1 correlates significantly with TOC for both LAs (Spearman $r = 0.96$, $p = 0.003$) and DAs (Spearman $r = 0.96$, $p = 0.007$). The Mantel test that contrasts BC dissimilarities among LAs with those among DAs shows a high Pearson correlation (Fig. 5a, Pearson $r = 0.83$, $p = 0.001$). Therefore, in spite of the overall compositional shift between LAs and DAs, both LAs and DAs are ordered similarly along an environmental gradient characterised by a decline in net sedimentation rate, grain size and sediment organic content. Both grab-scale and station-scale BC dissimilarities are highest at the Piran stations, as the 4 most abundant

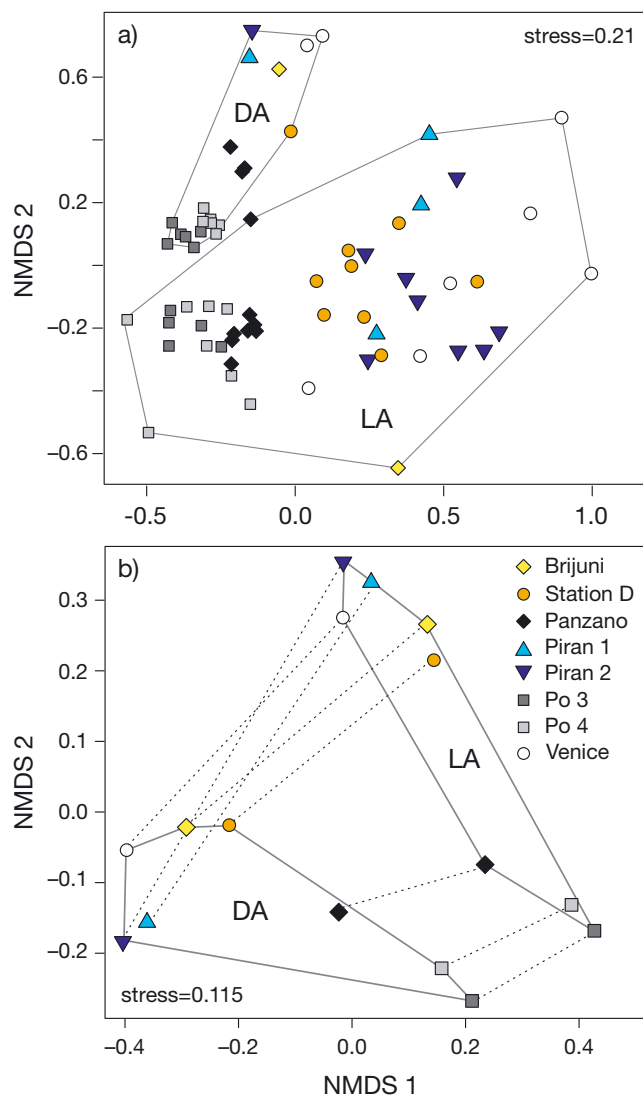


Fig. 4. (a) Ordination of proportional species abundances based on individual grab samples. (b) Ordination of pooled grab samples for each station. Dashed lines indicate the direction of change from the death assemblage (DA) to the living assemblage (LA). NMDS: non-metric multidimensional scaling

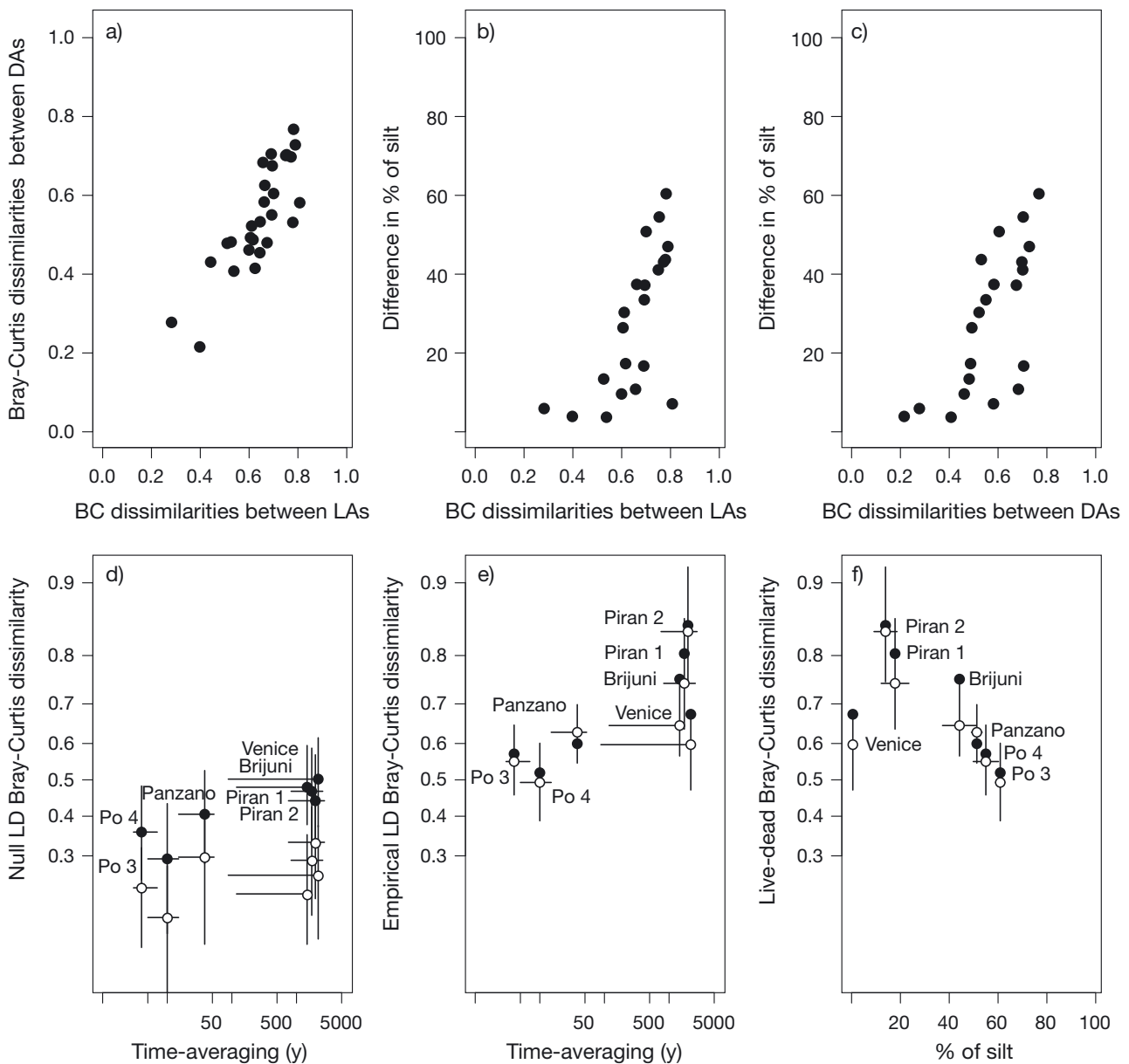


Fig. 5. (a) In spite of live–dead (LD) compositional differences within stations, the compositional gradient among stations is preserved as shown by the positive relationship of dissimilarities between LAs (living assemblages) with dissimilarities between DAs (death assemblages) in the Mantel test. Bray Curtis (BC) dissimilarities between LAs (b) and between DAs (c) correlate with between-station differences in silt percentage. (d) Relationship between time-averaging (interquartile range [IQR] of shell ages in years) and the null expectation of LD BC dissimilarity computed by subsampling of station-specific DAs to 2 assemblages (black circles) and by subsampling of station-specific LAs to 2 assemblages (white circles). The relationship is determined by a gradient in evenness of both LAs and DAs increasing towards stations with low sedimentation and thus high time-averaging. (e) LD mismatch represented by BC dissimilarity between centroids of LAs and DAs increases with time-averaging at grab scale (standardised to the minimum sample size per station, black circles) and at station scale (standardised to 41 individuals, white circles). (f) LD mismatch declines with total organic carbon concentration that covaries positively with silt percentage and total nitrogen concentration, and negatively with sediment accumulation rate. The relationships are similar if BC dissimilarity is computed between LAs and DAs by pooling grabs at each station. Error bars represent upper and lower confidence intervals

species of the DA are not present in the LA (Table 3, Fig. 5). At the other stations with high time-averaging (Brijuni and Venice), dissimilarities are also higher than at the stations with low time-averaging

(Po and Panzano). Here, *V. gibba*, *Kurtiella bidentata* and *N. nucleus* are within the 5 most abundant species in both DAs and LAs, and hence, dissimilarities are smaller (Fig. 5).

3.4. Gradients in functional composition

The most important functional changes driving LD mismatch are evident on the level of feeding guilds (Fig. 6a). Filter-feeding and detritus-feeding increase strongly in the LAs and become the dominant feeding types at all stations. Conversely, grazers, the second most important feeding guild in the DAs of low-sedimentation stations, are virtually absent in the LAs, and carnivores, scavengers and herbivores also decline (Fig. S2 in Supplement 1).

LAs are characterised by a substantial loss of abundance and diversity of epifaunal species. In the DAs, they constitute ~43% of all individuals and, on average, $48 \pm 6\%$ of species, and drop to a mere 2.1% and $17.6 \pm 12\%$ in abundance and species, respectively, in the LAs. This massive decline, which is particularly evident at Stns Piran, Brijuni and Venice, is

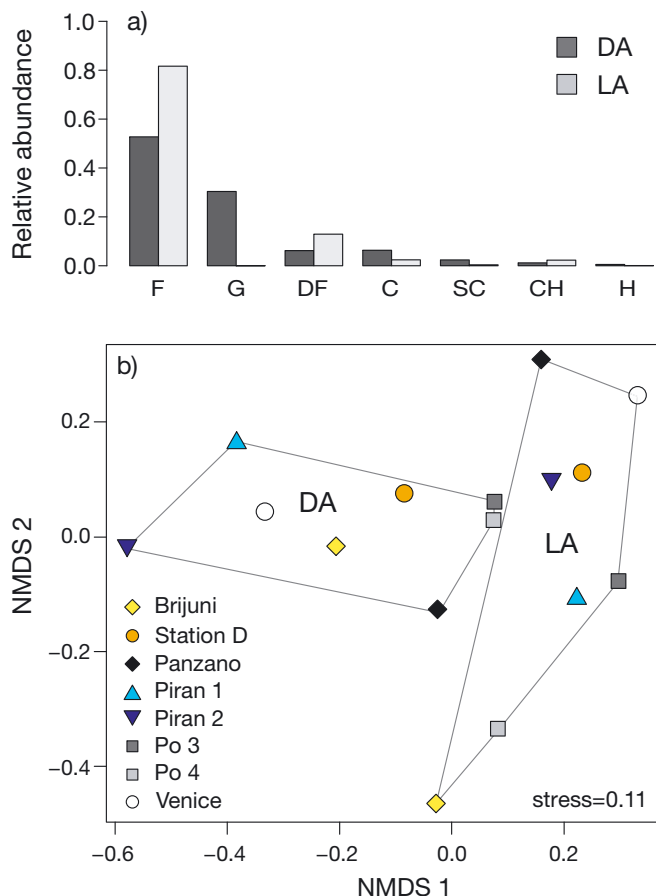


Fig. 6. (a) Proportional abundance of feeding guilds across stations. (b) Ordination of proportional abundances of feeding guilds for each station. DA: death assemblage; LA: living assemblage; F: filter feeders; G: grazers; DF: detritus feeders; C: carnivores and ectoparasites; SC: scavengers; CH: with chemosymbionts; H: herbivores; NMDS: non-metric multi-dimensional scaling

compensated by an increase in abundance of infaunal species, which make up between 73% and 100% in the LAs. The ordination of feeding guilds separates DAs and LAs along the first axis (Fig. 6b). The DAs of Stns Panzano, Po 3 and Po 4 are closest to the LA group, emphasising the functional affinity between DAs and LAs in muddy habitats. An increase in abundance of filter- and detritus-feeders (SIMPER: 29% and 28%, respectively) and the absence of grazers (SIMPER: 23%) in the LA contribute ~80% to the overall functional LD mismatch. Axis 1 of the NMDS plot thus reflects a gradient of increasing filter/detritus-feeding and decreasing grazing.

3.5. Relationship between LD mismatch, environmental variables, and time-averaging

PCA based on environmental variables shows the tight covariation of grain size with concentrations of TOC and TN (Fig. 7) aligning along the first axis, which explains 56% of environmental, between-station variation. BC dissimilarity correlates positively with time-averaging (IQR, Fig. 5b) at the grab (Fig. 5e, $r = 0.71$, $p = 0.08$) and station scale ($r = 0.75$, $p = 0.07$). The same rank correlations apply to the relationship

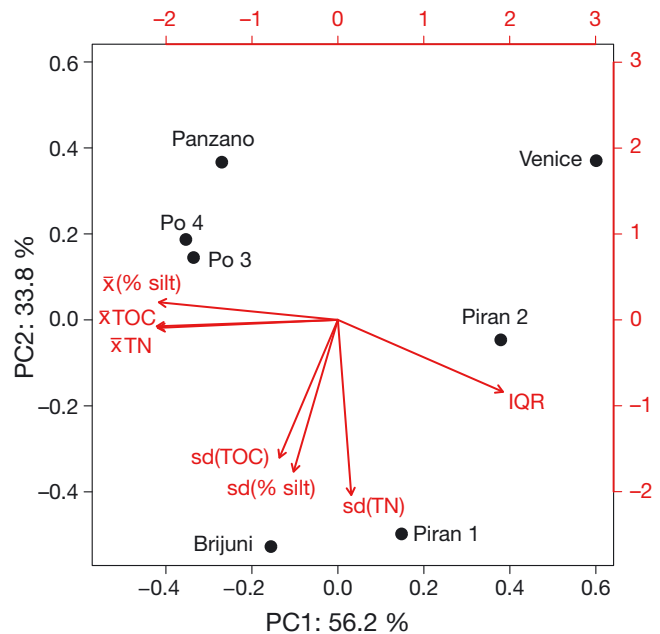


Fig. 7. Principal component (PC) analysis of the factors sediment type (% silt as proxy), sediment nutrient concentration (TOC: total organic carbon, and TN: total nitrogen as proxies), and time-averaging (IQR: interquartile range of shell ages). Means of environmental factors (\bar{x}) are used to characterise sedimentary conditions, and SD to express environmental variability within the uppermost 15 cm of the sediment column

between concentrations of TOC, TN and the silt percentage on the one hand, and BC dissimilarity on the other (r [grabs] = 0.75, p = 0.07; r [stations] = -0.78, p = 0.04; Fig. 5f). The environmental gradient underlying differences in BC dissimilarity is also illustrated by larger distances between low-sedimentation stations and higher distances between high-sedimentation stations in the NMDS (Fig. 4a,b).

However, the null-model LD dissimilarities (based on both LAs and DAs) also increase towards stations with low sedimentation rates, paralleling the general increase in evenness of benthic communities (Fig. 5d). Therefore, the LD mismatch increase towards stations with low sedimentation is expected even if other sources of mismatch would not increase along this gradient. The correlation between the null-model LD dissimilarities and IQR is positive for DAs (Fig. 5d, r = 0.82, p = 0.03), and positive but not significant for LAs (r = 0.5, p = 0.26). Hence, the geographic gradient in compositional mismatch, with higher LD mismatch at low-sedimentation stations, is to some degree determined by a higher evenness of habitat-specific species pools at sites with low sedimentation rate. The stratigraphic variability in TOC, TN and silt percentage (mainly contributing to the second PCA axis) does not correlate with the LD BC dissimilarity in any comparisons.

3.6. Species sensitive to BT

Relative abundance and richness of BT-sensitive species is considerably higher in the DAs of all stations (Fig. 8a,b). At Brijuni, the station with the highest level of protection, LD differences in sensitive species are least pronounced. At Stn Po 4, the LD mismatch is also pronounced, but in contrast to its unprotected counterpart Po 3, some sensitive species are still present in the LA. At the paired Piran stations, this pattern is reversed, with an increased richness of live sensitive species at the unprotected station Piran 2 and equal species abundances in both protected and unprotected LAs.

4. DISCUSSION

Two main patterns of LD mismatch follow from our analyses. First, living and dead mollusc assemblages displayed compositional and functional differences that showed a similar trend at all stations, in spite of major differences in grain size, organic enrichment, and time-averaging between them. These differences are primarily represented by an abundance increase of infaunal bivalve species in LAs associated with muddy, organic-rich sediments, a decline of epi-

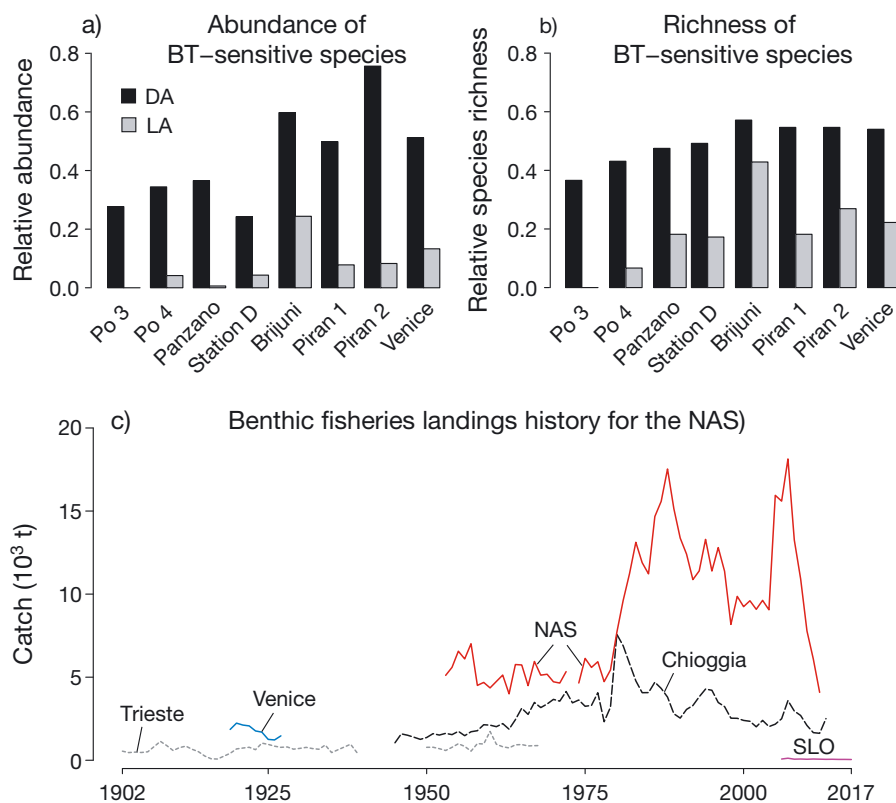


Fig. 8. (a) Proportional abundance of species sensitive to bottom trawling (BT) in death assemblages (DAs) and living assemblages (LAs) per station. (b) Relative richness of BT-sensitive species. (c) Time series of official benthic catches (fish, molluscs, and crustaceans) for individual Italian fish markets (Venice, Trieste, and Chioggia), for Slovenia (SLO), and for the upper northern Adriatic Sea (NAS; Italian catches only, regions Friuli-Venezia-Giulia and Veneto, regions selected to best match sampling area); data in (c) compiled from Fortibuoni et al. (2017)

faunal gastropods, and a functional impoverishment with a strong dominance of filter- and detritus feeders, an almost complete loss of grazers, and a decrease of carnivorous and herbivorous species in the living community. Second, LD mismatch increases to some degree with increasing grain size, decreasing organic enrichment, and increasing time-averaging. However, this gradient is partly determined by natural geographic gradients in evenness, even in non-time-averaged LAs. Random subsampling from even communities generates higher dissimilarities as random sampling of less-even communities, indicating that the stronger LD mismatch at stations with low sedimentation were not necessarily affected by stronger anthropogenic impacts. Although LD mismatch can arise from a true ecological shift in composition, with LAs reflecting the establishment of a new community state adapted to new environmental conditions (Kidwell 2007), several other factors can generate significant LD discordance (Kidwell & Tomašových 2013, Bürkli & Wilson 2017). These factors include undersampling of living communities, taphonomic biases generated by inter-specific differences in species durability, transport from other habitats, and time-averaging.

4.1. Undersampling, differences in durability, and transport effects

Several lines of evidence indicate that LD mismatch is not determined by undersampling of LAs. First, at each station, 8 replicates were taken, adding up to a total area of ~1 m² of sampled seafloor, a unit well within or beyond the range of sample areas used in comparable studies (e.g. Weber & Zuschin 2013, Zuschin & Ebner 2015). Second, size-standardised analyses at both the grab and station scales, with sample sizes of DAs rarefied to the sample sizes of LAs at each station, show the same segregation pattern in the ordination space as non-standardised analyses. Third, dissimilarities based on the null model where 2 subsamples are either drawn from the single, station-specific LA or DA are smaller than observed in empirical data at the same sample size (Fig. 5d,e).

Post-mortem transport and accumulation of species from other habitats in the DAs is also unlikely because all sampling stations except for Brijuni are located on a relatively uniform and shallow shelf not affected by transport of faunal elements from coastal hard bottoms. In addition, stations are located at water depths largely unaffected by wind-induced currents and influenced mainly by tidal currents or

the regional circulation system that cannot erode larger shells from the sediment and achieve cross-shelf transportation (e.g. Breman 1978). Also, for the Po and Panzano stations which can be affected by erosion from storm waves (Lipizer et al. 2012, Tesi et al. 2012), our previous analyses based on abundances of dated shells of *Varicorbula gibba* showed that the 20th century shell record is complete at the scale of decades (Tomašových et al. 2017, 2018). In contrast to steep, narrow shelves (Dominici & Zuschin 2005) and to deltaic settings (Trincardi et al. 2020), the effect of out-of-habitat transport is generally far less common on wide shelves as in most parts of the NAS (Collins 1986, Kidwell & Bosence 1991, Kidwell 2008, 2013).

At stations with low sedimentation rates, mollusc communities feature several species that are moderately or highly abundant alive but rare or completely missing in the DA. If these species are particularly fragile, and the species overrepresented in the DA are more durable, this can be generated by a taphonomic bias, because disintegration rates are expected to be higher in species with small, fragile shells (Kidwell 2002, Kosnik et al. 2009). Species such as *Phaxas pellucidus*, or *Hyala vitrea* and *Cylichna cylindracea*, are highly abundant in the LA and rare or missing in the respective DA (Fig. 3). Their underrepresentation in DAs, thus, can be interpreted as a consequence of low shell durability. On the other hand, species with robust shells are not overrepresented in the DA but occur in similar numerical proportions (abundant in LAs, rare in DAs) as the above-mentioned fragile species (e.g. *Timoclea ovata* and *Moerella distorta* at Piran, *Eulima glabra* at Stn Brijuni, *Turritellina tricarinata* at Stn D, Fig. 3). *T. ovata* is not only abundant in the DA of Stn Brijuni but also throughout a sediment core from this location covering the entire Holocene (Schnedl et al. 2018, Gallmetzer et al. 2019), which indicates that its rarity in the DAs at Piran is not caused by higher disintegration. Finally, species overrepresented in DAs, including *Gouldia minima* or *Cerithidium submammillatum* at Piran, *Parvicardium scabrum* at Stn D, or *Kurtiella bidentata* at Stn Panzano, possess shell size, thickness and structural attributes that are comparable to most other species and thus are not unusually durable.

Therefore, the absence or scarcity of an abundant live species in the DA, or shifts in rank abundance between LA and DA, do not reflect undersampling, interspecific differences in durability or transport effects, but rather document past ecological shifts in species and functional community composition in the wake of environmental change. This inference is fur-

ther supported by the observation that most species with high incidence alive and rare in the DA belong to the same functional category of soft-sediment infaunal, organic-loving suspension or deposit feeders, while many of the dead-only species are epifaunal taxa associated with detritic bottoms or vegetation. This regionally consistent turnover on the functional and live-habit level most likely mirrors a shift in ecological conditions.

4.2. Time-averaging

With increasing time-averaging, the composition of DAs is expected to diverge from LAs as within-habitat species fluctuations become more likely, dominant species become less abundant, and rare species can accumulate. The magnitude of this change depends on the evenness of the regional or habitat-specific species pool, on the extent of dispersal limitation between the species pool and local assemblages, and on temporal habitat variability at local scales (Tomašových & Kidwell 2009). In our study, the effect of time-averaging on LD mismatch is indicated by the significantly positive correlation between the IQR and BC dissimilarity. As IQR covaries negatively with net sediment accumulation rate and grain size and positively with organic enrichment (Fig. 7), LD mismatch also increases towards sites with coarse and organic-poor substrates. However, the increase in richness of DAs at more time-averaged stations can also be a direct consequence of naturally more diverse habitats with coarse sediments and low sediment accumulation rate rather than a secondary effect of time-averaging because the relationship between LD mismatch in composition and time-averaging observed in our study is predicted by the null model (Fig. 5d). This model indicates that among-site variability in LD mismatch is driven by a higher evenness of the habitat-specific species pool at sites with low sedimentation rate. These habitats are less disturbed and less organic-enriched and experienced hypoxia less frequently than sites at the Po Delta or in the Gulf of Trieste, and can hence support a higher species diversity. In turn, some variation in LD mismatch is associated with very limited time-averaging, i.e. DAs at the Po stations cover only a few years and thus do not effectively trace pre-anthropogenic community states. At these stations, sediments deposited during the late 20th century are found in core depths up to 70–80 cm (Tomašových et al. 2018). Although some older shells tend to be moved to the uppermost layers by burrowers, surface

DAs likely underestimate community states that existed prior to the major eutrophication and pollution of the shelf in the late 20th century. For example, baseline communities found below 70–80 cm were characterised by high abundance of *Turritellinella tricarinata*, which is rare in surface DAs. Rather, the LD mismatch observed at these stations at grab scales is thus underestimating the magnitude of ecological shift that occurred in this region.

Although time-averaging can disproportionately increase the relative abundance of rare species in DAs, the number of species with only 1 or 2 individuals in our DAs is not consistently higher at stations with high time-averaging (e.g. 33 rare species at Stn Venice [IQR = 2169 yr], 30 at Stn Panzano [IQR = 38 yr], 52 at Stn Brijuni [IQR = 1460 yr]). Furthermore, if species are abundant in the DA and absent in the LA, it is unlikely that this LD mismatch is caused by time-averaging; rather, it indicates that these species were dominant in the past and are now waning or extirpated in the wake of ecological change (Kidwell 2013). This is the case for several species at all sampling stations. Especially at Stns Piran 1 and 2, the most dominant species of the DA are either dead only or rare in the LA (Fig. 3; notably, many of these species are epifaunal or, if infaunal, associated with coarser grain size than prevailing at present).

Rarefied species richness of individual stations (Table 2) does not consistently increase with time-averaging. DAs at Stn Panzano, characterised by low time-averaging, feature the highest rarefied species richness owing to the high number of live specimens found at this station. Conversely, at Stn Piran 1, rarefied species richness of the DA is even smaller than the number of species collected alive. These results deviate from an expected relationship between taxonomic richness and time-averaging, and probably reflect the very small sample sizes of LAs at stations with low sedimentation.

4.3. Ecological change

Two main findings from our data strongly advocate that LD mismatch truly detects past ecological change: (1) the same direction of compositional change found at all sampling stations, irrespective of different environmental conditions: a trend towards infaunalisation and a decline of epifaunal grazing species; (2) LD mismatch also at stations with very low or modest time-averaging. The outlined functional shift was already apparent in the analysis of molluscan DAs from sediment cores taken at our sampling sta-

tions (except for Stn D; Gallmetzer et al. 2017, 2019, Tomašových et al. 2018, 2019). By comparing the stations among each other and by incorporating LAs into the analyses, the present-day dominance of infaunal, filter-feeding species across stations is further accentuated by the dominance of a few generalistic and opportunistic species in the LAs (e.g. *V. gibba*, *Timoclea ovata*, *Phaxas pellucidus*). These species appear in high numbers at stations where they were formerly rare (e.g. *T. ovata* at the Piran stations), or lead to highly uneven communities at stations with low time-averaging (*V. gibba* at Stn Panzano and the Po stations). The over-representation of *T. ovata* in the LAs is in line with other evidence indicating its recent expansion in the NAS (Nerlović et al. 2011, 2012) and its intermediate tolerance to pollution and organic enrichment reported from other regions (Simboura & Zenetos 2002, Wilding 2006, D'Alessandro et al. 2016). In the context of benthic ecological-status assessments, these findings suggest that the assignment of *T. ovata* to the group of tolerant species in the Bentix database is more accurate than its categorisation as a sensitive species in the AMBI database (Borja et al. 2000). The trend towards infaunalisation is only partly evident from environmental data measured in sediment cores (changes in sediment composition and organic content, e.g. at Stns Brijuni and Piran 1, Table 1, Fig. 7). This shows that ecological drivers that are difficult to trace geochemically will be underestimated in their effect, and that insights from the shell record are indispensable for a comprehensive understanding of community trajectories (Tomašových & Kidwell 2017). Previous local-scale analyses of sediment cores suggested that benthic communities in the NAS were affected by BT (Gallmetzer et al. 2019) and by an increased frequency of seasonal hypoxia mainly driven by eutrophication (Tomašových et al. 2018, 2020). Below, we assess the role of these drivers across all stations.

4.3.1. Bottom trawling

BT has been extensively practiced in Adriatic waters since the 18th century (Krisch 1900, Fortibuoni 2009), with an exponential increase in fishing effort after the industrialisation of fisheries in the 20th century, and steep catch peaks between the 1980s and the first decade of the 21st century. A sudden drop in fishing activity and capacity in recent years is related to a sharp decline in fishable biomass (our Fig. 8a; UNEP-MAP-RAC/SPA 2014, Damalas et al. 2015). Most of our stations (except for Brijuni) are located in

areas ranking among the most heavily trawled in the NAS in recent decades (Santelli et al. 2017, their Fig. 8). The impacts of BT on benthic habitats are manifold and include (1) the disturbance of the upper seabed layers, with a re-suspension of sediment and re-mineralisation of nutrients (and contaminants); (2) the direct removal, damage or displacement of epifaunal and endobenthic organisms; (3) the alteration of habitat structure (e.g. removal of biogenic frameworks or seagrass meadows) (Kaiser et al. 2001). Depending on the stability of the habitat (mud, sand, gravel, biogenic structures), the type of fishing gear (hydraulic dredges, otter trawl, beam trawl), and the intensity of the disturbance (rare or chronic), BT can have significant effects on benthic biota, ranging from shorter-term negative impacts and faster recovery on muddy and sandy habitats to the most severe effects suffered by biogenic habitats, with a drastic reduction in taxon abundance and only partial or altogether failing recovery over years or decades (Pranovi et al. 2000, Kaiser et al. 2001, 2006, Tillin et al. 2006, Kenchington et al. 2007). A dramatic example of a permanently altered benthic ecosystem as a result of repeated and intense bottom-fishing disturbance is represented by the soft-bottom communities in the area around the Piran stations, where extensive millennial mussel banks were eradicated by BT in the first half of the 20th century (Mautner et al. 2018, Gallmetzer et al. 2019, Tomašových et al. 2019).

The impact of BT on mollusc communities can be directly derived from an LD comparison by focussing on the functional traits of the constituent species. LD studies based on datasets from soft bottoms often fail in detecting a significant correlation between taxonomic composition and LD mismatch (Kidwell 2009), even in the case of gravel habitats whose communities are likely the most sensitive to trawling (Kaiser et al. 2006). If, however, a subset of species highly sensitive to BT is selected (all epifaunal bivalves and gastropods), the proportional abundance and richness of these species should vary significantly between LAs and DAs as a consequence of the impact of BT (Kidwell 2009). For all 8 sampling stations, this analysis revealed a marked LD mismatch (Fig. 8b,c). In the LAs of the Po and Piran stations, BT-sensitive species strongly decline in relative abundance and in the number of epifaunal species, indicating that the communities have undergone a drastic functional shift mainly characterised by the loss of grazing gastropods. Interestingly, this signal of BT was least pronounced at Stn Brijuni, suggesting that the relatively long-lasting (since 1983, see Fatović-Ferenčić 2006) and well-enforced protection from fishing at this

MPA site might have enabled a recovery of BT-sensitive species over the last few decades. Our analysis, thus, shows that considering the functional characteristics of individual species can improve the analytical power of LD comparisons and help recognise specific anthropogenic drivers of community shift such as BT that are not evident from species counts or abundance structures.

4.3.2. Eutrophication and hypoxia

The NAS is one of the most eutrophic regions in the Mediterranean Sea, especially the coastal areas influenced by rivers with densely populated and intensively managed watersheds (Degobbis et al. 2000, Viaroli et al. 2015). In the second half of the 20th century, increasing inputs of nitrogen and phosphorus from industry, agriculture, livestock and wastewater via the Po and other rivers have accelerated marine eutrophication significantly (Talaber et al. 2018), leading to the formation of algal blooms, mucilage events and severe oxygen depletion in water depths below the seasonal thermocline (Druon et al. 2004, Danovaro et al. 2009, Djakovac et al. 2012, Kralj et al. 2019). Environmental measures eventually led to a reversal in the eutrophication trend during the early 2000s (Mozetič et al. 2010, Giani et al. 2012, Djakovac et al. 2015, Viaroli et al. 2015). During the last decade, however, this trend seemed to attenuate (Totti et al. 2019). The frequency of seasonal hypoxic events remained high near the Po Delta (Alvisi & Cozzi 2016), and recurrence of bottom-water hypoxia was observed in the Gulf of Trieste in 2015 and 2016 (Kralj et al. 2019).

LD mismatch showed that *Nucula nucleus* and *V. gibba* are exceptionally abundant in the LAs at Po and Panzano. Both species are known to tolerate hypoxia; *V. gibba* can even survive anoxic conditions for days (Holmes et al. 2002, Nerlović et al. 2011, Riedel et al. 2014), and outbreaks of this species are a common response to anoxia-induced mass mortality events (Holmes & Miller 2006, Hrs-Brenko 2006, Tomašových et al. 2018). This signal is enforced by the scarcity or absence of hypoxia-sensitive species such as *T. tricarinata* and pectinids in the LA. These taxa are present in the DA and dominate the assemblages in sediment depths below the mixed layer, where they mark community states preceding the high frequency of hypoxic disturbances in the late 20th century. Analyses of sediment cores from the Po and Panzano stations showed that both proportional abundance and shell size of *V. gibba* increased sig-

nificantly in the late 20th century, correlating strongly with the increased frequency of seasonal hypoxic events (Gallmetzer et al. 2017, Tomašových et al. 2018, 2020). The proportional abundance of *V. gibba* above 50% and its shell size >10 mm as observed in the late 20th century increments exceed the values that were typical of *V. gibba* assemblages in the entire Holocene successions in the NAS (Scarponi & Kowalewski 2004, Tomašových et al. 2020). Although eutrophication can lead to increased sedimentation rates resulting in benthic changes, core-based estimates showed that sediment accumulation remained constant during the 20th century at the Po stations (10–20 mm yr⁻¹) and slightly declined at Panzano relative to earlier centuries (Tomašových et al. 2017, 2018). The compositional and size turnover with the unprecedented dominance and size structure of *V. gibba* was detected at ~80 cm sediment depth at the Po stations and at ~15 cm at Stn Panzano. Therefore, the mismatch observed in the LD comparison is underestimating the magnitude of the ecological shift because surface Van Veen grabs do not penetrate into older layers that contain assemblages from the 19th century and earlier.

The bivalves *V. gibba*, *N. nucleus*, and *T. ovata* are also prominent in the LAs of Brijuni and Piran. High abundances of these species at stations with differing grain size and organic enrichment indicate that eutrophication and hypoxia contribute to restructuring the mollusc assemblages across habitat boundaries, forcing a community homogenisation over large parts of the northern Adriatic basin. While DAs represent habitat-specific communities with a broad range of feeding guilds and substrate relations, most notably epifaunal species associated with vegetation (Piran) or detritic bottoms (Brijuni), LAs are compositionally similar across stations, as they are dominated by the same small set of infaunal suspension or detritus feeders typical for soft bottoms with high mud content (*N. nucleus*, *T. ovata*, *P. pellucidus*, *V. gibba*, and *M. distorta*). These species are primarily responsible for LD mismatch at most stations (Fig. 6). The siltation of habitats coupled with organic enrichment of the sediment, particularly evident at Piran and Brijuni (Fig. 7), contribute to community shifts that emerge as a new ecosystem baseline strongly influenced by the impact of BT and eutrophication.

4.4. Effects of protection

For the 3 protected stations Po 4, Piran 1, and Brijuni, no significant effects of protection can be

deduced from the applied fidelity measures. Mismatch between LAs and DAs is either very similar to the unprotected counterparts (Stns Po 3 and Piran 2) or, in the case of Stn Brijuni, similar to other stations with comparable DA time-averaging. Oceanographic buoys, which have a protected perimeter of 50 m, are removed for maintenance at regular intervals and then relocated, sometimes not exactly at the same position; they can also be occasionally moved or detached by heavy storms (e.g. Ivkić et al. 2019). The protection they provide, therefore, is not only spatially limited but also temporally restricted to a few years at most, which might not be sufficient to enable appreciable recovery (Bastari et al. 2016). This is reflected in the analysis of BT-sensitive species, which do not consistently increase in the LA of the bouy-protected Stns Po 4 and Piran 1. Stn Brijuni, on the other hand, is a national park, where in contrast to many MPAs that lack effective protection (Claudet et al. 2020), strict regulations have been well enforced for almost 40 yr (Di Franco et al. 2014). The high time-averaging of the DA and taphonomic inertia (Kidwell 2007) at this station might conceal the relatively short-term potential structural changes from protection. However, abundance and proportional richness of sensitive species are significantly higher than at all other stations, suggesting that the absence of trawling enabled some of these species to recover.

Protective boundaries of buoys or MPAs can reduce the impact of fishing, but not exclude the effects of other stressors such as eutrophication, anoxia, or siltation. At Stn Brijuni, therefore, the positive effect of a fishing ban might easily be offset by the impact of high nutrient and sediment input (Schnedl et al. 2018, Gallmetzer et al. 2019), which enforces the dominance of infaunal and opportunistic species.

5. CONCLUSIONS

We found consistent across-shelf LD mismatch in the NAS in habitats differing in sediment accumulation rate, grain size and organic enrichment, despite differences in time-averaging observed among surface DAs. This observation indicates that LD mismatch does not result merely from methodological constraints, taphonomic processes or time-averaging but represents a true ecological signal. LD mismatch reflects a similar trend at all stations; infaunal species increase in number and abundance in the live community, while epifaunal species, often prominent in the DAs, decrease or vanish from LAs. On the func-

tional level, important feeding guilds of DAs such as grazers, herbivores and carnivores decline or altogether disappear from LAs, where the vast majority of species are now suspension and detritus feeders. This basin-wide trend of infaunalisation and community homogenisation indicates a substantial change of soft-bottom environments characterised by a loss of marine vegetation and bioherm structures (mussel beds) and the establishment of a new ecological baseline replacing the former, more heterogeneous habitats. BT, eutrophication and oxygen crises emerged as the main anthropogenic drivers of this development on the northern Adriatic shelf.

Small-scale and short-term protection from BT as in the case of protected perimeters of oceanographic buoys fails to yield clear evidence for structural changes of LAs compared to impacted areas. This suggests that longer-term protection on a larger scale as provided by MPAs is needed for benthic communities, to reverse the infaunalisation trend shaping modern northern Adriatic soft-bottom biota.

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LITERATURE CITED

- ✦ Agiadi K, Albano PG (2020) Holocene fish assemblages provide baseline data for the rapidly changing eastern Mediterranean. *Holocene* 30:1438–1450
- ✦ Albano PG, Sabelli B (2011) Comparison between death and living molluscs assemblages in a Mediterranean infralittoral off-shore reef. *Palaeogeogr Palaeoclimatol Palaeoecol* 310:206–215
- ✦ Albano PG, Tomašových A, Stachowitsch M, Zuschin M (2016) Taxonomic sufficiency in a live–dead agreement study in a tropical setting. *Palaeogeogr Palaeoclimatol Palaeoecol* 449:341–348
- ✦ Albano PG, Gallmetzer I, Haselmair A, Tomašových A, Stachowitsch M, Zuschin M (2018) Historical ecology of a biological invasion: The interplay of eutrophication and pollution determines time lags in establishment and detection. *Biol Invasions* 20:1417–1430
- ✦ Alin SR, Cohen AS (2004) The live, the dead, and the very dead: taphonomic calibration of the recent record of paleoecological change in Lake Tanganyika, East Africa. *Paleobiology* 30:44–81
- ✦ Alvisi F, Cozzi S (2016) Seasonal dynamics and long-term trend of hypoxia in the coastal zone of Emilia Romagna (NW Adriatic Sea, Italy). *Sci Total Environ* 541:1448–1462
- ✦ Aronson RB, Macintyre IG, Lewis SA, Hilbun NL (2005) Emergent zonation and geographic convergence of coral reefs. *Ecology* 86:2586–2600

- ✦ Bastari A, Micheli F, Ferretti F, Pusceddu A, Cerrano C (2016) Large marine protected areas (LMPAs) in the Mediterranean Sea: the opportunity of the Adriatic Sea. *Mar Policy* 68:165–177
- ✦ Borja A, Franco J, Pérez V (2000) A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Mar Pollut Bull* 40:1100–1114
- ✦ Breitburg D, Levin LA, Oschlies A, Grégoire M and others (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240
- ✦ Breman E (1978) Species diversity of ostracode shells in bottom sediments of the Adriatic Sea. *Palaeogeogr Palaeoclimatol Palaeoecol* 25:277–313
- ✦ Bürkli A, Wilson AB (2017) Explaining high-diversity death assemblages: undersampling of the living community, out-of-habitat transport, time-averaging of rare taxa, and local extinction. *Palaeogeogr Palaeoclimatol Palaeoecol* 466:174–183
- ✦ Caswell BA, Frid CLJ, Borja A (2019) An ecological status indicator for all time: Are AMBI and M-AMBI effective indicators of change in deep time? *Mar Pollut Bull* 140: 472–484
- Chiantore M, Bedulli D, Cattaneo-Vietti R, Schiaparelli S, Albertelli G (2001) Long-term changes in the mollusc-echinoderm assemblages in the north and coastal middle Adriatic Sea. *Atti Assoc Ital Oceanol Limnol* 14:63–75
- ✦ Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- ✦ Claudet J, Loiseau C, Sostres M, Zupan M (2020) Underprotected marine protected areas in a global biodiversity hotspot. *One Earth* 2:380–384
- Collins MJ (1986) Taphonomic processes in a deep water *Modiolus*–brachiopod assemblage from the west coast of Scotland. PhD thesis, University of Glasgow
- Correggiari A, Miserocchi S, Tesi T, Albertazzi S and others (2014) Linking deltaic sedimentation and the pollution history: an integrated approach in the Po River delta, Italy. Poster presentation at the Ocean Science Meeting, Honolulu, HI, 23–28 Feb 2014
- ✦ Covelli S, Fontolan G, Faganeli J, Ogrinc N (2006) Anthropogenic markers in the Holocene stratigraphic sequence of the Gulf of Trieste (northern Adriatic Sea). *Mar Geol* 230:29–51
- ✦ Covelli S, Langone L, Acquavita A, Piani R, Emili A (2012) Historical flux of mercury associated with mining and industrial sources in the Marano and Grado Lagoon (northern Adriatic Sea). *Estuar Coast Shelf Sci* 113: 7–19
- ✦ Crema R, Castelli A, Prevedelli D (1991) Long term eutrophication effects on macrofaunal communities in northern Adriatic Sea. *Mar Pollut Bull* 22:503–508
- ✦ Cronin KE, Dietl GP, Kelley PH, Edie SM (2018) Life span bias explains live–dead discordance in abundance of two common bivalves. *Paleobiology* 44:783–797
- ✦ D’Alessandro M, Esposito V, Giacobbe S, Renzi M and others (2016) Ecological assessment of a heavily human-stressed area in the Gulf of Milazzo, Central Mediterranean Sea: an integrated study of biological, physical and chemical indicators. *Mar Pollut Bull* 106:260–273
- ✦ Damalas D, Maravelias CD, Osio GC, Maynou F, Sbrana M, Sartor P (2015) ‘Once upon a time in the Mediterranean’ long term trends of Mediterranean fisheries resources based on fishers’ traditional ecological knowledge. *PLOS ONE* 10:e0119330
- ✦ Danovaro R, Fonda Umani S, Pusceddu A (2009) Climate change and the potential spreading of marine mucilage and microbial pathogens in the Mediterranean Sea. *PLOS ONE* 4:e7006
- ✦ Degobbi D, Precali R, Ivancic I, Smodlaka N, Fuks D, Kveder S (2000) Long-term changes in the northern Adriatic ecosystem related to anthropogenic eutrophication. *Int J Environ Pollut* 13:495–533
- ✦ Dietl GP, Durham SR, Smith JA, Tweitmann A (2016) Mollusk assemblages as records of past and present ecological status. *Front Mar Sci* 3:169
- Di Franco A, Bodilis P, Piante C, Di Carlo G, Thiriet P, Francour P, Guidetti PM (2014) Fishermen engagement, a key element to the success of artisanal fisheries management in Mediterranean marine protected areas. *MedPAN North Project*. WWF France Port-Cros National Park
- ✦ Djakovac T, Degobbi D, Supić N, Precali R (2012) Marked reduction of eutrophication pressure in the northeastern Adriatic in the period 2000–2009. *Estuar Coast Shelf Sci* 115:25–32
- ✦ Djakovac T, Supić N, Bernardi Aubry F, Degobbi D, Giani M (2015) Mechanisms of hypoxia frequency changes in the northern Adriatic Sea during the period 1972–2012. *J Mar Syst* 141:179–189
- ✦ Dominici S, Zuschin M (2005) Infidelities of fossil assemblages. *Lethaia* 38:381–382
- ✦ Druon JN, Schrimpf W, Dobricic S, Stips A (2004) Comparative assessment of large-scale marine eutrophication: North Sea area and Adriatic Sea as case studies. *Mar Ecol Prog Ser* 272:1–23
- ✦ Fatović-Ferenčić S (2006) Brijuni Archipelago: story of Kuppelwieser, Koch, and cultivation of 14 islands. *Croat Med J* 47:369–371
- Fortibuoni T (2009) La pesca in Alto Adriatico dalla caduta della Serenissima ad oggi: un’analisi storica ed ecologica. PhD thesis, Università degli studi di Trieste
- ✦ Fortibuoni T, Libralato S, Arneri E, Giovanardi O, Solidoro C, Raicevich S (2017) Fish and fishery historical data since the 19th century in the Adriatic Sea, Mediterranean. *Sci Data* 4:170104
- ✦ Gallmetzer I, Haselmair A, Tomašových A, Stachowitsch M, Zuschin M (2017) Responses of molluscan communities to centuries of human impact in the northern Adriatic Sea. *PLOS ONE* 12:e0180820
- ✦ Gallmetzer I, Haselmair A, Tomašových A, Mautner AK and others (2019) Tracing origin and collapse of Holocene benthic baseline communities in the northern Adriatic Sea. *Palaios* 34:121–145
- ✦ García-Ramos DA, Albano PG, Harzhauser M, Piller WE, Zuschin M (2016) High dead–live mismatch in richness of molluscan assemblages from carbonate tidal flats in the Persian (Arabian) Gulf. *Palaeogeogr Palaeoclimatol Palaeoecol* 457:98–108
- ✦ Giani M, Djakovac T, Degobbi D, Cozzi S, Solidoro C, Umani SF (2012) Recent changes in the marine ecosystems of the northern Adriatic Sea. *Estuar Coast Shelf Sci* 115:1–13
- ✦ Gilad E, Kidwell SM, Benayahu Y, Edelman-Furstenberg Y (2018) Unrecognized loss of seagrass communities based on molluscan death assemblages: historic baseline shift in tropical Gulf of Aqaba, Red Sea. *Mar Ecol Prog Ser* 589:73–83
- Gofas S, Moreno D, Salas C (eds) (2011) *Moluscos marinos de Andalucía*, Vol 1. Servicio de Publicaciones e Intercambio Científico, Universidad de Málaga, Málaga

- Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. *Science* 319:948–952
- He F, Legendre P (2002) Species diversity patterns derived from species–area models. *Ecology* 83:1185–1198
- Holmes SP, Miller N (2006) Aspects of the ecology and population genetics of the bivalve *Corbula gibba*. *Mar Ecol Prog Ser* 315:129–140
- Holmes SP, Miller N, Weber A (2002) The respiration and hypoxic tolerance of *Nucula nitidosa* and *N. nucleus*: factors responsible for determining their distribution? *J Mar Biol Assoc UK* 82:971–981
- Hrs-Brenko M (2006) The basket shell, *Corbula gibba* Olivi, 1792 (bivalve mollusks) as a species resistant to environmental disturbances: a review. *Acta Adriat* 47:49–64
- Huntley J, Scarponi D (2015) Geographic variation of parasitic and predatory traces on mollusks in the northern Adriatic Sea, Italy: implications for the stratigraphic paleobiology of biotic interactions. *Paleobiology* 41:134–153
- Ivkić A, Steger J, Galil BS, Albano PG (2019) The potential of large rafting objects to spread Lessepsian invaders: the case of a detached buoy. *Biol Invasions* 21:1887–1893
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637
- Justić D (1991) Hypoxic conditions in the northern Adriatic Sea: historical development and ecological significance. In: Tyson RV, Pearson TH (eds) *Modern and ancient continental shelf anoxia*. *Spec Publ Geol Soc Lond* 58:95–105
- Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2001) Impacts of fishing gear on marine benthic habitats. In: Sinclair M, Valdimarsson G (eds) *Responsible fisheries in the marine ecosystem*. FAO, Rome, p 197–217
- Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14
- Kenchington EL, Kenchington TJ, Henry LA, Fuller S, Gonzalez P (2007) Multi-decadal changes in the megabenthos of the Bay of Fundy: the effects of fishing. *J Sea Res* 58:220–240
- Kidwell SM (2002) Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. *Geology* 30:803–806
- Kidwell SM (2007) Discordance between living and death assemblages as evidence for anthropogenic ecological change. *Proc Natl Acad Sci USA* 104:17701–17706
- Kidwell SM (2008) Ecological fidelity of open marine molluscan death assemblages: effects of post-mortem transportation, shelf health, and taphonomic inertia. *Lethaia* 41:199–217
- Kidwell S (2009) Evaluating human modification of shallow marine ecosystems: mismatch in composition of molluscan living and time-averaged death assemblages. In: Dietl GP, Flessa KW (eds) *Conservation paleobiology: using the past to manage for the future*. *Paleontological Society Papers*, Portland, OR, p 113–139
- Kidwell S (2013) Time-averaging and fidelity of modern death assemblages: building a taphonomic foundation for conservation palaeobiology. *Palaeontology* 56: 487–522
- Kidwell SM, Bosence DW (1991) Taphonomy and time-averaging of marine shelly faunas. In: Allison PA, Briggs DE (eds) *Taphonomy, releasing the data locked in the fossil record*. Plenum Press, New York, NY, p 115–209
- Kidwell SM, Tomašových A (2013) Implications of time-averaged death assemblages for ecology and conservation biology. *Annu Rev Ecol Syst* 44:539–563
- Kosnik MA, Hua Q, Kaufman DS, Wust RA (2009) Taphonomic bias and time-averaging in tropical molluscan death assemblages: differential shell half-lives in Great Barrier Reef sediment. *Paleobiology* 35:565–586
- Kowalewski M (2009) The youngest fossil record and conservation biology: Holocene shells as eco-environmental recorders. In: Dietl GP, Flessa KW (eds) *Conservation paleobiology: using the past to manage for the future*. *Paleontological Society Papers*, Portland, OR, p 1–23
- Kowalewski M, Wittmer JM, Dexter TA, Amorosi A, Scarponi D (2015) Differential responses of marine communities to natural and anthropogenic changes. *Proc R Soc B* 282:20142990
- Kralj M, Lipizer M, Čermelj B, Celio M and others (2019) Hypoxia and dissolved oxygen trends in the northeastern Adriatic Sea (Gulf of Trieste). *Deep Sea Res II* 164: 74–88
- Krisch A (1900) *Fischerei im Adriatischen Meere mit besonderer Berücksichtigung der österreichisch-ungarischen Küsten*. Carl Gerold's Sohn, Vienna
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13
- Leshno Y, Benjamini C, Edelman-Furstenberg Y (2016) Ecological quality assessment in the Eastern Mediterranean combining live and dead molluscan assemblages. *Mar Pollut Bull* 104:246–256
- Lipizer M, De Vittor C, Falconi C, Comici C, Tamberlich F, Giani M (2012) Effects of intense physical and biological forcing factors on CNP pools in coastal waters (Gulf of Trieste, Northern Adriatic Sea). *Estuar Coast Shelf Sci* 115:40–50
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809
- Lotze HK, Coll M, Dunne JA (2011) Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14:198–222
- Marini M, Jones BH, Campanelli A, Grilli F, Lee CM (2008) Seasonal variability and Po River plume influence on biochemical properties along western Adriatic coast. *J Geophys Res Oceans* 113:C05S90
- Mautner AK, Gallmetzer I, Haselmair A, Schnedl SM, Tomašových A, Zuschin M (2018) Holocene ecosystem shifts and human-induced loss of *Arca* and *Ostrea* shell beds in the north-eastern Adriatic Sea. *Mar Pollut Bull* 126:19–30
- Mavric B, Orlando-Bonaca M, Bettoso N, Lipej L (2010) Soft-bottom macrozoobenthos of the southern part of the Gulf of Trieste: faunistic, biocoenotic and ecological survey. *Acta Adriat* 51:203–216
- Mozetič P, Solidoro C, Cossarini G, Socal G and others (2010) Recent trends towards oligotrophication of the northern Adriatic: evidence from chlorophyll *a* time series. *Estuar Coasts* 33:362–375
- Mozetič P, Francé J, Kogovšek T, Talaber I, Malej A (2012) Plankton trends and community changes in a coastal sea (northern Adriatic): bottom-up vs. top-down control in relation to environmental drivers. *Estuar Coast Shelf Sci* 115:138–148

- Munari C, Mistri M (2010) Towards the application of the Water Framework Directive in Italy: assessing the potential of benthic tools in Adriatic coastal transitional ecosystems. *Mar Pollut Bull* 60:1040–1050
- Nerlović V, Doğan A, Hrs-Brenko M (2011) Response to oxygen deficiency (depletion): bivalve assemblages as an indicator of ecosystem instability in the northern Adriatic Sea. *Biologia (Bratisl)* 66:1114–1126
- Nerlović V, Hrs-Brenko M, Dogan A (2012) Long-term changes in the transitional community of detritic bottoms of the northern Adriatic Sea: dynamic of the bivalve assemblages. *Fresenius Environ Bull* 21:3600–3613
- Occhipinti-Ambrogi A, Savini D, Forni G (2005) Macrobenthos community structural changes off Cesenatico coast (Emilia Romagna, northern Adriatic), a six-year monitoring programme. *Sci Total Environ* 353:317–328
- Oksanen J, Blanchet G, Kindt R, Legendre P and others (2016) *vegan*: community ecology package. R package version 2.3-5. <https://cran.r-project.org/package=vegan>
- Olszewski TD (1999) Taking advantage of time-averaging. *Paleobiology* 25:226–238
- Palinkas CM, Nittrouer CA (2007) Modern sediment accumulation on the Po shelf, Adriatic Sea. *Cont Shelf Res* 27: 489–505
- Palinkas CM, Nittrouer CA, Wheatcroft RA, Langone L (2005) The use of ⁷Be to identify event and seasonal sedimentation near the Po River delta, Adriatic Sea. *Mar Geol* 222–223:95–112
- Powell EN, Ewing AM, Kuykendall KM (2020) Ocean quahogs (*Arctica islandica*) and Atlantic surfclams (*Spisula solidissima*) on the Mid-Atlantic Bight continental shelf and Georges Bank: the death assemblage as a recorder of climate change and the reorganization of the continental shelf benthos. *Palaeogeogr Palaeoclimatol Palaeoecol* 537:109205
- Pranovi F, Raicevich S, Franceschini G, Farrace MG, Giovannardi O (2000) Rapido trawling in the northern Adriatic Sea: effects on benthic communities in an experimental area. *ICES J Mar Sci* 57:517–524
- Rabalais NN, Díaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J (2010) Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7:585–619
- Riedel B, Pados T, Pretterebner K, Schiemer L and others (2014) Effect of hypoxia and anoxia on invertebrate behaviour: ecological perspectives from species to community level. *Biogeosciences* 11:1491–1518
- RStudio Team (2018) *RStudio: integrated development for R*. RStudio, Boston, MA. www.rstudio.com
- Santelli A, Cvitković I, Despalatović M, Fabi G and others (2017) Spatial persistence of megazoobenthic assemblages in the Adriatic Sea. *Mar Ecol Prog Ser* 566:31–48
- Scardi M, Crema R, Di Dato P, Fresi E, Orel G (1999) Le comunità bentoniche dell' alto Adriatico: un'analisi preliminare dei cambiamenti strutturali dagli anni '30 ad oggi. In: Giovanardi O (ed) *Impact of trawl fishing on benthic communities*. Proceedings ICRAM. Istituto Centrale per la Ricerca Scientifica e Tecnologica Applicata al Mare (ICRAM), Rome, p 95–108
- Scarponi D, Kowalewski M (2004) Stratigraphic paleoecology: bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy. *Geology* 32:989–992
- Schnedl SM, Haselmair A, Gallmetzer I, Mautner AK, Tomašových A, Zuschin M (2018) Benthic communities at Brijuni Islands (northern Adriatic Sea) were shaped by Holocene sea-level rise and recent human impact. *Holocene* 28:1801–1817
- Simboura N, Zenetos A (2002) Benthic indicators to use in Ecological Quality classification of Mediterranean soft bottom marine ecosystems, including a new Biotic Index. *Mediterranean Marine Science* 3:77–111
- Simonini R, Ansaloni I, Bonvicini Pagliai AM, Prevedelli D (2004) Organic enrichment and structure of the macrozoobenthic community in the northern Adriatic Sea in an area facing Adige and Po mouths. *ICES J Mar Sci* 61: 871–881
- Simonini R, Grandi V, Massamba-N'Siala G, Iotti M, Montanari G, Prevedelli D (2009) Assessing the ecological status of the north-western Adriatic Sea within the European Water Framework Directive: a comparison of Bentix, AMBI and M-AMBI methods. *Mar Ecol* 30: 241–254
- Spillman CM, Imberger J, Hamilton DP, Hipsey MR, Romero JR (2007) Modelling the effects of Po River discharge, internal nutrient cycling and hydrodynamics on biogeochemistry of the northern Adriatic Sea. *J Mar Syst* 68: 167–200
- Stachowitsch M (1991) Anoxia in the northern Adriatic Sea: rapid death, slow recovery. In: Tyson RV, Pearson TH (eds) *Modern and ancient continental shelf anoxia*. *Spec Publ Geol Soc Lond* 58:119–129
- Talaber I, Francé J, Flander-Putrlé V, Mozetič P (2018) Primary production and community structure of coastal phytoplankton in the Adriatic Sea: insights on taxon-specific productivity. *Mar Ecol Prog Ser* 604:65–81
- Tesi T, Miserocchi S, Goñi MA, Turchetto M and others (2011) Influence of distributary channels on sediment and organic matter supply in event-dominated coastal margins: the Po prodelta as a study case. *Biogeosciences* 8:365–385
- Tesi T, Langone L, Goñi MA, Wheatcroft RA, Miserocchi S, Bertotti L (2012) Early diagenesis of recently deposited organic matter: a 9-yr time-series study of a flood deposit. *Geochim Cosmochim Acta* 83:19–36
- Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45
- Tomašových A, Kidwell SM (2009) Fidelity of variation in species composition and diversity partitioning by death assemblages: time-averaging transfers diversity from beta to alpha levels. *Paleobiology* 35:94–118
- Tomašových A, Kidwell SM (2010) Predicting the effects of increasing temporal scale on species composition, diversity, and rank-abundance distributions. *Paleobiology* 36: 672–695
- Tomašových A, Kidwell SM (2011) Accounting for the effects of biological variability and temporal autocorrelation in assessing the preservation of species abundance. *Paleobiology* 37:332–354
- Tomašových A, Kidwell SM (2017) Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. *Proc R Soc B* 284:20170328
- Tomašových A, Gallmetzer I, Haselmair A, Kaufman DS, Vidović J, Zuschin M (2017) Stratigraphic unmixing reveals repeated hypoxia events over the past 500 years in the northern Adriatic Sea. *Geology* 45:363–366
- Tomašových A, Gallmetzer I, Haselmair A, Kaufman DS and others (2018) Tracing the effects of eutrophication on

molluscan communities in sediment cores: outbreaks of an opportunistic species coincide with reduced bioturbation and high frequency of hypoxia in the Adriatic Sea. *Paleobiology* 44:575–602

- ✦Tomašových A, Gallmetzer I, Haselmair A, Kaufman D, Mavrič B, Zuschin M (2019) A decline in molluscan carbonate production driven by the loss of vegetated habitats encoded in the Holocene sedimentary record of the Gulf of Trieste. *Sedimentology* 66:781–807
- ✦Tomašových A, Albano PG, Fuksi T, Gallmetzer I and others (2020) Ecological regime shift preserved in the Anthropocene stratigraphic record. *Proc R Soc B* 287: 20200695
- ✦Totti C, Romagnoli T, Accoroni S, Coluccelli A and others (2019) Phytoplankton communities in the northwestern Adriatic Sea: interdecadal variability over a 30-years period (1988–2016) and relationships with meteorological drivers. *J Mar Syst* 193:137–153
- ✦Trincardi F, Amorosi A, Bosman A, Correggiari A, Madricardo F, Pellegrini C (2020) Ephemeral rollover points and clinothem evolution in the modern Po Delta based on repeated bathymetric surveys. *Basin Res* 32:402–418
- ✦Tweitmann A, Dietl GP (2018) Live–dead mismatch of molluscan assemblages indicates disturbance from anthropogenic eutrophication in the Barnegat Bay–Little Egg Harbor estuary. *J Shellfish Res* 37:615–624
- ✦Tyler CL, Kowalewski M (2017) Surrogate taxa and fossils as reliable proxies of spatial biodiversity patterns in marine benthic communities. *Proc R Soc B* 284:20162839
- UNEP-MAP-RAC/SPA (2014) Status and conservation of fisheries in the Adriatic Sea (H. Farrugio & Alen Soldo). Draft internal report for the purposes of the Mediterranean Regional Workshop to Facilitate the Description of Ecologically or Biologically Significant Marine Areas, Malaga, 7–11 April 2014
- Vatova A (1949) La fauna bentonica dell' Alto e Medio Adriatico. *Nova Thalassia* 1:1–110
- ✦Viaroli P, Nizzoli D, Pinardi M, Soana E, Bartoli M (2015) Eutrophication of the Mediterranean Sea: a watershed–cascading aquatic filter approach. *Rend Fis Acc Lincei* 26:13–23
- ✦Weber K, Zuschin M (2013) Delta-associated molluscan life and death assemblages in the northern Adriatic Sea: implications for palaeoecology, regional diversity and conservation. *Palaeogeogr Palaeoclimatol Palaeoecol* 370: 77–91
- ✦Wilding TA (2006) The benthic impacts of the Loch Linnhe artificial reef. *Hydrobiologia* 555:345–353
- Wilson JG (1979) The burrowing of *Tellina tenuis* Da Costa and *Tellina fabula* Gmelin in relation to sediment characteristics. *J Life Sci R Dublin Soc* 1:91–98
- ✦Yonge CM (1939) The protobranchiate mollusca: a functional interpretation of their structure and evolution. *Philos Trans R Soc B* 230:79–147
- ✦Yonge CM (1946) On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*. *J Mar Biol Assoc UK* 26:358–376
- ✦Zavatarelli M, Raicich F, Bregant D, Russo A, Artegiani A (1998) Climatological biogeochemical characteristics of the Adriatic Sea. *J Mar Syst* 18:227–263
- ✦Zuschin M, Ebner C (2015) Actupaleontological characterization and molluscan biodiversity of a protected tidal flat and shallow subtidal at the northern Red Sea. *Facies* 61:5
- ✦Zuschin M, Stachowitsch M (2009) Epifauna-dominated benthic shelf assemblages: lessons from the modern Adriatic Sea. *Palaios* 24:211–221

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