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Delta-associated molluscan life and death assemblages in the northern Adriatic Sea: Implications for paleoecology, regional diversity and conservation

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ABSTRACT

Life–death (LD) studies of shelly macrofauna are important to evaluate how well a fossil assemblage can reflect the original living community, but can also serve as a proxy for recent ecological shifts in marine habitats and in practice this has to be distinguished using taphonomic preservation pattern and estimates of time-averaging. It remains to be rigorously evaluated, however, how to distinguish between sources of LD disagreement. In addition, death assemblages (DAs) also preserve important information on regional diversity which is not available from single censuses of the life assemblages (LAs). The northern Adriatic Sea is an ecosystem under anthropogenic pressure, and we studied the distribution and abundance of living and dead bivalve and gastropod species in the physically stressful environments (tidal flat and shallow sublittoral soft bottoms) associated with the delta of the Isonzo River (Gulf of Trieste). Specifically we evaluated the fidelity of richness, evenness, abundance, habitat discrimination and beta diversity. A total of 10,740 molluscs from fifteen tidal flat and fourteen sublittoral sites were analyzed for species composition and distribution of living and dead molluscs. Of 78 recorded species, only eleven were numerically abundant. There were many more dead than living individuals and rarefied species richness in the DA was higher at all spatial scales, but the differences are lower in habitats and in the region than at individual stations. Evenness was always higher in death assemblages, and probably due to temporally more variable LAs the differences are stronger in the sublittoral habitats. Distinct assemblages characterized intertidal and sublittoral habitats, and the distribution and abundance of empty shells generally corresponded to that of the living species. Death assemblages have lower beta diversity than life assemblages, but empty shells capture compositional differences between habitats to a higher degree than living shells. More samples would be necessary to account for the diversity of living molluscs in the study area, which is, however, well recorded in the death assemblages. There is no indication of a major environmental change over the last decades in this area, but due to the long history of anthropogenic pressure here, such a potential impact might be preserved in historical layers of the deeper sedimentary record.

1. Introduction

The study of living and empty shelly assemblages in modern environments is important for several reasons. Assessing fidelity of abundance and diversity is crucial to evaluate how accurately paleocommunities reflect the original living community (Cadée, 1968; Staff et al., 1986; Greenstein and Pandolfi, 1997; Kidwell, 2001; Kowalewski et al., 2003; Lockwood and Chastant, 2006; Ferguson and Miller, 2007; Zuschin and Stachowitsch, 2007; Albano and Sabelli, 2011; Tietze and De Francesco, 2012; for reviews see Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Tomašových and Kidwell, 2011). Death assemblages (DAs) can also be a valuable tool in assessing the regional diversity composition, especially when information on the living assemblage (LA) is limited (Bouchet et al., 2002; Warwick and Light, 2002; Warwick and Turk, 2002; Zuschin and Oliver, 2005). Additionally, the degree of agreement between the composition of life- and death assemblages of taphonomically relevant macrofauna (e.g. molluscs) can serve as a proxy for recent ecological shifts (Kidwell, 2007, 2009; Kowalewski, 2009). Life–death (LD) agreement seems to be high in many pristine settings and to decrease with increasing environmental modification by anthropogenic impact, most notably eutrophication and bottom trawling, but the ability of such LD analyses to detect past anthropogenic impacts needs to be tested further (Kidwell, 2007, 2009). The northern Adriatic is particularly suited to study ecosystem modifications under human pressure. Lotze et al. (2006) list the Adriatic among the most degraded marine ecosystems worldwide, with a long history of intense human impact that started already in Roman times. During the last centuries, the dense urbanization along its coasts and the pollution of its main tributary, the Po River, led to strong eutrophication and coastal degradation, especially in its northern part (Revelante and Gilmartin, 1977; Barmawidjajaa et al., 1995; Degobbis et al., 2000; Covelli et al., 2006; Lotze et al., 2006).

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The molluscan fauna of the northern Adriatic Sea is well known (Vatova, 1949; Riedl, 1963; D'Angelo and Gargiullo, 1979; Cossignani et al., 1992). Recent quantitative studies treated molluscan assemblages in the intertidal and sublittoral of the Gulf of Trieste (Sawyer and Zuschin, 2010), but the distribution pattern and diversity of bivalves and gastropods is still poorly known and no study has yet investigated how well the death assemblage reflects the living community composition and how well potential differences may reflect environmental change, anthropogenic impact and differences in species preservation and time-averaging. This study investigates the distribution and abundance of living and dead bivalve and gastropod species in environments with high temporal variation in salinity, oxygen and temperature (tidal flat and shallow sublittoral soft bottoms) associated with the delta of the Isonzo River. We ask whether there are differences in the abundances, distribution and diversity of common species in different habitats of the intertidal and the sublittoral and whether empty shells reflect distribution patterns of living molluscs, which would allow the use of death assemblages for gradient analysis. Specifically we focus on fidelity in species richness, evenness and beta diversity between live and dead molluscs at different spatial scales.

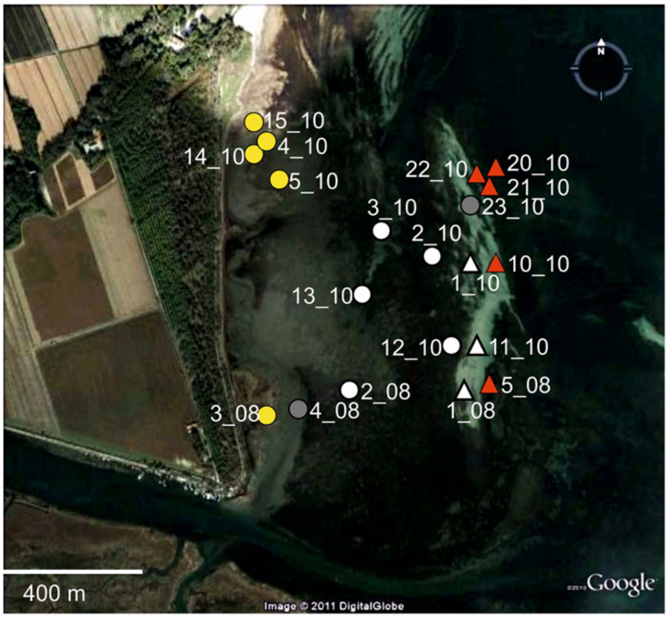

Fig. 2. Sample stations on the tidal flat – the inner tidal flat (yellow circles), outer tidal flat (white circles), channel (gray circles), sandbar (white triangles) – and in the shallow sublittoral zone in front of the sandbar (red triangles).

2. Study area

The studied tidal flat of the Isonzo River is located in the Gulf of Trieste in the northern Adriatic Sea (Fig. 1) and reaches a maximum width of approximately 800 m. The tides are semidiurnal and the average tide is 64 cm. At the time of spring tides the maximum tidal range is 132 cm (Stravisi et al., 1986). The highest elevations in the tidal flat are situated 10 cm above, the deepest regions 85 cm below the midwater-level (Hohenegger et al., 1989). The fieldwork was conducted in June and July 2010. Additional material was available from a previous sampling campaign in July 2008. Stations were chosen to permit a broad-ranged, overall survey of the intertidal and shallow sublittoral mollusc distribution (maximum water depth 2.5 m). Standardized samples were collected from fifteen tidal flat and fourteen sublittoral stations (see below) (Figs. 2, 3). Tidal flat samples were collected at times of spring tide low water north of the mouth of the Isonzo River (Figs. 1, 2).

Four sampling areas were distinguished in the intertidal. The inner tidal flat (5 samples) is nearest to the marsh belt line and thus least flooded. The sediment was silty and contained a high organic matter content of decomposing seagrass leaves. The outer tidal flat (5 samples) has a sparse seagrass cover. The sandbar (3 samples) is exposed only at low spring tide level. Channels (2 samples) are located on the tidal flat but are permanently flooded (Fig. 2). Three sampling areas were

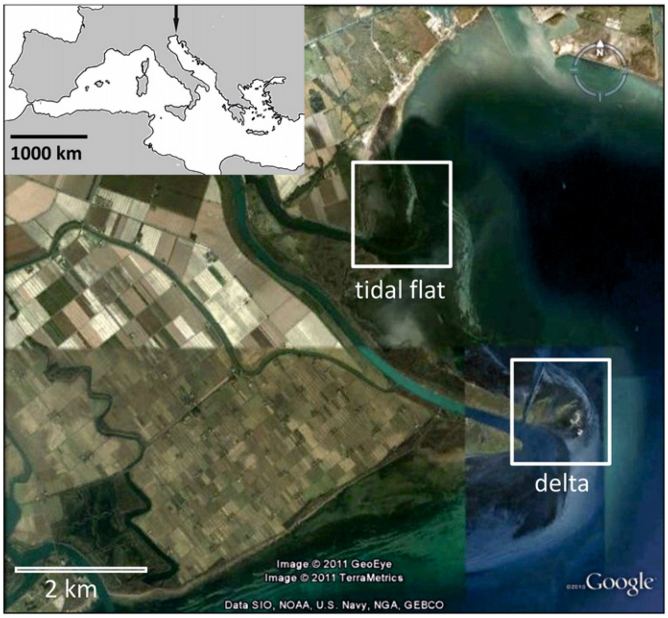

Fig. 1. The estuary of the Isonzo River, located in the Gulf of Trieste in the northernmost part of the Adriatic Sea, Italy. The molluscan fauna was analyzed on the tidal flat and in the delta.

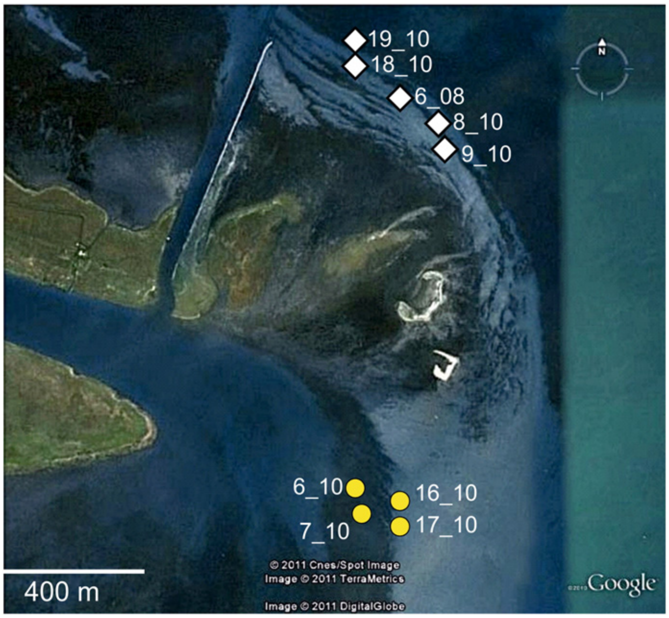

Fig. 3. Sample stations in the delta zone include seagrass meadows (white rhombuses) and a sand ridge in front of the river mouth (yellow circles).

distinguished in the sublittoral. Seven samples were taken in front of the sandbar in a water depth of 30 to 100 cm (Fig. 2). The sediment there was sandy and, at a water depth of about 30 cm below the spring tide line, there were meadows of *Zostera* (*Zostera*) *marina*. Another four samples were collected on the sand ridge of the Isonzo Delta at a water depth of about 100 cm, and five more in seagrass meadows of the delta at a water depth of about 250 cm (Fig. 3). The positions were recorded using a global positioning system (GPS).

3. Material and methods

Abiotic conditions at the sampling sites were measured using a WTW Multi 350 i Universal Pocket Meter. A SenTix 41-3 pH-Electrode was used to determine the pH-value, and a ConOx-oxygen sensor to measure oxygen levels and temperature. Measurements in the early morning showed strong fluctuations of temperature (22.4 °C to 24.4 °C), pH (7.51 to 7.83), salinity (20 to 24 psu) and oxygen content (1.06 to 3.33 mg/l) across the tidal flat.

Each sample consisted of 4500 cm^3 sediment collected from the uppermost 5 cm (including seagrass leaves) using a 30 cm by 30 cm metal frame which was randomly positioned. On the same day, all samples were washed through a 1 mm sieve using freshwater. Living individuals were separated and dried. Unbroken shells (>90% complete) were counted. Molluscs were sorted and identified to species level (D'Angelo and Gargiullo, 1979; Cossignani et al., 1992; taxonomic information was updated using the World register of marine Species (WoRMS)) and differentiated in individuals collected alive or as empty shells. Dead bivalves included shells that were empty but still articulated and single valves and were counted using the maximum number of individuals approach (Gilinsky and Bennington, 1994). Shell preservation is generally good, without indication of major taphonomic biases between habitats. It was difficult to consistently determine whether individuals of the abundant gastropod species *Bittium reticulatum* (Cerithiidae) and *Rissoa membranacea* (Rissoidae) were alive or empty. Therefore these two species were excluded from all live–dead assemblage analyses.

Our evaluations of species richness of life and death assemblages are based on rarefied data to account for sample-size differences. Richness of LAs and DAs at all scales (stations, habitats, region) is compared at a minimum sample size of 25 individuals. At station level this limits the number of comparisons to 16 out of 29, because in many LAs less than 25 living specimens were available.

The Simpson index, which is affected by the 2–3 most abundant species, and the Shannon–Wiener index, which is more strongly affected by species in the middle of the rank sequence of species, were used as measures of evenness (see Gray, 2000 for discussion). The Simpson index (1-D) was calculated with the equation

$$D = \sum_{i=1}^{S} p_i^2$$

Table 1
Number of living bivalves and gastropods and their empty shells. Note that the abundant gastropods *Bittium reticulatum* and *Rissoa membranacea* were not included in our study because we were not able to consistently distinguish living and dead individuals.

Category	Number of species		Number of individuals	
	living	dead	living	dead
Bivalves	24	49	2097	7423
Gastropods	8	29	93	1127
total	32	78	2190	8550

Table 2
List of bivalve and gastropod species found living (l), dead (d) or both (l/d) in the study. Note that all species found alive where also found dead. *Species not included in our quantitative evaluation of the data set (see Table 1).

Family	Species		Status
Nuculidae	*Nucula nucleus*	(Linnaeus, 1758)	d
	Nuculana pella	(Linnaeus, 1767)	d
Arcidae	*Arca noae*	Linnaeus, 1758	d
	Anadara juv.		d
Anomiidae	*Anomia ephippium*	Linnaeus, 1758	l/d
Limidae	*Limaria hians*	(Gmelin, 1791)	d
Glycimerididae	*Glycymeris* sp. juv.		d
Mytilidae	*Mytilus* sp. juv.		d
	Mytilus galloprovincialis	Lamarck, 1819	l/d
	Modiolus sp. juv (barbatus)		l/d
	Gibbomodioloa adriatica	(Lamarck, 1819)	d
	Gregariella petagnae	(Scacchi, 1832)	l/d
	Mytilaster sp.		d
	Amygdalum politum	(Verrill & Smith in Verrill, 1880)	l/d
Pectinidae	*Mimachlamys* sp. juv.		d
	Mimachlamys varia	(Linnaeus, 1758)	d
	Flexopecten glaber	(Linnaeus, 1758)	d
Ostreidae	*Ostrea edulis*	Linnaeus, 1758	d
Lucinidae	*Loripes lucinalis*	(Lamarck, 1818)	l/d
	Lucinella divaricata	(Linnaeus, 1758)	l/d
	Anodontia sp.		l/d
Montacutidae	*Kurtiella bidentata*	(Montagu, 1803)	d
	Hemilepton nitidum	(Turton, 1822)	d
Cardiidae	*Cerastoderma glaucum*	(Bruguière, 1789)	l/d
	Acanthocardia tuberculata	(Linnaeus, 1758)	d
	Parvicardium sp.		d
	Papillicardium papillosum	(Poli,1795)	l/d
Mactridae	*Spisula subtruncata*	(da Costa, 1778)	d
	Mactra stultorum	(Linnaeus, 1758)	d
Solenidae	*Solen marginatus*	Pulteney, 1799	d
Veneridae	*Chamelea gallina*	(Linnaeus, 1758)	l/d
	Dosinia lupinus	(Linnaeus, 1758)	l/d
	Venerupis decussata	(Linnaeus, 1758)	l/d
	Venerupis phillipinarum	(A. Adams & Reeve, 1850)	l/d
	Venerupis juv.		l/d
	Polititapes cf. *virgineus*	(Linnaeus, 1767)	l/d
	Pitar rudis	(Poli, 1795)	d
Tellinidae	*Moerella* cf. *donacina*	(Linnaeus, 1758)	d
	Tellina cf. *pulchella*	Lamarck, 1818	d
	Angulus tenuis	da Costa, 1778	l/d
	Tellinidae indet		d
	Angulus fabula	(Gmelin, 1791)	l/d
	Gastrana fragilis	(Linnaeus, 1758)	d
Donacidae	*Donax* cf. *trunculus*	Linnaeus, 1758	l/d
	Donax cf. *semistriatus*	Poli, 1795	d
Semelidae	*Scrobicularia plana*	(da Costa, 1778)	l/d
	Abra segmentum	(Récluz, 1843)	d
Corbulidae	*Lentidium mediterraneum*	(O. G. Costa, 1829)	l/d
	Corbula gibba	(Olivi, 1792)	d
Gastrochaenidae	*Gastrochaena* sp.		d
Thraciidae	*Thracia* sp.		d
Trochidae	*Gibbula* sp. 1		l/d
	Gibbula magus	(Linnaeus, 1758)	d
	Gibbula albida	(Gmelin, 1791)	d
	Gibbula sp. 2		d
	Calliostoma sp.		d
	Trochidae juv. *indet.*		d
Cerithiidae	*Bittium reticulatum*	(da Costa, 1778)	l/d*
	Cerithium vulgatum	Bruguière, 1792	d
Muricidae	*Ocinebrina aciculata*	(Lamarck, 1822)	d
	Hexaplex trunculus	(Linnaeus, 1758)	l/d
	Muricidae indet.		d
Calyptraeidae	*Calyptraea chinensis*	(Linnaeus, 1758)	d
Hydrobiidae	*Hydrobia* sp.		l/d
Phasianellidae	*Tricolia* sp.		d
Truncatellidae	*Truncatella* sp.		d
	Truncatella subcylindrica	(Linnaeus, 1758)	d

(continued on next page)

Table 2 (*continued*)

Family	Species		Status
Rissoidae	*Rissoa membranacea*	(J. Adams, 1800)	l/d*
	Rissoa variabilis	(Von Mühlfeldt, 1824)	d
	Alvania lineata	Risso, 1826	l/d
	Alvania sp.		d
Nassariidae	*Cyclope neritea*	(Linnaeus, 1758)	l/d
	Nassarius pygmaeus	(Lamarck, 1822)	d
	Nassarius reticulatus	(Linnaeus, 1758)	l/d
Turridae	*Turridae indet.*		d
	Bela sp.		d
	Mangelia costulata	Risso, 1826	d
	Mangelia sp.		d
Retusidae	*Retusa truncatula*	(Bruguière, 1792)	d
Opisthobranchia	*Lymnaea* sp.		d
	Haminoea navicula	(da Costa, 1778)	d

where S = the total number of species and p_i = the proportion of individuals found in the ith species. The Shannon–Wiener index was calculated with the equation

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where S = the total number of species, and p_i = the proportion of individuals found in the ith species. Species richness, the Simpson index and the Shannon–Wiener index were chosen because they are the most commonly employed measures of diversity (Lande, 1996). The underlying statistical distribution of a sample will, however, generally influence the constancy of evenness measures and the Shannon–Wiener index is particularly sensitive to sample size (Lande, 1996; Magurran, 2004; Buzas and Hayek, 2005).

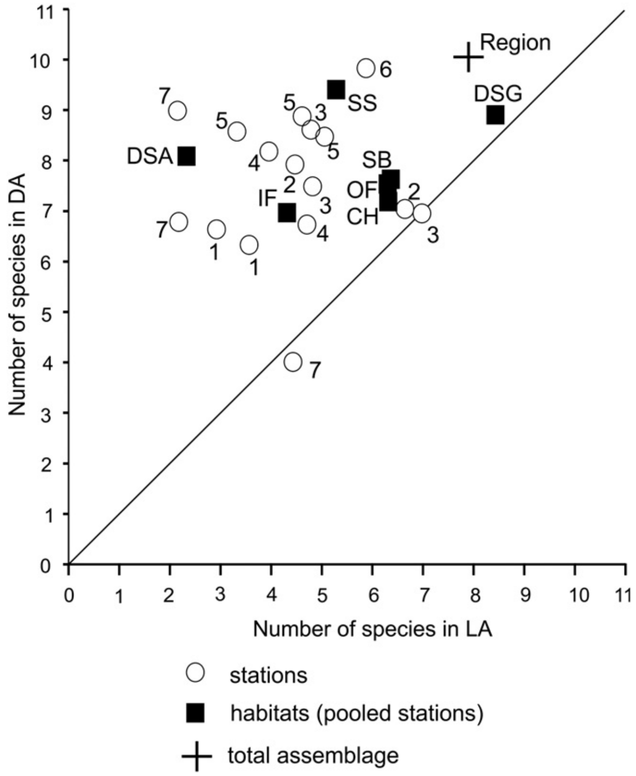

Fig. 4. Rarefied species richness for LAs and DAs of stations, habitats and the region. Numbers assign stations to habitats (1 = IF, 2 = OF, 3 = SB, 4 = CH, 5 = SS, 6 = DSG, 7 = DSA). IF: inner flat, OF: outer flat, SB: sandbar, CH: channel, SS: shallow sublittoral, DSG: delta seagrass, DSA: delta sand.

Relations between stations and environments and the LD fidelity were analyzed using ordination and clustering methods. For the cluster analysis the Bray–Curtis index was used. For non-metrical multidimensional scaling (nMDS), all pairwise distances among stations were calculated with the Bray–Curtis distance measure (Clarke and Warwick, 2001). The nMDS ordination was specified for two dimensions. The goodness of fit, termed stress, was calculated with the Kruskal's method (Clarke and Warwick, 2001). Results of cluster analyses were superimposed on the nMDS-figures, because the two methods complement each other. The number of individuals per sample was highly variable; therefore, data for nMDS and cluster analysis were standardized (i.e., percentages were used) and square root transformed to de-emphasize the importance of the most abundant species (Clarke and Warwick, 2001). Diversity indices and

Table 3
Ratio in diversity between DAs and LAs for stations, habitats and in the region at fixed numbers of individuals. The number of individuals was rarefied to 25 at all spatial scales and additionally to 50 in habitats and for the region. Consider that 13 stations had less than 25 living specimens and are therefore not included. Habitats and the region are pooled from stations. D/L = ratio in diversity between death assemblages and life assemblages.

Scale	Station no.	Habitat	D/L
stations_25	14_10	IF	1.77
	15_10	IF	2.27
	3_10	OF	1.06
	13_10	OF	1.77
	1_08	SB	1.00
	1_10	SB	1.80
	11_10	SB	1.55
	5_08	SS	1.92
	20_10	SS	2.58
	21_10	SS	1.67
	4_08	CH	2.07
	23_10	CH	1.43
	6_08	DSG	1.67
	7_10	DSA	0.90
	16_10	DSA	3.12
	17_10	DSA	4.18
	Median		1.77
	Mean		1.92
	Stdev		0.83

Scale	No. of stations	Habitat	D/L
habitats_ 25	5	IF	1.61
	5	OF	1.19
	3	SB	1.19
	2	CH	1.15
	5	SS	1.78
	5	DSG	1.06
	4	DSA	3.46
	Median		1.19
	Mean		1.63
	Stdev		0.85

Scale	No. of stations	Habitat	D/L
habitats_50	5	IF	1.76
	5	OF	1.32
	3	SB	1.24
	2	CH	1.19
	5	SS	1.88
	5	DSG	1.08
	4	DSA	4.13
	Median		1.32
	Mean		1.80
	Stdev		1.07

Scale	No. of stations	No. of habitats	D/L
region_25	29	7	1.27
region_50	29	7	1.42

individual rarefaction were calculated with the original data. To study similarities between the live and death assemblages within individual stations and within the seven predefined habitats, we used the Spearman's rank order coefficient (r_s) and the R statistic of analysis of similarity (ANOSIM) (Clarke and Warwick, 2001). To check which species are responsible for differences between LA and DA of habitats we performed a similarity percentage analysis (SIMPER) (Clarke and Warwick, 2001). Statistical analysis was performed with the package Past (Hammer et al., 2001).

4. Results

4.1. Basic structure of the molluscan assemblages

A total of 10,740 complete individual molluscs (calculated from articulated and disarticulated bivalves and gastropods) were collected in fifteen intertidal and fourteen sublittoral samples and identified to species level. These shells represented 78 species from 32 families (Tables 1, 2). 2190 (25.6%) of all individuals were collected alive.

4.2. Fidelity of richness

Rarefied species richness in DAs was higher than in LAs at almost all stations, in all habitats and in the region. At the habitat scale the surplus of dead species is particularly high in the delta sand, in the shallow sublittoral and on the inner tidal flat (Fig. 4). For fixed numbers of individuals (rarefied to 25 at stations, in habitats and in the region) the differences in diversity decrease with increasing scale. With increasing number of individuals (25 versus 50 in habitats and region), however, diversity differences increase (Table 3).

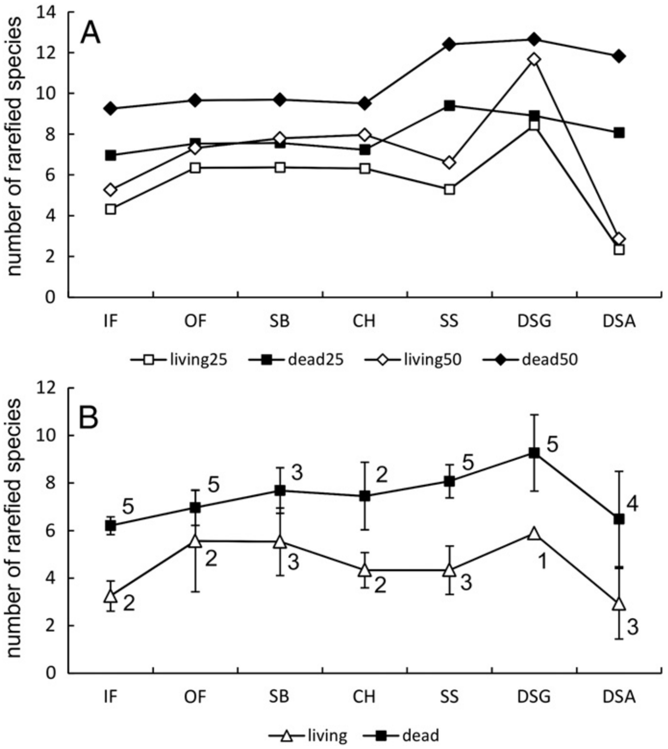

Fig. 5. Trends of rarefied species richness for LA and DA along a gradient from the inner tidal flat to the delta sand. A. Trends of pooled species richness of habitats rarefied to 25 and 50 individuals. B. Trends of mean species richness (±95% confidence intervals) of stations within habitats. Numbers in B are numbers of stations with at least 25 individuals. IF: inner flat, OF: outer flat, SB: sandbar, CH: channel, SS: shallow sublittoral, DSG: delta seagrass, DSA: delta sand.

Rarefied species richness of pooled stations per habitat (Fig. 5A) shows a moderate increase of the LA across the tidal flat, followed by a decrease into the shallow sublittoral and delta sand. There is, however, a distinct peak in richness in the delta seagrass. The death assemblage in contrast, shows relatively uniform species richness on the tidal flat and in the sublittoral, with values in the sublittoral being distinctly higher but without a distinct peak in the delta seagrass (Fig. 5A). Mean species richness of stations within habitats (Fig. 5B) shows for the LA a very similar trend to that of the pooled stations of habitats, but the peak in delta seagrass is comparatively moderate. The DA here shows a continuous increase from the inner flat to the delta seagrass and again a decrease into the delta sand.

4.3. Fidelity of evenness

The Shannon–Wiener- and the Simpson index show very similar patterns (Fig. 6), which also closely correspond to those of rarefied species richness (Fig. 5). Evenness was higher in DAs than in the LAs, but differences were stronger in the three sublittoral habitats (shallow sublittoral, delta seagrass and delta sand) than in the four tidal flat habitats (except for inner flat). In the life assemblage evenness showed a strong increase from the inner to outer tidal flat, was high on the sand bar and in the channel and decreased strongly towards the three sublittoral habitats, with a peak in the delta seagrass. The death assemblage, however, showed a weak trend of increasing evenness along the tidal flat into the shallow sublittoral, a distinct

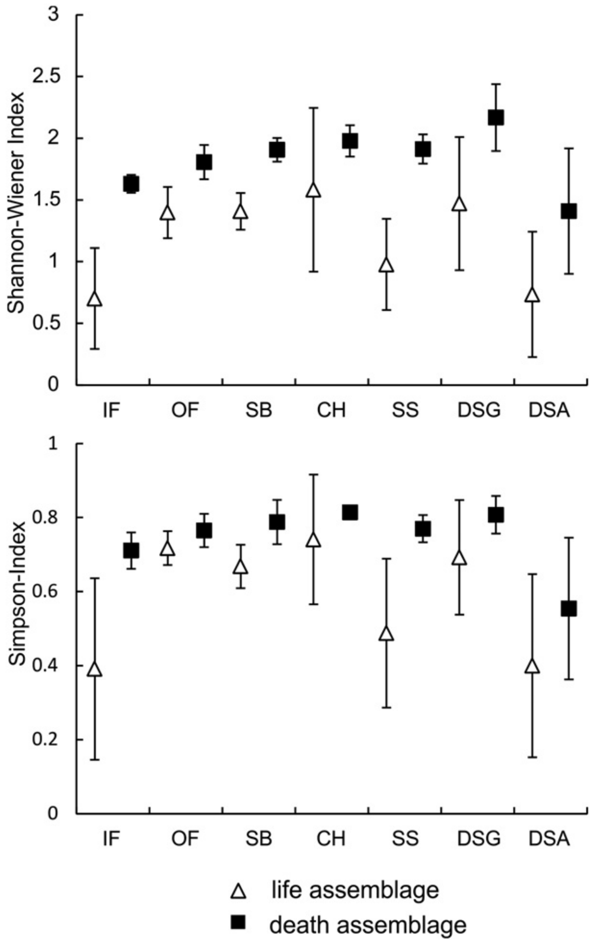

Fig. 6. Evenness (±95% confidence intervals) for the LA and the DA in the different habitats (IF: inner flat, OF: outer flat, SB: sandbar, CH: channel, SS: shallow sublittoral, DSG: delta seagrass. DSA: delta sand).

peak in the delta seagrass and a strong decrease towards the delta sand (Fig. 6), a trend particularly similar to mean rarefied species richness of the death assemblages in habitats (see Fig. 5B).

4.4. Fidelity of abundance

The single habitat with more living than dead individuals is the delta sand. On sublittoral sand and on the sand bar the proportion of living individuals is also relatively high, but in all other habitats dead shells strongly dominate (Fig. 7).

The most abundant species in the LA were the bivalves *Cerastoderma glaucum* (Cardiidae), *Chamelea gallina* (Veneridae), *Scrobicularia plana* (Semelidae), and *Lentidium mediterraneum* (Corbulidae). *Chamelea* dominated in four habitats, the other three habitats were dominated by *Scrobicularia*, *Cerastoderma* and *Lentidium*, respectively. DAs of the 7 habitats were dominated by *Lentidium* (2 habitats), *Chamelea* (2 habitats), *Scrobicularia*, *Cerastoderma* and the lucinid bivalve *Loripes lucinalis*. Typically, species which dominated in the LA were also abundant in the DA and vice versa. A notable exception is *L. mediterraneum*, which dominated alive in the delta sand, was relatively abundant alive in the delta seagrass and channel, but was among the abundant species of the DA in three additional habitats. Similarly, *Gibbula* sp. 1 was widely distributed in DAs, but never occurred alive (Fig. 8, Tables 4, 5). Species with higher rank abundance in the LAs were also ranked high in the DAs (Table 5). Spearman's rank order correlations were statistically significant for the region, all habitats (Table 6A) and almost all stations

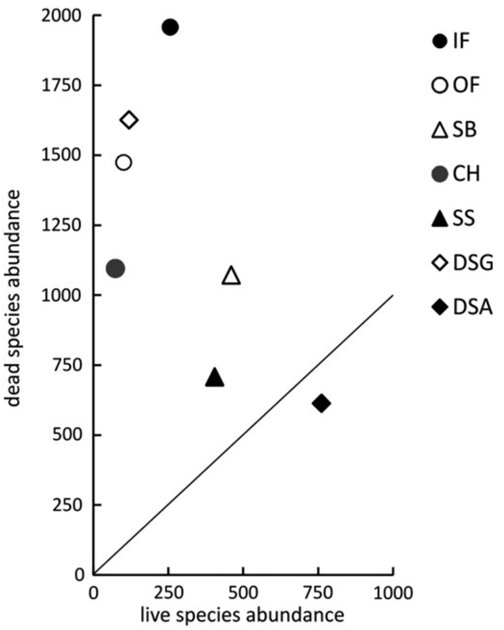

Fig. 7. Bivariate plot of species abundance in the LA and in the DA for all habitats.

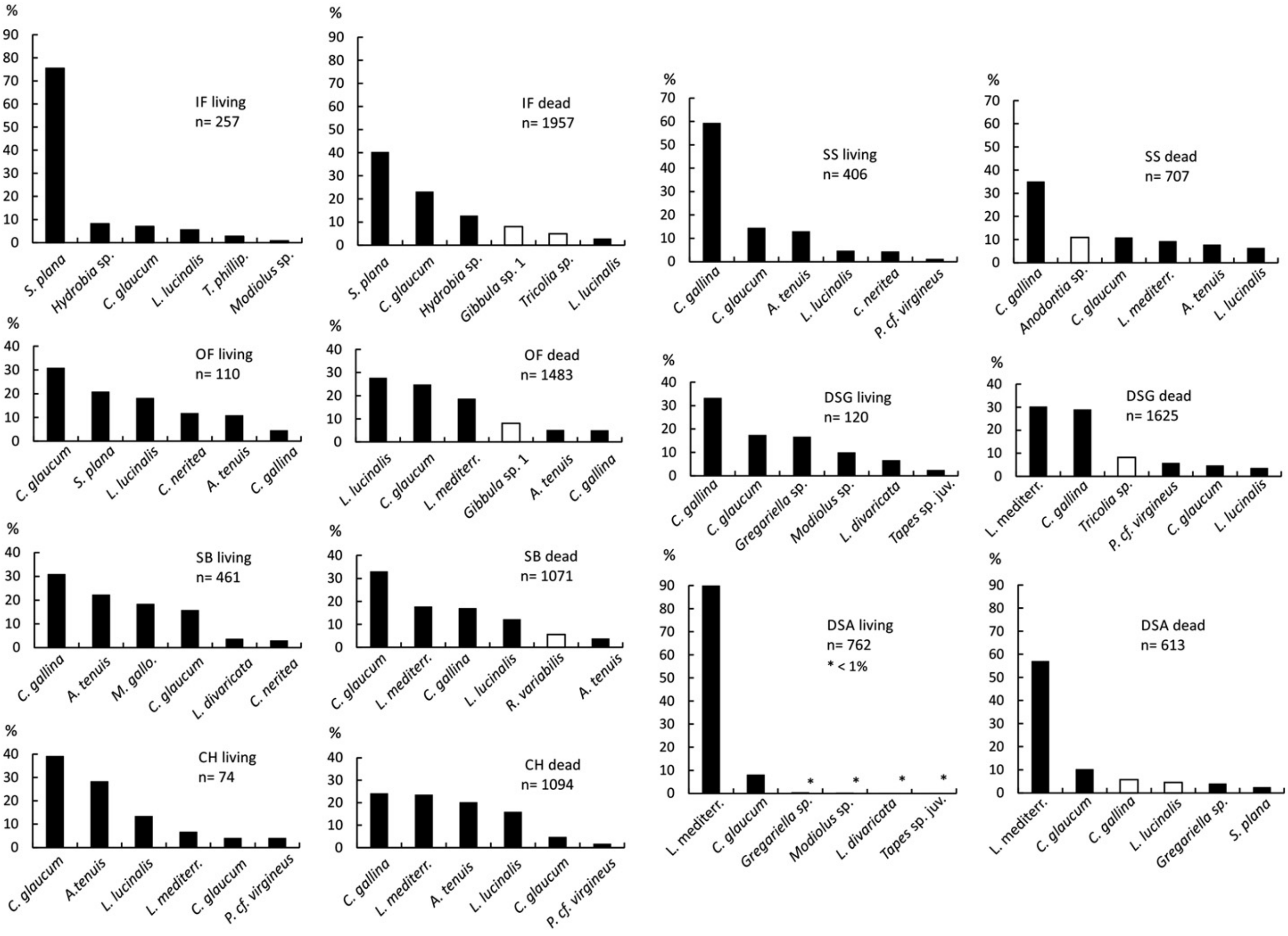

Fig. 8. The six most abundant species in the LA and in the DA for all habitats. Solid bars indicate live (or dead) species also found dead (or live). Open bars indicate dead species which were not found alive. Note that there were no species found only alive.

Table 4
Abundances of the most common species in the LA and DA of the investigated habitats.

	Habitat (number of samples)	Category	*Cerastoderma glaucum*	*Chamelea gallina*	*Angulus tenuis*	*Scrobicularia plana*	*Loripes lucinalis*	*Lentidium mediterraneum*	*Venerupis phillipinarum*	*Lucinella divaricata*	*Hydrobia* sp.	*Gregariella petagnae*	*Cyclope neritea*	All species
Intertidal	Inner flat (5)	LA	18	0	0	194	14	0	7	0	21	0	0	257
		DA	454	16	1	789	57	7	8	0	250	3	2	1957
	Outer flat (5)	LA	34	5	12	23	20	1	0	0	0	0	13	110
		DA	369	75	77	40	412	277	4	12	2	0	12	1483
	Sandbar (3)	LA	73	143	103	0	8	2	0	17	0	0	14	461
		DA	354	183	41	1	131	190	2	14	0	0	13	1071
	Channel (2)	LA	3	29	21	0	10	5	0	0	0	0	0	74
		DA	52	265	221	15	174	258	2	10	0	0	14	1094
Sublittoral	Shallow subtidal (5)	LA	59	241	53	0	19	2	0	2	0	1	18	406
		DA	77	248	55	3	45	66	0	16	0	0	12	707
	Delta seagrass (5)	LA	1	40	2	0	12	20	0	12	0	0	8	120
		DA	77	472	36	39	59	493	3	47	13	1	14	1025
	Delta sand (4)	LA	62	0	0	1	0	686	1	2	0	4	0	762
		DA	63	35	7	15	28	350	2	8	9	25	4	613
	Total (29)	LA	250	458	191	218	83	716	8	33	21	5	53	2190
		DA	1446	1294	438	902	906	1641	21	107	274	29	71	8550

(Table 6B) and they were typically higher at habitat and regional scale than at individual stations (Fig. 9).

4.5. Fidelity of community structure

For living and dead molluscs the cluster- and scaling methods and ANOSIM showed similar patterns in faunal compositions between stations and environments: inner and outer tidal flat samples are more similar to each other in the living fauna than in the dead fauna and delta sand stations are quite heterogeneous in all analyses. The dendrogram of the living individuals only (Fig. 10A) formed three clusters at the similarity level of 0.25. One cluster contained nine out of ten inner and outer tidal flat stations. Another big cluster contained all sandbar, channel and shallow sublittoral stations. A third, smaller cluster contained two stations from the delta sand and one from the delta seagrass. Two other delta sand stations showed affinities to tidal flat stations. nMDS of the living individuals plotted the inner and outer tidal flat and two of the delta sand stations close to each other, indicating high similarity of the species composition in both areas. Channel, sandbar, shallow sublittoral and seagrass stations were similar to each other with one exception: two delta sand stations were distinct (Fig. 11A). R-values confirm that for the LA the difference between inner and outer tidal flat is small, and also between the sandbar, the channel, the shallow sublittoral and the delta seagrass. The delta sand is well separated from most habitats, except the channel (Table 7).

Empty shells form one inner flat cluster at the 0.5 similarity level, all other stations are fused, with the exception of three delta sand stations and one delta seagrass station (Fig. 10B). nMDS of the empty shells (Fig. 11B), shows distinct inner flat stations, whereas outer flat stations became more similar to the shallow sublittoral and sandbar stations. With one exception, stations of the delta seagrass showed high similarity. Stations of the sandbar, the channel and the shallow sublittoral were also very similar to each other. Delta sand stations are widely dispersed. R-values in accordance show strong differences for the dead fauna between the inner and outer tidal flat, but considerable overlaps between the sandbar, the channel, the shallow sublittoral and the delta seagrass. The delta sand is again poorly separated from the channel (Table 7).

4.6. Fidelity of between habitat discrimination

DAs capture differences between habitats better than LAs. In 14 out of 21 pairwise comparisons between habitats, the R-values are higher for the DA than for the LA and the median R-values are almost identical (Table 7). Differences between LA and DA are mostly due to numerically abundant living species that were present in the dead fauna with even higher abundances. Notable exceptions include *Lentidium mediterraneum* in the delta sand and *L. mediterraneum* and *Angulus tenuis* on the sand bar, which were more important in the LA. Numerically relatively unimportant species, which were restricted to dead fauna only, also contributed to differences between LAs and DAs, but significant differences were never due to species restricted to the LA (Table 8, compare also Fig. 8).

4.7. Fidelity of beta diversity

The nMDS of living and dead fauna shows that LAs were much more heterogeneous than the DAs, as indicated by much wider scattering of stations in the ordination plot (Fig. 12). Beta diversity is therefore higher in LA than in the DA. nMDS also shows that group centroids are consistently segregated between LAs and DAs, with no overlap at all, which is in contrast to Spearman rank correlations (see Table 6). The similarities between life and death assemblages were strongest in the shallow sublittoral and on the sandbar, where life and death assemblages plot closer to each other than in other habitats (Fig. 12).

Table 5
Rank order of the most abundant species of LAs and DAs of the total assemblage and the habitats: inner flat (IF), outer flat (OF), sandbar (SB), channel (CH), shallow sublittoral (SS), delta seagrass (DSG) and delta sand (DSA). Only species with at least 10 living individuals or empty shells in a habitat were included. (a: *Lentidium mediterraneum*, b: *Chamelea gallina*, c: *Cerastoderma glaucum*, d: *Scrobicularia plana*, e: *Angulus tenuis*, f: *Mytilus galloprovincialis*, g: *Loripes lucinalis*, h: *Cyclope neritea*, i: *Lucinella divaricata*, k: *Hydrobia* sp., l: *Polititapes* cf. *virgineus*, m: *Gibbula* sp.1, n: *Tricolia* sp., o: *Modiolus* sp., p: *Anodontia* sp., q: *Plagiocardium papillosum*, r: *Gregariella petagnae*, s: *Venerupis decussata*).

Habitat		Total		IF		OF		SB		CH		SS		DSG		DSA	
Assemblage		L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
$n_{species}$		32	78	7	42	9	37	13	29	9	31	13	32	18	50	9	27
Rank	1	a	a	d	d	c	g	b	c	b	b	b	b	b	a	a	a
	2	b	c	k	c	d	c	e	a	e	a	c	p	i	b	c	c
	3	c	b	c	k	g	a	f	b	g	e	e	c	a	n		b
	4	d	g	g	m	k	m	c	g		g	g	a	g	l		g
	5	e	d		n	e	e	i	e		c	h	e		c		r
	6	f	e		g		b	h	m		l		g		g		d
	7	g	m		o		d		i		m		m		i		l
	8	h	k		b		l		l		d		i		d		r
	9	i	n		s		h		o		h		q		e		d
	10	k	l				i		h				h		h		l
	11	l	i						f						m		o
	12	m	h												k		

5. Discussion

5.1. Formation of the death assemblage

More than 80% of the collected individuals were empty shells. This strong surplus is typical for LD studies from sediments and is the main reason for the higher species richness in death assemblages (Fig. 2.1 in Kidwell, 2009). Due to the accumulative effect of time-averaging, the number of rarefied species is much higher for the DAs in our study than for the LAs (Fig. 4). This pattern is typical for DAs, even after accounting for the higher number of shells (Kidwell, 2002; Olszewski and Kidwell, 2007; Tomašových and Kidwell, 2009a). This higher rarefied species richness in DAs may result from within habitat time-averaging in a dispersal-limited metacommunity or from introduction of species that would not be expected to co-occur alive in the same habitat (Kidwell and Bosence, 1991; Olszewski and Kidwell, 2007; Tomašových and Kidwell, 2010). In our study all species found alive were also found dead, and abundant living species were typically also abundant (or at least present) in the DA. In contrast, there were only few dead-only-species abundant in the DA of some habitats and there were no live-only-species at all (Fig. 8, Table 8). This results in high rank order correlation of LAs and DAs (Table 6) and indicates that environmental condensation or large-scale redistribution of shelly remains (out-of-habitat transport) is of limited importance for the studied DAs, as has been reported in many other case studies of shallow sublittoral and intertidal environments (e.g., Miller, 1988; Poirier et al., 2010; Albano and Sabelli, 2011; for review see Kidwell, 2008). For fixed numbers of individuals the differences in diversity between LAs and their corresponding DAs decrease with increasing scale (i.e., from stations to habitats to the region, see Table 3) and in the study area the higher species richness of DAs at all scales is accompanied by lower beta diversity in the death assemblage (Fig. 12), which both point to an important role of within-habitat time-averaging (Tomašových and Kidwell, 2009a, 2010). In accordance with these findings, the rank order correlation of species abundance is higher at habitat and regional scale than at individual stations (see Fig. 9)

Table 6
Spearman's rank order coefficient of live and death assemblages at habitat scale (A) and at station scale (B).

Habitat	Spearmans r_s	Significance
Inner flat	0.3991	<0.001
Outer flat	0.5185	<0.001
Sandbar	0.5741	<0.001
Shallow subtidal	0.5297	<0.001
Channel	0.5794	<0.001
Delta seagrass	0.4447	<0.001
Delta sand	0.4448	<0.001
Region	0.5649	<0.001

Habitat	Sample	Spearmans r_s	Significance
Inner flat	3_08	0.5219	<0.001
	4_10	0.253	0.023
	5_10	0.4776	<0.001
	14_10	0.4125	<0.001
	15_10	0.3953	<0.001
Outer flat	2_08	0.493	<0.001
	2_10	0.5586	<0.001
	3_10	0.5947	<0.001
	12_10	0.5649	<0.001
	13_10	0.443	<0.001
Sandbar	1_08	0.5958	<0.001
	1_10	0.5151	<0.001
	11_10	0.5278	<0.001
Shallow subtidal	5_08	0.6856	<0.001
	10_10	0.5041	<0.001
	20_10	0.2075	0.063
	21_10	0.4876	0.001
	22_10	0.2075	0.063
Channel	4_08	0.6579	<0.001
	23_10	0.5166	<0.001
Delta seagrass	6_08	0.3033	0.006
	8_10	0.4697	<0.001
	9_10	0.3532	0.001
	18_10	0.3633	<0.001
	19_10	0.3705	<0.001
Delta sand	6_10	0.4633	<0.001
	7_10	0.1031	0.360
	16_10	0.4306	<0.001
	17_10	0.3589	<0.001

5.2. Preservation and trends of species richness and evenness

Species richness and evenness are higher in the studied DAs but trends of diversity in the LAs are better preserved in the DAs of the tidal flat than in those of the sublittoral habitats (Figs. 4–6). We relate the strong similarities in diversity of LAs and DAs in most tidal flat habitats to a comparatively simple and persistent species-abundance structure, where the most abundant and the species in the middle of the rank sequence hardly ever change. In the sublittoral habitats in contrast, frequent changes in the rank sequence in the life assemblage will result in a strong increase of evenness during time-averaging. This agrees with modeling results, where at any point in the time, living assemblages were not colonized by all species that were adapted to a specific habitat, because they were rare or slow colonizers. With increasing time

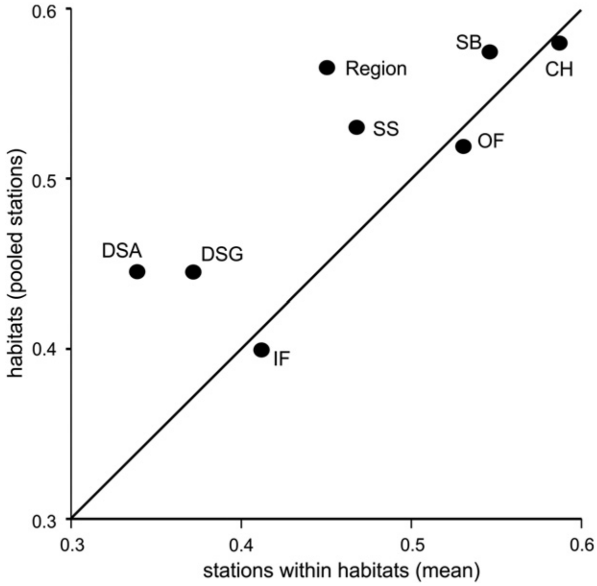

Fig. 9. Spearman's rank order correlation of live and death assemblages at stations versus habitats and the region. IF: inner flat, OF: outer flat, SB: sandbar, CH: channel, SS: shallow sublittoral, DSG: delta seagrass, DSA: delta sand.

averaging, however, they eventually colonized living assemblages for a short period, thereby increasing richness and evenness of the death assemblages (Olszewski and Kidwell, 2007; Tomašových and Kidwell, 2010).

A distinct peak in species richness and evenness is present in the LAs and DAs of the delta seagrass. We tentatively relate this to the structuring effect of seagrasses, which typically harbor more species than unvegetated surrounding areas (Duffy, 2006) and this peak of life assemblages is well preserved in the death assemblage here, except for the species richness of pooled habitats (Figs. 5, 6).

5.3. Abundance and distribution of common species

Intertidal and sublittoral habitats differed in the abundance and distribution of common species (Fig. 8, Tables 4, 5) and are accordingly characterized by distinct communities (Figs. 10, 11).

A common species in both the tidal flat and sublittoral environments was the bivalve *Loripes lucinalis*. It belongs to the family Lucinidae, which occur infaunally in sandy silts in the intertidal or in the shallow sublittoral. Symbiosis with sulfide-oxidizing bacteria enables them to inhabit anoxic environments with high levels of sulfide (Beesley et al., 1998; Taylor and Glover, 2000). Therefore, live individuals of this species were most abundant in those environments with fine-grained sediments and a high organic content of decomposing seagrass leaves, such as the inner and outer flat, the shallow sublittoral and the delta seagrass. Its empty shells were found at all stations, but they were far most abundant in the outer flat, in the channel and on the sandbar.

Lucinella divaricata is a lucinid bivalve inhabiting fine sand or mud just below the low tide line to a depth of 60 m (Pennec et al., 1995). This species lived on the sandbar and in the delta seagrass and in very low numbers in the shallow sublittoral and the delta sand. In general, *L. divaricata* occurred in rather low numbers in all environments and was absent in the inner flat.

C. glaucum, family Cardiidae, is a shallow burrower in soft substrata ranging from muds to coarse sands (Beesley et al., 1998) and prefers estuarine conditions (Boyden and Russel, 1972). It was the only species found alive in all environments, but occurred in high abundances on the sandbar, in the delta sand, in the shallow sublittoral and on the outer flat. Numbers of its shelly remains, however, were highest in the inner flat and decreased on the flat towards the sea. In the shallow sublittoral and in the delta sand the proportion of live and empty shells was similar.

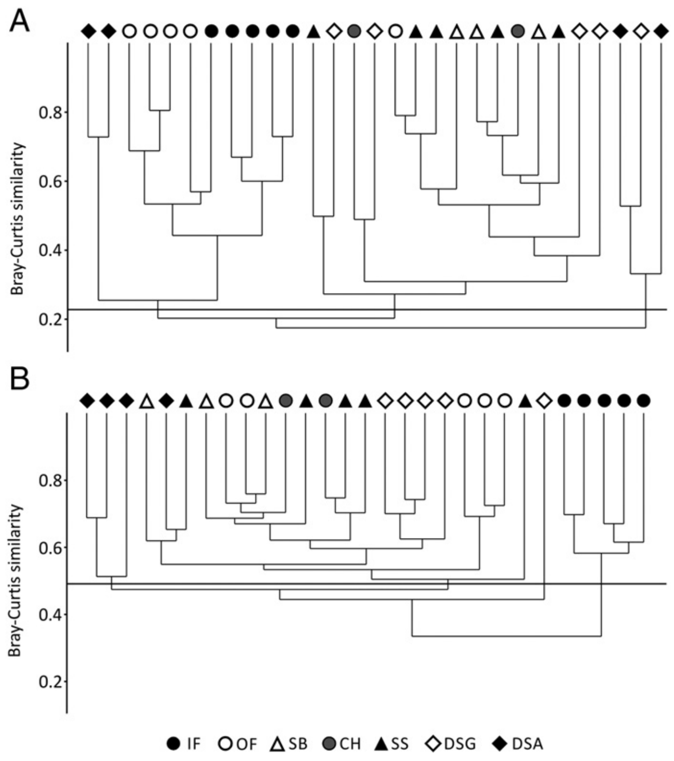

Fig. 10. Cluster analysis for the live assemblage (A) and the death assemblage (B). Symbols represent habitats. IF: inner flat, OF: outer flat, SB: sandbar, CH: channel, SS: shallow sublittoral, DSG: delta seagrass. DSA: delta sand.

C. gallina is a venerid bivalve. Most members of this family live in shallow marine and occasionally estuarine habitats. They are infaunal filter-feeders with an active, powerful and compressed foot, which enables them to bury themselves when they fall dry (Beesley et al., 1998). Living *C. gallina* were highly frequent in the shallow sublittoral and on the sandbar, but were present in all environments except for the inner flat and the delta sand. High numbers of empty shells were found in the delta seagrass, the channel and the shallow sublittoral.

Another common species was the bivalve *A. tenuis* (Tellinidae). It occurs from mid-tide level down to a few meters below low water. It lives a few centimeters below the sand surface, generally on its left side, and feeds on plankton and organic detritus through an inhalant siphon (Trevallion, 1971). Living *A. tenuis* were abundant on the sandbar, in the shallow sublittoral, in the channel and on the outer flat, but absent on the inner flat and the delta sand. Highest abundances of empty shells occurred in the channel.

S. plana, a member of the Semelidae, is an infaunal inhabitant of muddy bays and feeds on deposits along the mud surface if the water table remains at the surface (Hughes, 1970). Living individuals were most abundant on the inner tidal flat. Some individuals, but far fewer, lived on the outer tidal flat and only one living individual was found in seagrass. Dead *S. plana* were correspondingly most frequent on the inner flat.

L. mediterraneum belongs to the Corbulidae, a genus of ciliary suspension feeders with cosmopolitan distribution. Its foot is compressed and grooved and associated with a byssal gland which produces threads to anchor the animal to small rocks or other hard surfaces within the substratum. They are shallow burrowers in sandy and muddy substrata in sublittoral settings and are common in estuaries and embayments, usually at depths below 4 m (Hallan and Willian, 2010). *L. mediterraneum* is typical in Mediterranean intertidal to shallow-water environments (Poppe and Goto, 1993).

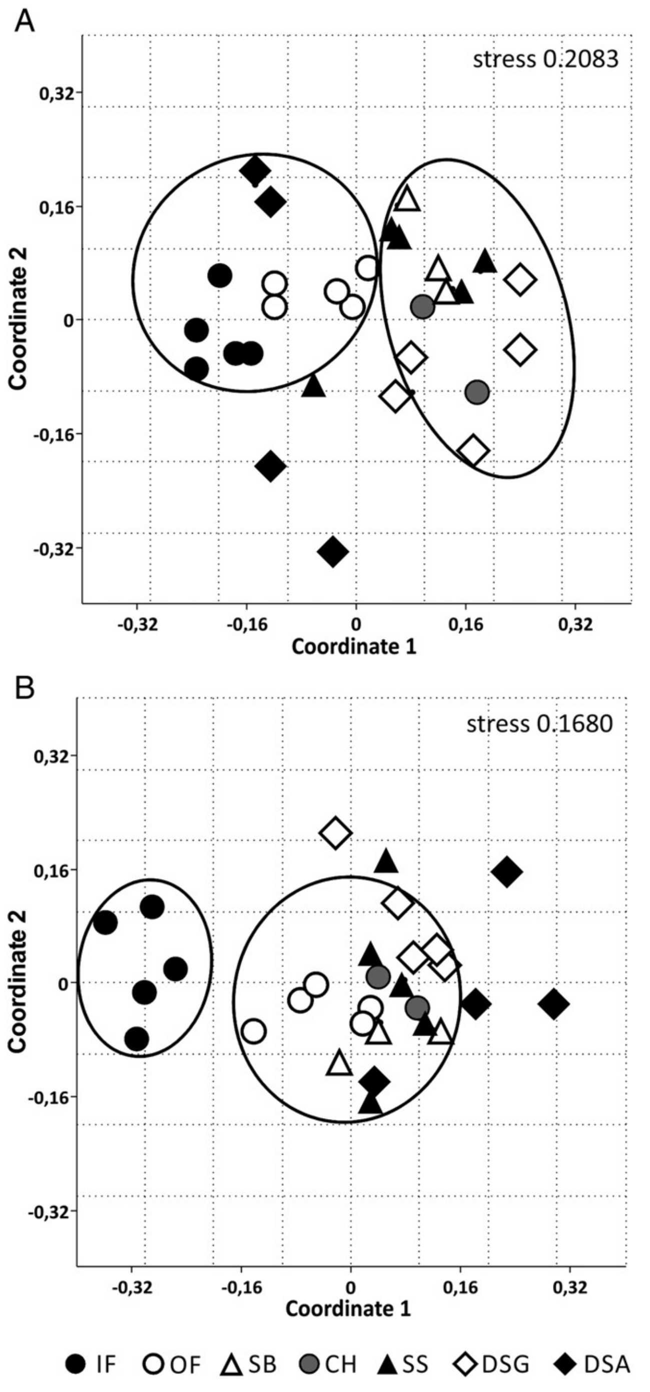

Fig. 11. nMDS of the LA (A) and the DA (B). Clusters formed at Bray–Curtis similarities of 0.25 and 0.5 (B) are superimposed as ellipses on ordination of LAs and DAs, respectively. Symbols represent habitats. IF: inner flat, OF: outer flat, SB: sandbar, CH: channel, SS: shallow sublittoral, DSG: delta seagrass. DSA: delta sand.

Living individuals were extraordinarily abundant in the delta sand, but rare in any other habitat. In contrast, its empty shells were found in all habitats, with high abundances in the delta seagrass and delta sand, the outer flat and the sandbar.

Hydrobia is a genus of small brackish water snails in the family Hydrobiidae. Hydrobiid snails belong to the most important deposit feeding invertebrates in estuaries. They ingest sediment and assimilate the microorganisms attached to mineral and detrital particles (Fenchel, 1975). They protect from predators or desiccation with an operculum. *Hydrobia* sp. occurred in high numbers on the inner tidal flat but was absent or rare in all other environments.

Table 7
R-values of ANOSIM for LAs and DAs of habitats.

	Living	Dead
Inner flat–outer flat	0.21	0.88
Inner flat–sandbar	0.89	0.84
Inner flat–channel	0.67	1
Inner flat–shallow sublittoral	0.69	1
Inner flat–delta seagrass	0.89	0.97
Inner flat–delta sand	0.66	0.92
Outer flat–sandbar	0.92	0.46
Outer flat–channel	0.76	0.80
Outer flat–shallow sublittoral	0.40	0.84
Outer flat–delta seagrass	0.63	0.74
Outer flat–delta sand	0.62	0.74
Sand bar–channel	0.08	−0.08
Sandbar–shallow sublittoral	−0.16	0.36
Sandbar–delta seagrass	0.30	0.22
Sandbar–delta sand	0.50	0.09
Channel–shallow sublittoral	−0.18	0.33
Channel–delta seagrass	−0.25	0.09
Channel–delta sand	0.14	0.43
Shallow sublittoral–delta seagrass	0.19	0.22
Shallow sublittoral–delta sand	0.71	0.51
Delta seagrass–delta sand	0.52	0.28
Median	0.52	0.51
Mean	0.44	0.55
Stdev.	0.36	0.34

Two species, *B. reticulatum and R. membranacea* were very abundant in the study area but not investigated quantitatively here because we were not able to consistently distinguish living and dead individuals. *B. reticulatum* is a member of the family Cerithiidae, which inhabit a variety of substrata, generally in the shallow sublittoral and intertidal, and are micro-algal feeders. They show remarkable adaptive radiations within a variety of marine and estuarine habitats (Fernandez et al., 1988). *B. reticulatum* is often found together with *Zostera* spp.; therefore the tidal flats offer optimal living conditions for this species. Empty shells occurred in great numbers in all habitats, but especially on the tidal flat (Weber, 2011). Interestingly, living *B. reticulatum* were present in only one of the inner flat and one of the outer flat stations. The distribution of *Zostera* on the flat was patchy, and – although not evaluated quantitatively – *Bittium* was found live only in seagrass-covered sediments (Weber, 2011). Also very common was *R. membranacea*. The genus *Rissoa* occurs worldwide in shallow seas, especially in the mid to lower littoral zones; a few species inhabit brackish water. They feed on diatomaceous films covering macroalgae or on foraminiferans or are selective deposit feeders (Beesley et al., 1998). We did not distinguish live and dead individuals in this gastropod, but shells were highly abundant on the tidal flat (Weber, 2011).

The species composition of the investigated Isonzo Delta region matches closely the well-established Mediterranean biocoenoses of previous authors. For example, fine sands are a widely distributed habitat of the Northern Adriatic Sea in which molluscs like *C. gallina*, *L. mediterraneum*, *A. tenuis*, *Donax semistriatus*, *Donax trunculus* form a distinct biocenosis. The gastropod *Cyclope neritea* is typical for fine sand with changing salinity and *C. glaucum* and *S. plana* together with other species (e.g. *Loripes lucinalis*), characterize the eurythermal and euryhaline lagoons (Vatova, 1949; Peres and Picard, 1964).

5.4. Preservation of community structure and beta diversity

The living molluscan fauna of the studied tidal flat and delta was not randomly distributed: individual species had their peak distribution in particular environments and this distribution is well reflected in the death assemblage (Fig. 8). Two main compositions in molluscan assemblages were evident in both life and death assemblages: one characterized the intertidal and the other one the sublittoral, with the delta sand being rather unique in its composition. In the LAs, however, samples of the outer tidal flat showed stronger relations to those of the inner tidal

Table 8
Results of SIMPER analysis.

Inner tidal flat (IF)				
Overall avarage dissimilarity: 82.1				
			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Living	Dead
Scrobicularia plana	29.8	36.3	38.8	158
Cerastoderma glaucum	21.32	62.26	3.6	90.8
Hydrobia sp.	9	72.95	4.2	50
Gibbula sp. 1	8	82.19	0	31.4
Tricolia sp.	4	87.47	0	19.2
Loripes lucinalis	3	91.45	2.8	11.4
Venerupis decussata	1	92.69	0	2.6
Outer tidal flat (OF)				
Overall avarage dissimilarity: 87.86				
			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Species	Contribution
Loripes lucinalis	26.3	29.93	4	82.4
Cerastoderma glaucum	21.92	54.88	6.8	73.8
Lentidium mediterraneum	13.47	70.21	0.2	55.4
Gibbula sp.1	8	79.58	0	23.8
Angulus tenuis	4	84.17	2.4	15.4
Chamelea gallina	4	88.44	1	15
Venerupis cf. *rhomboides*	3	91.42	0	8
Sandbar (SB)				
Overall avarage dissimilarity: 74				
			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Species	Contribution
Cerastoderma glaucum	18.2	24.59	24.3	118
Lentidium mediterraneum	11.8	40.53	667	63.3
Chamelea gallina	11.05	55.46	47.7	61
Angulus tenuis	7.84	66.05	34.3	13.7
Loripes lucinalis	8	76.27	2.67	43.7
Mytilus galloprovincialis	6	84.2	28.3	4
Rissoa variabilis	3	88.34	0	20
Lucinella divaricata	2	90.83	5.67	4.67
Channel (CH)				
Overall avarage dissimilarity: 83.09				
			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Species	Contribution
Chamelea gallina	21.45	25.81	14.5	133
Lentidium mediterraneum	18.22	47.74	2.5	129
Angulus tenuis	15.12	65.94	10.5	111
Loripes lucinalis	11.63	79.93	5	87
Cerastoderma glaucum	5	85.35	1.5	26
Gibbula sp. 1	3	89.04	0	9
Cyclope neritea	2	91.23	0	7
Shallow subtidal (SS)				
Overall avarage dissimilarity: 67.21				
			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Species	Contribution
Chamelea gallina	24.9	37.05	48.2	49.6
Cerastoderma glaucum	9	50.36	11.8	15.4
Lentidium mediterraneum	6.24	59.65	0.4	13.2
Anodontia sp.	6	68.56	0	15.4
Loripes lucinalis	4	75.21	3.8	9
Angulus tenuis	4	80.87	10.6	11
Polititapes cf. *virgineus*	2	84.49	1	6.2
Gibbula sp. 1	2	87.3	0	4.8

(continued on next page)

Table 8 (*continued*)

Shallow subtidal (SS)

Overall avarage dissimilarity: 67.21

			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Species	Contribution
Cyclope neritea	2	89.9	3.6	2.4
Lucinella divaricata	1	91.82	0.4	3.2

Delta seagrass (DSG)

Overall avarage dissimilarity: 87.16

			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Species	Contribution
Lentidium mediterraneum	20.99	24.09	4	98.6
Chamelea gallina	20.95	48.12	8	94.4
Tricolia sp.	11.76	61.62	0	26.6
Venerupis cf. *rhomboides*	5	67.45	0.4	19
Cerastoderma glaucum	4	72.58	0.2	15.4
Lucinella divaricata	3	76.07	4.2	9.4
Loripes lucinalis	3	79.5	2.4	11.8
Scrobicularia plana	3	82.91	0	7.8
Angulus tenuis	2	85.61	0.4	7.2
Plagiocardium papillosum	1	87.09	0.2	2.2
Spisula subtruncata	1	88.42	0.2	2.6
Gibbula sp.1	1	89.39	0	2.6
Cyclope neritea	0.97	90.51	1.6	2.8

Delta sand (DSA)

Overall avarage dissimilarity: 76.54

			Mean abundance	Mean abundance
Species	Contribution	Cumulative %	Species	Contribution
Lentidium mediterraneum	46.83	61.19	172	87.5
Cerastoderma glaucum	10.39	74.76	15.5	15.8
Chamelea gallina	5	80.71	0	8.75
Loripes lucinalis	3	84.82	0	7
Gregariella sp.	2	87.22	1	6.25
Polititapes cf. *virgineus*	1.54	89.23	0	3.25
Scrobicularia plana	1	90.65	0.25	3.75

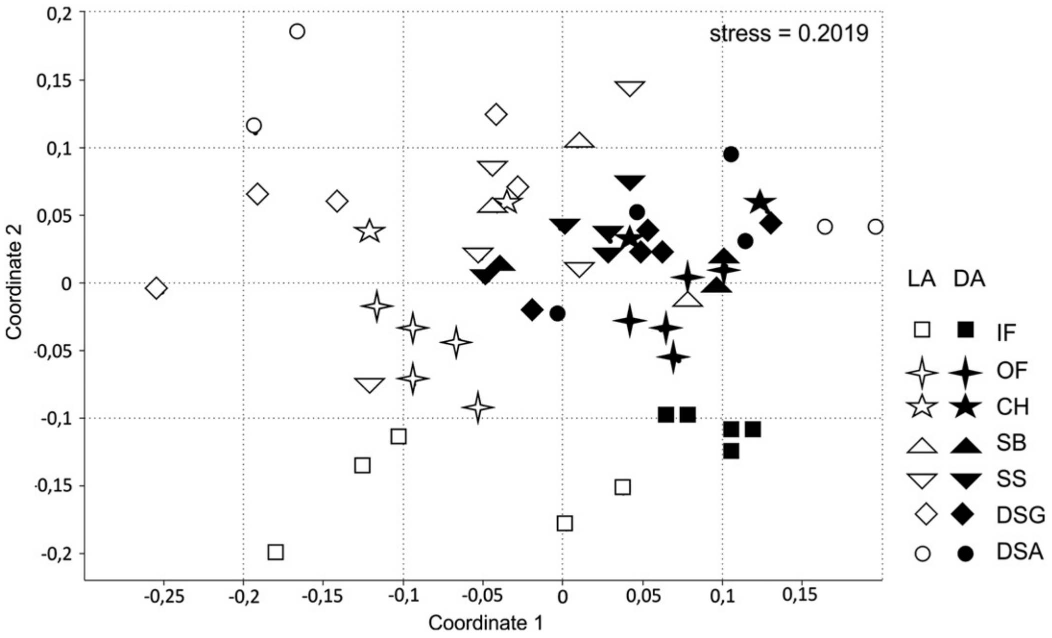

Fig. 12. nMDS of the LAs (white symbols) and DAs (black symbols). Symbols represent habitats. IF: inner flat, OF: outer flat, SB: sandbar, CH: channel, SS: shallow sublittoral, DSG: delta seagrass. DSA: delta sand.

flat, but in the DAs they showed stronger affinities to the shallow sublittoral and to the delta seagrass (Figs. 10, 11).

The stations of the inner and outer tidal flat and the delta seagrass showed high similarity of species composition in living and empty shells, and each of these habitats formed well-defined groups in all analyses, with LAs and DAs consistently separated in nMDS. In contrast, in all analyses, delta sand stations were widely separated from each other. The sandbar, channel and shallow sublittoral stations, finally, plotted together in all analyses, but were also always close to the stations from the outer tidal flat and the sublittoral seagrass (Figs. 10–12). Ordination and cluster analysis show that adjacent stations tended to have a similar faunal composition. In the living fauna this is interpreted to result from similar habitat preferences and possibly also from spatial autocorrelation, which can result from patchy dispersal (Tomašových and Kidwell, 2009b). In the analysis of the shelly remains, both original habitat preferences and a common response to taphonomic processes may cause the close association of nearby stations (Fürsich and Flessa, 1991) or alternatively preservation pathways may not strongly differ between the studied habitats (cf. Tomašových and Kidwell, 2009b). Due to time-averaging and spatial mixing of the fauna, beta diversity is predicted to be lower in DAs (Tomašových and Kidwell, 2009a). This was confirmed by the more homogeneous death versus living assemblages in our study because DAs occupy much smaller portions of nMDS space than LAs (see Fig. 12). In some habitats, both assemblages differ more strongly from each other than in others, but DAs are generally better suitable to distinguish between habitats than LAs (Table 7), In accordance with other similar case studies (e.g., Miller, 1988; Ferguson and Miller, 2007) and meta-analyses (Tomašových and Kidwell, 2009b) we therefore conclude that the dead molluscan fauna can be used to reliably define intertidal and sublittoral habitats.

Although nMDS plots indicate significant differences, a strong similarity of rank order abundance between life and death assemblages in our study is evident (see Table 6), which is probably inflated by temporal autocorrelation between a death- and its source life assemblage (Tomašových and Kidwell, 2011). This can result from a dominance of recently dead cohorts in the death assemblage (Kosnik et al., 2007; Krause et al., 2010).

5.5. Conservation paleobiology

Recognizing and evaluating environmental changes in the younger history of human civilization is crucial to assess the type, magnitude and rate of change, to clarify the underlying causes and to assess historical baselines of "pristine" ecosystem conditions that may serve as targets for restoration and management efforts (Jackson et al., 2001). Modern ecological studies investigating ecosystem responses to environmental changes in marine systems normally use a perspective restricted to annual or decadal time scales at the longest. This is because quantitative biological monitoring data are not available for time intervals preceding the onset of extensive anthropogenic ecosystem modification. Nonetheless, the relatively recent past can be used to identify environmental change beyond timescales of direct human experience (Kowalewski et al., 2000; Flessa, 2002; Edgar and Samson, 2004; Ferguson, 2008; Dietl and Flessa, 2011). One of the methods applied to assess the response to past environmental changes in marine ecosystems involves studying life and death assemblages of shelly fauna. A mismatch between the composition of a time-averaged death assemblage of molluscan skeletal remains and the associated living assemblage can be reliable and conservative evidence for human-induced change (e.g. dredging or nutrient input) in shallow marine habitats if taphonomic sources can be ruled out (Staff and Powell, 1990; Kidwell, 2007; Olszewski and Kidwell, 2007; Ferguson, 2008; Kidwell, 2009).

Lotze et al. (2006) list the Adriatic among the most degraded marine ecosystems worldwide, with a long history of intense human impact that started back in Roman times. Our study indicates significant differences between living and death assemblages on the tidal flat and shallow sublittoral environments associated with the Isonzo River, but these can largely be explained by the process of time-averaging and small-scale redistribution of dead shells and therefore do not point to any major recent impact on this ecosystem. The long history of anthropogenic impact in the northern Adriatic Sea, however, makes it likely that the traces of the transition from "natural" to anthropogenically modified benthic communities are buried in somewhat deeper sediment layers (Kidwell, 2009). In fact, the study of historical sediment layers (down to 30 cm depth) from the same area indicates a strong shift in community composition with time on the tidal flat (unpublished boxcore data, Sawyer and Zuschin). Even here, however, changes are only among the same set of species and suggest a gradual environmental change with time. Whether this is natural or due to anthropogenic impact remains to be determined.

6. Conclusions

The studied molluscan faunas show consistent patterns in the life and death assemblages. Two intertidal (inner and outer tidal flat) and one sublittoral habitat (delta seagrass) are always characterized by well-defined station groups, three habitats (channel, sandbar and shallow sublittoral) always show close affinities to each other and mark a transition from the intertidal to the sublittoral, and the sublittoral delta sand is consistently characterized by a heterogeneous faunal composition.

The species composition of the investigated Isonzo delta region matches closely the well-established Mediterranean biocoenoses of previous authors. Some species were highly characteristic for intertidal or sublittoral settings. *Hydrobia* sp. lived exclusively at and living specimens of *S. plana* were largely restricted to the tidal flat, whereas *L. mediterraneum* was found live mostly in sublittoral settings. Living *C. gallina* were most abundant in the transition zone from the tidal flat to the sublittoral environments. *C. glaucum* was the only species found live in all habitats, with peak abundances in the LA of the outer tidal flat and of the channel.

Due to time-averaging, DAs are more homogeneous than LAs, indicating lower beta diversity in death assemblages, but strong rank order correlation of living and dead fauna suggests that no large-scale redistribution of shelly remains occurred. We conclude that the dead molluscan fauna can be used to reliably define intertidal and sublittoral habitats and to study environmental gradients.

There were many more dead than living individuals, and due to the prominent role of within habitat time-averaging this results in higher rarefied species richness in DAs, a difference that decreases with increasing spatial scale. Strong similarities in species richness and evenness of LAs and DAs in most tidal flat habitats are related to a comparatively simple and persistent species-abundance structure. In the sublittoral habitats in contrast, frequent changes in the rank sequence of the life assemblage resulted in a strong increase of evenness during time-averaging. Evenness of LAs was lowest in the physically structured habitats of the inner tidal flat and delta sand and a peak in the complex delta seagrass habitat is preserved in the DA.

Empty shells faithfully record overall diversity in the region and our study does not indicate a strong faunal turnover on the tidal flat and in shallow sublittoral habitats associated with the Isonzo River. Therefore no major human-induced change affected community composition during the last decades in this area. This, however, remains to be tested by careful study of historical sediment layers, which may record previous anthropogenic impact on this ecosystem.

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