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MASTERARBEIT

Titel der Masterarbeit

Distribution of molluscs on the intertidal flat and in the
delta of the Isonzo River (Gulf of Trieste, northern
Adriatic Sea, Italy)

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1. Introduction

Tidal flat deposits are frequently found in the Lower and Middle Miocene fossil record of the Central Paratethys (Zuschin et al., 2004; Zuschin et al., accepted) but actualistic studies in such environments are rare (Fürsich and Flessa, 1991a). To provide a dataset for comparison with fossil examples from Austria we studied appropriate environments at the northern Adriatic Sea.

The molluscan fauna of the northern Adriatic Sea is well known (D'Angelo and Gargiullo, 1979; Cossignani et al., 1992). Recent quantitative studies treated molluscan assemblages in the intertidal and subtidal of the Gulf of Trieste (Sawyer and Zuschin, 2010), but the distribution of bivalves and gastropods of the transitional zone between intertidal and subtidal environments is poorly known. This work investigates the distribution and abundance of bivalve and gastropod species on the tidal flats, the shallow subtidal in front of the tidal flat and the delta zone of the Isonzo River.

1.1. Isonzo River tidal flat

Tidal flats are plane and sediment-covered areas at the shore, influenced by the periodically flooding of the tides. Depending on the balance of deposition and erosion the sediment types range from sandy to silty bottoms. By trend, the grain size of the sediments decreases landwards (Reineck, 1970). The consistency and stability of the sediment is a basic physical factor for the colonization of a tidal flat (Sommer, 2005).

The tide is the most important environmental factor influencing life in the intertidal zone. The duration of exposure is most important because during that time marine organisms will be subjected to the greatest temperature ranges and the possibility of desiccation. Mobile organisms can move into moist cracks or burrow into the sediment. Some gastropods have opercula that completely seal off the aperture and thus reducing water loss (Nybakken and Bertness, 2005). Wave action exerts huge influence on organisms in the intertidal zone. Due to the permanent rearrangement of the sediment, the most characteristic species are infaunal. The sediment surface is only settled by organisms with low need of substrate like crabs. Since hard substrata for settling are rare, the filter-feeding epifauna (like bivalves of the families Mytilidae and Ostreidae) is less important than the sediment-feeding endofauna (e.g. Semelidae) (Sommer, 2005). Most intertidal molluscs are adapted to wave action by possessing a strong, enlarged foot that clamps them to the substrate and a shell that is low and flat, offering little resistance (Nybakken and Bertness, 2005). Wave energy can also cause drifting and accumulation of dead shells. Naturally accumulated death assemblages are important to palaeontology and ecology, where longer temporal perspectives on community composition are needed to discriminate natural or anthropogenic factors in ecosystem change (Kidwell, 2001).

Salinity on the tidal flat may change in two situations. First, flooding of river water or heavy rains may greatly reduce salinity. The second situation concerns tide pools that retain seawater at low tide and may show increased salinity due to evaporation. For organisms to survive and successfully colonize this area, they must possess certain adaptations such as burrowing into mud and osmoregulatory ability (Nybakken and Bertness, 2005). Tidal flats in close distance to river mouth have both freshwater and salt water influence. Depending on the amount of freshwater input into an environment there are two types of fauna inhabiting intertidal and nearby subtidal areas: marine and brackish water fauna. Furthermore marine fauna includes two subgroups: stenohaline animals which are barely able to tolerate changes in salinity (psu minimum 25) like *Gibbula* and *Tricolia*, and euryhaline animals which tolerate changes in salinities (between 30 and 15 psu) like *Ostrea*, *Scrobicularia plana*, *Hydrobia* (Nybakken and Bertness, 2005).

Zostera marina is a temperate seagrass that often grows within a distinct band extending from the intertidal to water depths ranging from several to tens of meters (Meyer and Nehring, 2006). *Z. marina* meadows develop structure and complexity of marine habitats. It reduces currents, tide and wave action and therefore causes accumulation and stabilization of sediment. The seagrass has high biomass, dead leaves accumulate and decompose, and especially in the inner tidal flat it forms thick mats.

The tidal flat of the Isonzo River is situated in the Gulf of Trieste in the Northern Adriatic Sea (Fig. 1). It covers an area of a maximum width of approximately 800 m. The tides are semidiurnal and the average tide, that is the difference between the mean low water and the mean high water, is 64 cm. At the time of spring tides, i.e. when the gravitational pulse of the sun and the moon are acting together, 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).

1.2. Research Question

The aim of the study was to investigate the distribution pattern of living and dead mollusc shells in view of the particularly stressful and rigorous habitat of the intertidal flat and the estuary delta of the Isonzo River.

- Are there differences in the abundances of common species in different zones of the intertidal and the subtidal?
- Are there differences in the diversity of the zones of the intertidal and the subtidal?
- Do the dead shells reflect distribution patterns of living molluscs, or is there drifting by wave action?
- Are there differences in the abundances and size frequency distribution of living and dead shells?



Figure 1. The estuary of the Isonzo River, located in the Gulf of Trieste in the northern-most part of the Adriatic Sea, Italy. Molluscan fauna was analysed on the tidal flat and in the delta.

2. Material and Methods

2.1. Study area

The fieldwork was carried out in June and July 2010 in the northernmost section of the Adriatic Sea in the Gulf of Trieste, Bay of Panzano. Additionally, material was available from a previous sampling campaign in July 2008. Sample sites were chosen to permit a broad-ranged, overall survey of the tidal and sublittoral mollusc distribution (Fig. 1). Standardized samples were collected from fifteen tidal flat and fourteen sublittoral delta locations (see below) (Figs. 2 and 3).

Tidal flat samples were collected at times of spring tide low water north of the mouth of the Isonzo River (Fig. 1 and 2). The intertidal flat extends between the marsh belt line and the low spring tide line over a length of about 650 m.

Four sampling areas can be distinguished. The first one was the inner tidal flat (Fig. 2, dark green dots), which is nearest to the marsh belt line and thus least flooded. The sediment was silty and contained high organic content of decomposing seagrass leaves (Fig. 4, A). The second area was the

outer tidal flat (Fig. 2, bright green dots), with sparse seagrass cover (Fig. 4, B). The last sampling area of the tidal flat was the sandbar (Fig. 2, yellow), which is only exposed to air at low spring tide level (Fig. 4 C). Two samples were taken in channels; both are located on the tidal flat but are permanently flooded (Fig. 2, purple).

Subtidal samples were collected in three different areas. Seven samples were taken in front of the sand bar of the tidal flat in water depth of 30 to 100 cm (Fig. 2, red dots). Sediment there was sandy and at a water depth of about 30 cm below the spring tide line there were meadows of *Zostera marina*. Another four samples were collected on the sand ridge in the estuary of the Isonzo at a water depth of about 100 cm (Fig. 3, dark blue dots) and five in seagrass meadows of the delta at water depth of about 250 cm (Fig. 3, bright blue dots; Fig. 4, D).

The positions were recorded by means of global positioning system (GPS).

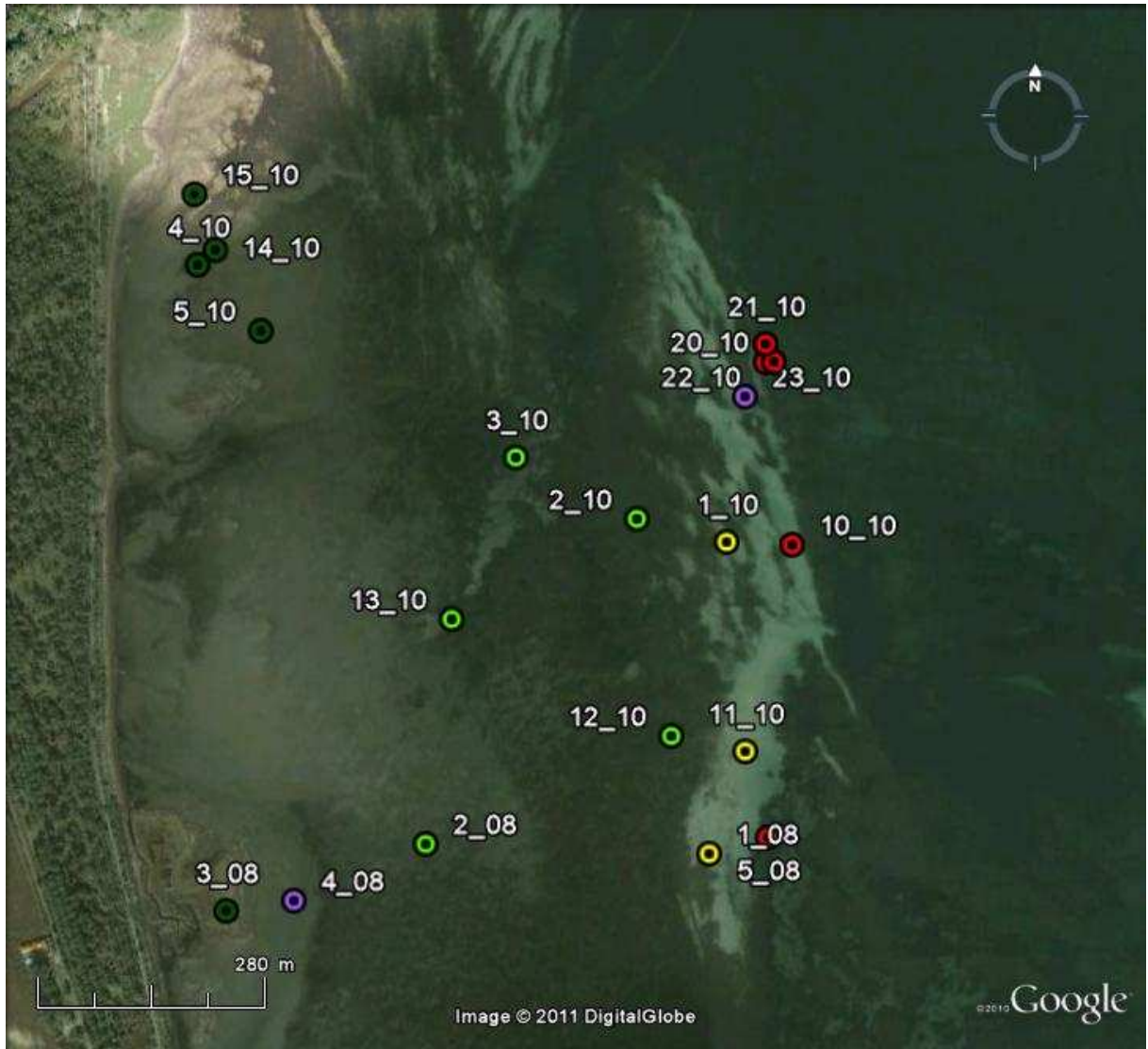


Figure 2. Sample sites on the tidal flat: the inner tidal flat (dark green dots), the outer tidal flat (bright green dots), the channel (purple dots), the sandbar (yellow dots) and in the shallow subtidal zone in front of the sandbar (red dots).



Figure 3. Samples in the delta zone were collected on sand patches inside seagrass meadows (bright blue) and on a sand ridge in front of the river mouth (dark blue).

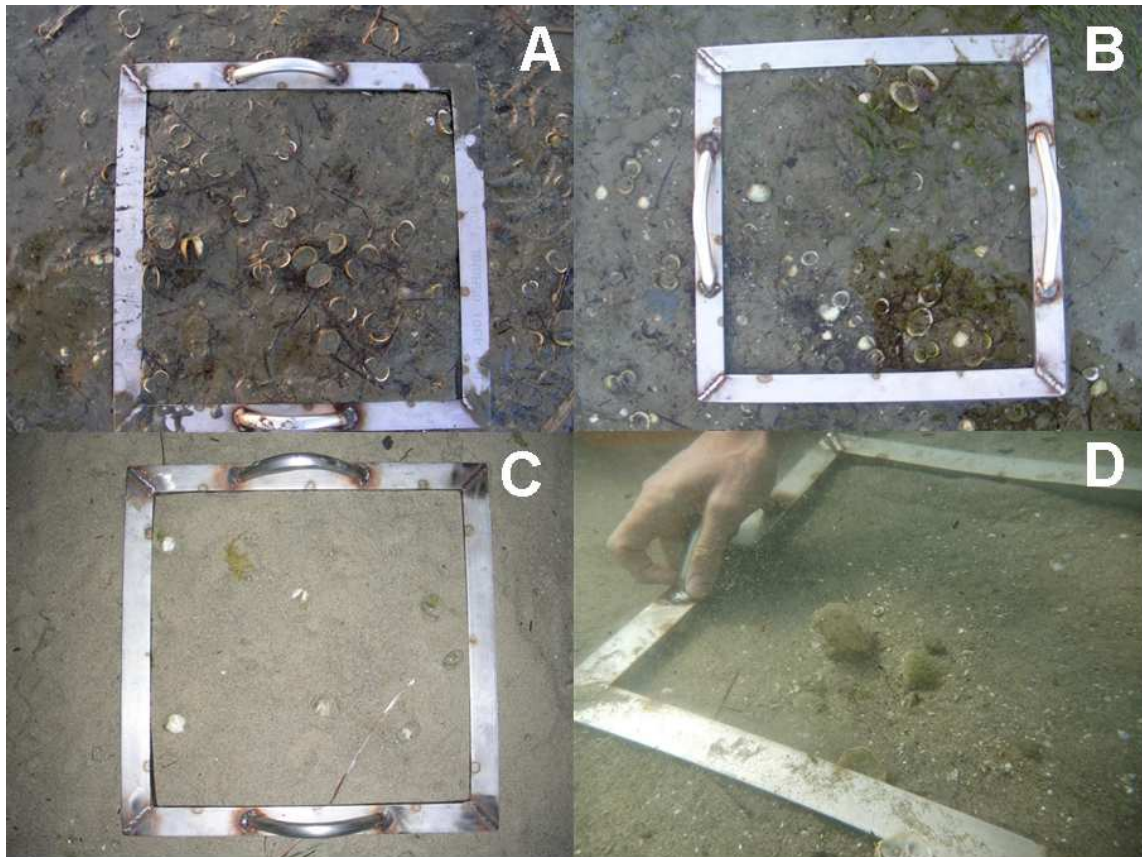


Figure 4. Photographs of sampling: (A) inner tidal flat, (B) outer tidal flat, (C) sandbar, (D) delta.

2.2. Field work

Each sample consisted of 4500 cm³ sediment collected using a 30 cm by 30 cm by 5 cm metal frame which was randomly positioned. At the same day, all sediment was 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).

Gastropods were differentiated in individuals collected alive or as dead shells. It is difficult to determine whether shells of the species *Bittium reticulatum* are inhabited or empty when they are exposed to air. Therefore five small extra samples (unstandardized size of approximately one shovel) were taken in July 2010 on the tidal flat samples sites (see chapter 2.1 for details) and are correspondingly termed 11_10a, 12_10a, 13_10a, 14_10a and 15_10a in the text. The gastropods were examined in small bowls of sample water. Living individuals started moving after short while and were then separated from the dead and dried for further work.

Bivalves were separated into three categories: first, individuals collected alive, second, shells which were empty, but still articulated by the ligament and third, single valves.

In samples which contained living molluscs, I measured all categories of the respective species. The applied number of size-classes depended on the size variation of each taxon. Taxa showing large size variations were given more size-classes than those with a low variation. Measurements were taken with a vernier calliper to 0.01 mm (gastropods spire to the base of the operculum, and bivalves anterior-posterior axis and dorsal-ventral axis).

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.

2.3. Statistical analysis

Statistical analysis was performed with Microsoft Excel and the package Past (Hammer et al., 2001).

Diversity was estimated as species richness, comparing the total number of species and individuals per sample. Additionally diversity indices were calculated to reduce the multispecies complexity of assemblage data into a single index. The Shannon-Wiener index is affected by species in the middle of the rank sequence of species (at base of 10 [$H' = - \sum_i p_i \log (p_i)$; p_i is the proportion of the total count arising from the i th species];). The Simpson index [$1-D = 1-(\sum p_i^2)$] is affected by the 2-3 most abundant species and the Margalef index does not assess the relative dominances of the species [$d = (S-1) / \log N$, in which S = number of species and N = number of individuals] (Magurran, 2004).

Rarefaction is a technique to compare species richness computed from samples of different size and allows the construction of rarefaction curves. Number of individuals is plotted on the x-axis against number of species on the y-axis. The sample sizes may differ widely between stations, but the relevant sections of the curves can still be compared (Magurran, 2004).

Cluster analysis sorts through the raw data and groups them into clusters and demonstrates the similarity of the samples to each other. Objects in a cluster are similar to each other and dissimilar to objects outside the cluster, particularly objects in other clusters (Clarke and Warwick, 2001). For the cluster analysis the Bray-Curtis index was used.

For non-metrical multidimensional scaling (nMDS) all pair wise distances among samples were calculated with the Bray-Curtis distance measure. nMDS uses non-metric algorithms, respecting only the relative ordering of the input dissimilarities (Clarke and Warwick, 2001). The MDS ordination was performed on a 2 dimensions distance matrix. The goodness of fit is called stress and was calculated with the Kruskal's method (Clarke and Warwick, 2001). Results of cluster analyses were superimposed on the nMDS-figures, as the two methods complement each other.

Number of individuals per sample was highly variable; therefore data for non-metric multidimensional scaling (nMDS) and cluster analysis was standardized (i.e., percentages were used)

and square root transformed to deemphasize the importance of the most important species (Clarke and Warwick, 2001). Diversity indices and individual rarefaction were calculated with the original data.

A comparison of shell size was performed only in samples with more than three individuals of both living and dead shells. Double-valved empty shells were treated as dead animals.

Dependent on the size range of a species up to six size classes were used to describe the size-distribution of living and dead molluscs.

Normal distribution of the size of living and dead shells was rejected; therefore Man-Whitney U-Test was used for statistical comparison. This is a non-parametric statistical test and does not assume a normal distribution.

3. Results

3.1. Physical conditions

Physical parameters were measured only once per location, to get insight into abiotic conditions. Measurements were made in the early morning hours on the tidal flat and in the afternoon in the delta waters.

Temperature ranged from 22.4 °C to 24.4 °C in the tidal flat (Fig. 5, A). Subtidal water was warmer and ranged between 25.4 °C to 26.3 °C: the temperature of the water at the surface of the Isonzo River was 23.3 °C (Fig. 5, B).

pH in the intertidal ranged from 7.51 to 7.83 (Fig. 5, A), in the subtidal the pH was more alkaline and ranged from 8.18 to 8.41 (Fig. 5, B).

Salinity increased from about 20 psu in the inner tidal flat up to 24 on the sandbar (Fig. 5, C). The water in the estuary is stratified; water close to the bottom is more saline than surface waters (Fig 5, D).

Oxygen content of the tidal samples ranged from 1.06 to 3.33 mg/l (Fig. 5, C). In contrast, the subtidal samples contained higher oxygen levels from 6.4mg/l to 7.99mg/l (Fig. 5, D).

Altogether the intertidal and the subtidal habitats differ in each of the four measured parameters, whereas fluctuations of temperature, pH, salinity and oxygen content are stronger in the intertidal.

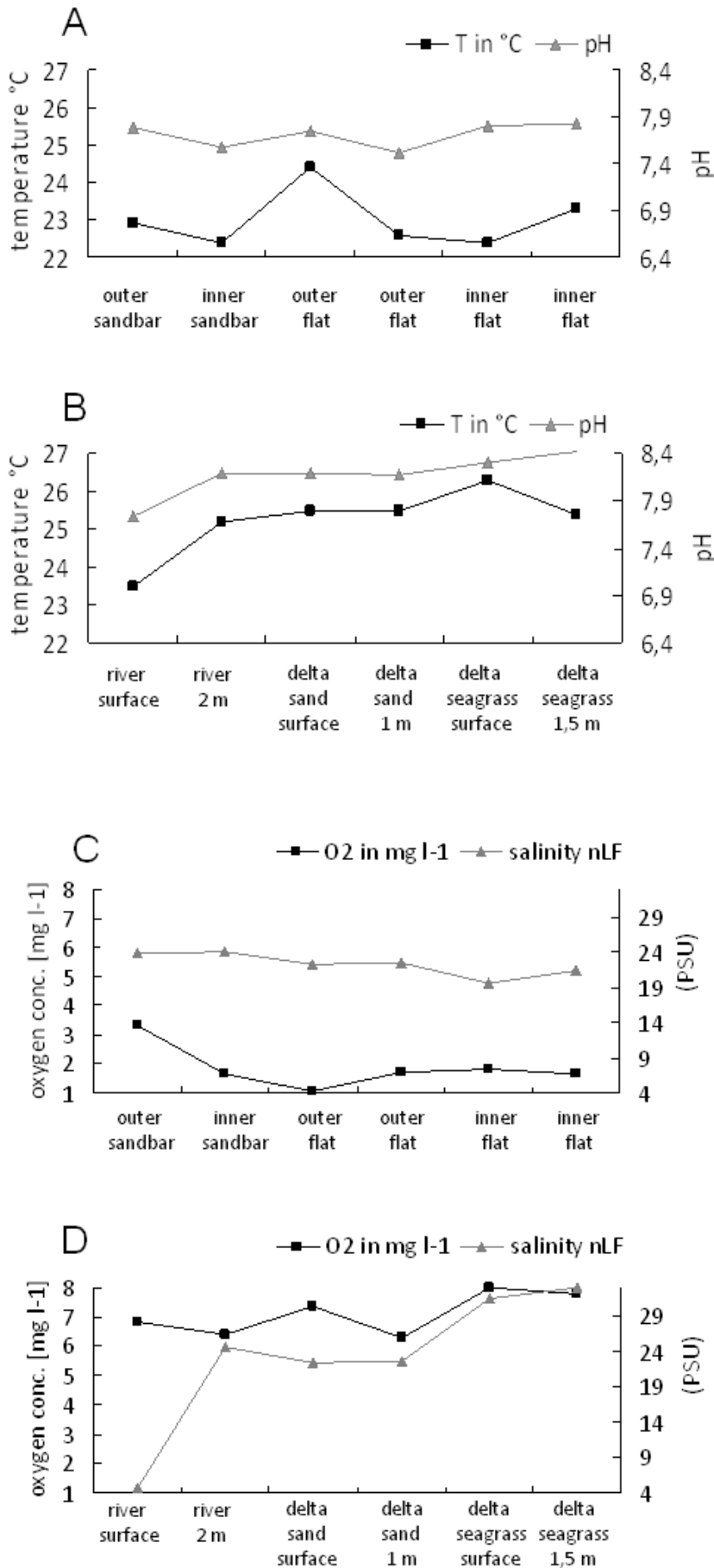


Figure 5. Measurements of physical factors in the intertidal flat (A, C) and different water depth of subtidal locations (B, D). Temperature, pH, oxygen levels and salinity are higher in the subtidal samples. The samples from deeper water show higher salinity than surface water (D).

3.2. Basic structure of the molluscan assemblages

A total of 24,922 complete individual molluscs (calculated from articulated and disarticulated bivalves, gastropods and scaphopods) were collected in fifteen intertidal and fourteen subtidal samples and identified to species level. These shells represent 83 species from 33 families. Only 1162 (5%) of all shells were collected alive. The proportion of dead shells is overestimated because the abundant gastropods *Bittium reticulatum* and *Rissoa labiosa* were all counted as dead, as detection of living individuals was impossible for us in the dried state. Excluding *R. labiosa* and *B. reticulatum* the proportion of shells collected alive is 20 %.

In the extra tidal flat samples (11_10a, 12_10a, 13_10a, 14_10a, 15_10a) a total of 616 *B. reticulatum* was counted. Living *B. reticulatum* were found only in one outer and one inner flat sample (see chapter 3.8) and the percentage of living shells in the total of these five samples was 23 % (range from 0 to 38 %).

3.3. Abundances of species

For each tidal and subtidal region the six most abundant species are shown as percentage of the total of molluscs of each sample.

In the **inner tidal flat** the most abundant species were the gastropods *B. reticulatum* and *R. labiosa*, and the bivalves *Scrobicularia plana* and *Cerastoderma glaucum*, all other species made up less than 10 % in the samples (Fig. 6, A).

In the **outer tidal flat** samples the abundance of *B. reticulatum* is striking, *R. labiosa*, *C. glaucum* and *Loripes lacteus* were found frequently but other species were rare (Fig. 6, B).

On the **sandbar** there was no trend of single dominant species, but the composition of abundant species is heterogeneous between the samples (Fig. 6, C). Abundant species on the sandbar were *B. reticulatum*, and the bivalves *C. gallina*, *C. glaucum*, *T. tenuis*, *L. mediterraneum*, *L. lacteus*.

The two **channel** samples did not contain percentages of more than 32 % of one single species (Fig. 7, A). *B. reticulatum*, *Chamelea gallina*, *Lentidium mediterraneum*, *Tellina tenuis*, *L. lacteus* and *R. labiosa* were abundant, and the percentage of species summed up as “others” is in both samples rather high.

In the **shallow subtidal** in front of the tidal flat abundances of species varied between the samples, but *B. reticulatum*, *C. gallina* were common (Fig. 7, B) *C. glaucum*, *R. labiosa* and *T. tenuis* showed high abundances only in single samples, but the amount of “other” species ranged from 12 % to 30 %.

The samples taken in **seagrass-covered delta** sediments contained *B. reticulatum*, *C. gallina* and *L. mediterraneum*, but the amount of “others” is highest in this environment, making up more than 20% in each of the four samples (Fig. 7, C).

In the **delta sand** the most abundant species was *L. mediterraneum*, making up 30 % to 83 % of the individuals, whereas the amount of other species varied between the samples (Fig. 8).

In general, the composition of the total of shells in the intertidal samples was dominated by few highly abundant species whereas in the subtidal several species showed high percentages.

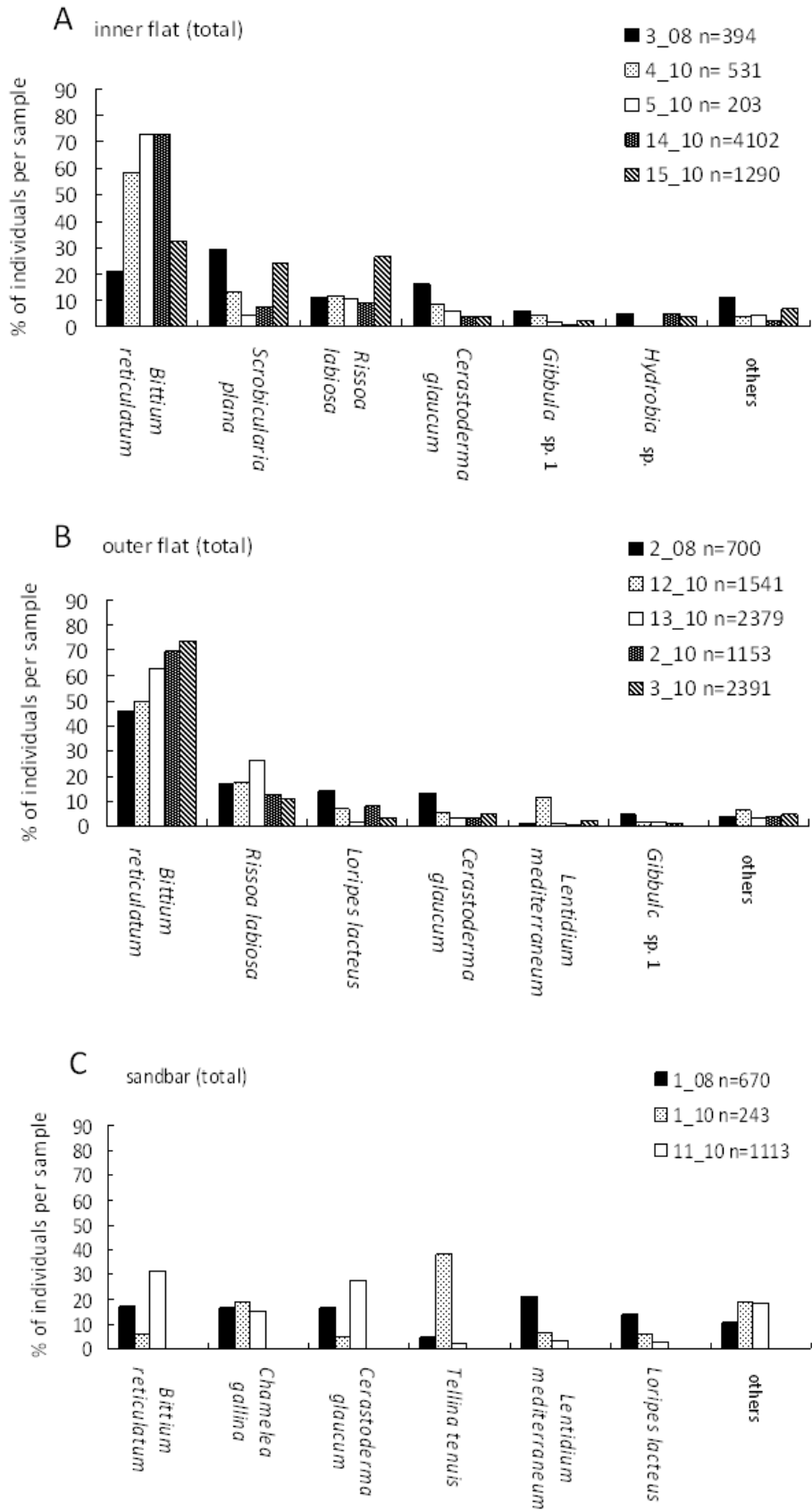


Figure 6. Percentage abundances of the six most frequent species of the intertidal zones: (A) inner tidal flat, (B) outer tidal flat, (C) sandbar.

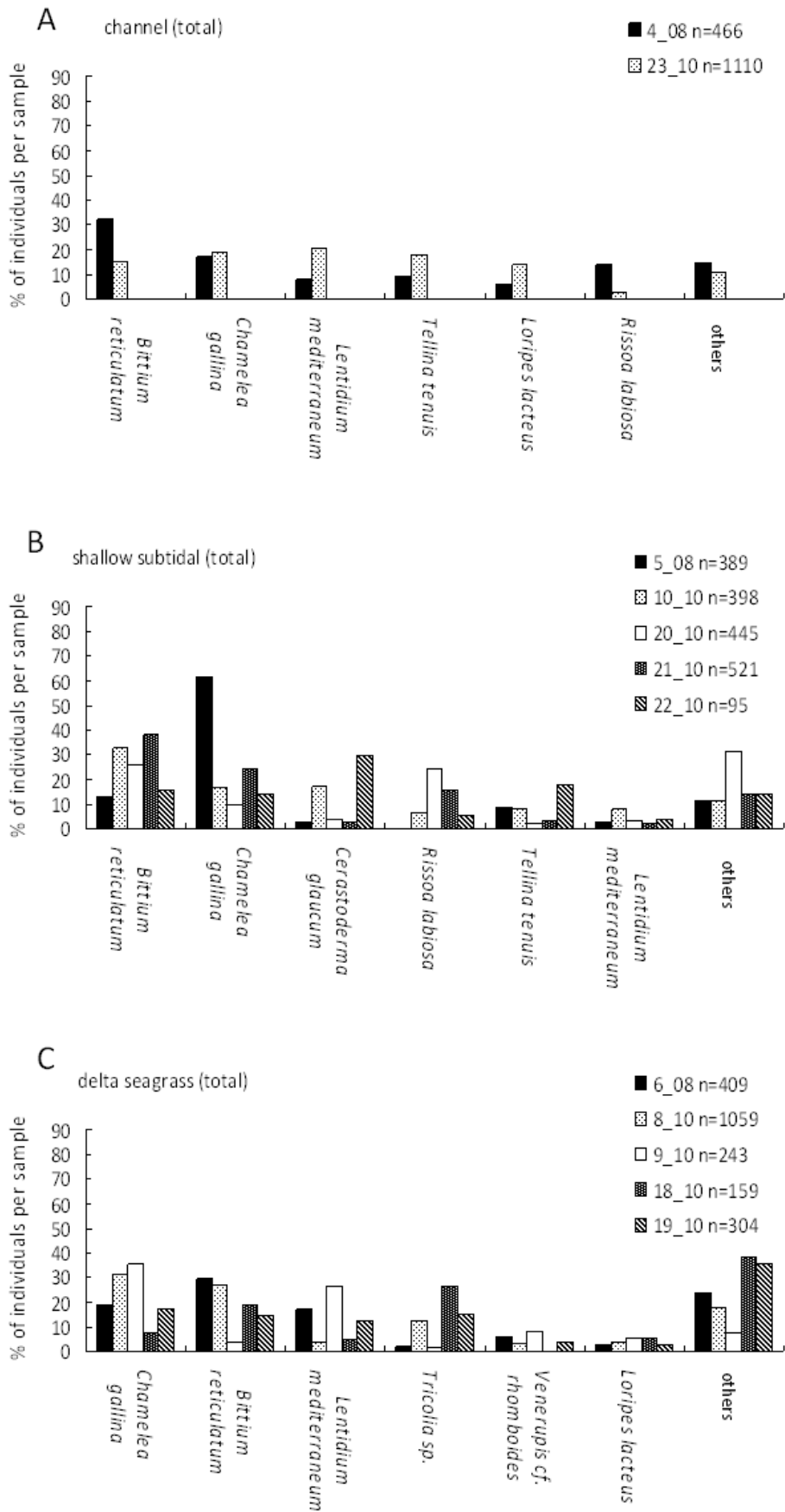


Figure 7. Percentage abundances of the six most frequent species of (A) channel, (B) shallow subtidal, (C) delta seagrass.

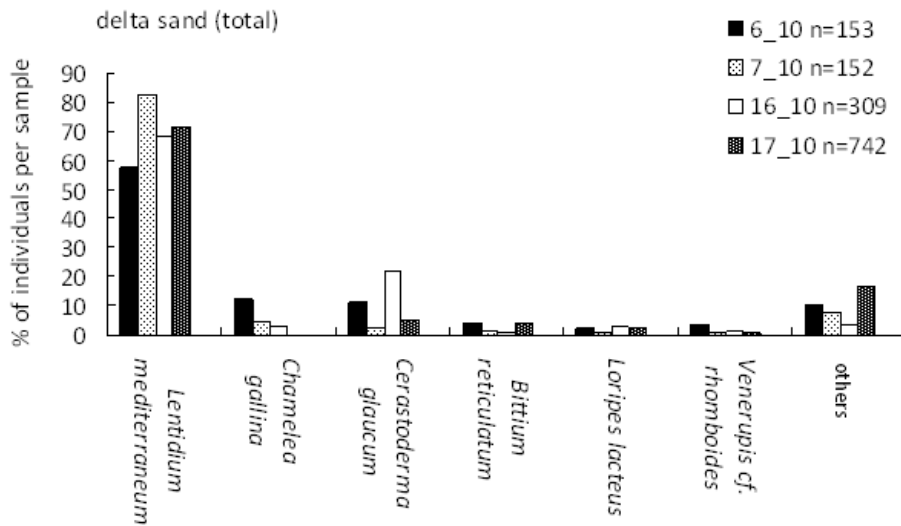


Figure 8. Abundances of the six most frequent species of the delta sand. Total of individuals (n) is 100% in each sample (different pattern).

3.4. Diversity

3.4.1. Diversity of the total assemblage

3.4.1.1. Environments

Diversity indices for the seven environments were calculated for the total of shells and show that the molluscan fauna in the inner and outer flat and in the delta sand have low evenness in contrast to the delta seagrass (Fig. 9), which were dominated by few species (Fig. 10).

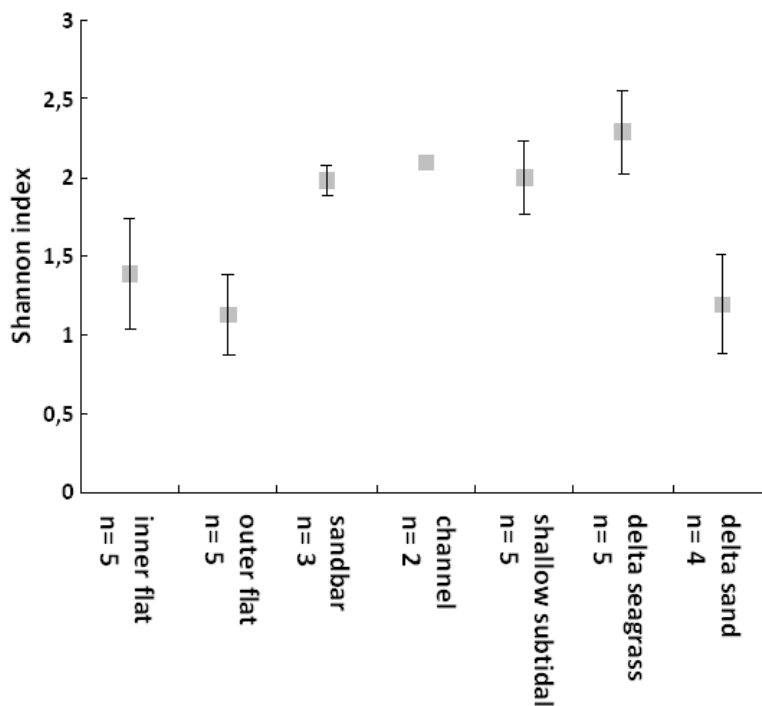


Figure 9. Shannon diversity and 95% confidence intervals for the total of shells in the different environments. Molluscan fauna in the inner and outer flat and in the delta sand shows low diversity.

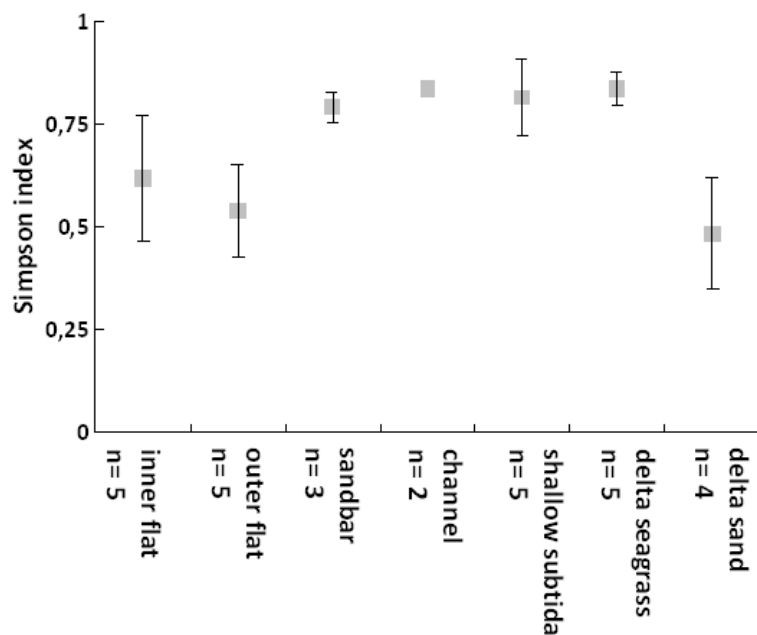


Figure 10. Simpson diversity (D-1) and 95% confidence intervals for the seven environments (total of shells). Inner and outer flat and delta sand are dominated by few species.

3.4.1.2. Samples

In a first step, diversity in the individual samples is illustrated as the number of species, compared to the number of individuals. High number of species paired with low numbers of individuals suggests high diversity. Lowest number of species per sample was 12 in a shallow subtidal sample in front of the sandbar; the highest number was 32 in a delta seagrass sample (Fig. 11). 4012 individuals were found in one inner tidal sample, of which almost three quarters belonged to one gastropod species, *B. reticulatum*.

Intertidal samples contained significantly (mean= 1364, SE= 276; $p= 0.0028$) more shells than the subtidal (mean=384, SE= 75). Species richness was similar in both habitats (intertidal: mean= 19, SE= 1; subtidal: mean= 22, SE= 2).

Diversity indices were used to reduce the complexity of assemblage data into a single index (Fig. 12). The Margalef index does not assess the relative dominances of the species, and therefore the curve is quite similar to the number of species in Fig. 11, showing high diversity in samples with high number of species.

The Shannon diversity is highest in the seagrass-covered subtidal areas, indicating high evenness. In contrast it is variable in the intertidal and delta sand samples.

Another commonly used measure is the Simpson index (here given as 1-D). It is low in intertidal and sandy subtidal samples, indicating strong dominance of a few species. In contrast, the Simpson index of the sandbar, shallow subtidal and delta seagrass samples is high around 0.8, indicating low dominance.

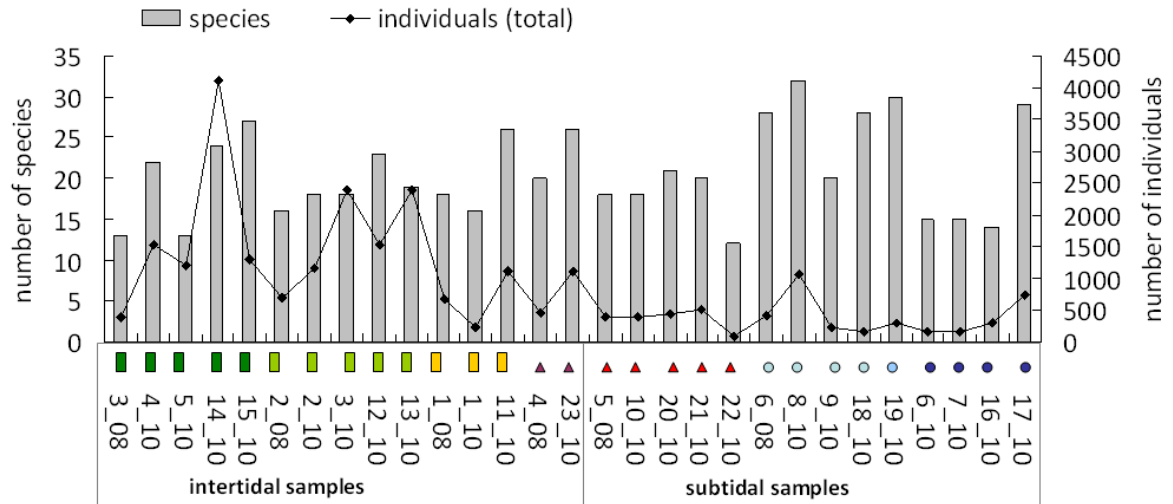


Figure 11. Overview diversity (total). Number of species compared to the number of individuals per sample. Sampling zones are illustrated in the x-axis with colours of the maps in Fig. 2 and Fig. 3. Low number of individuals paired with high number of species suggests high diversity. Tidal flat samples generally show higher numbers of individuals per sample but have fewer species than subtidal samples.

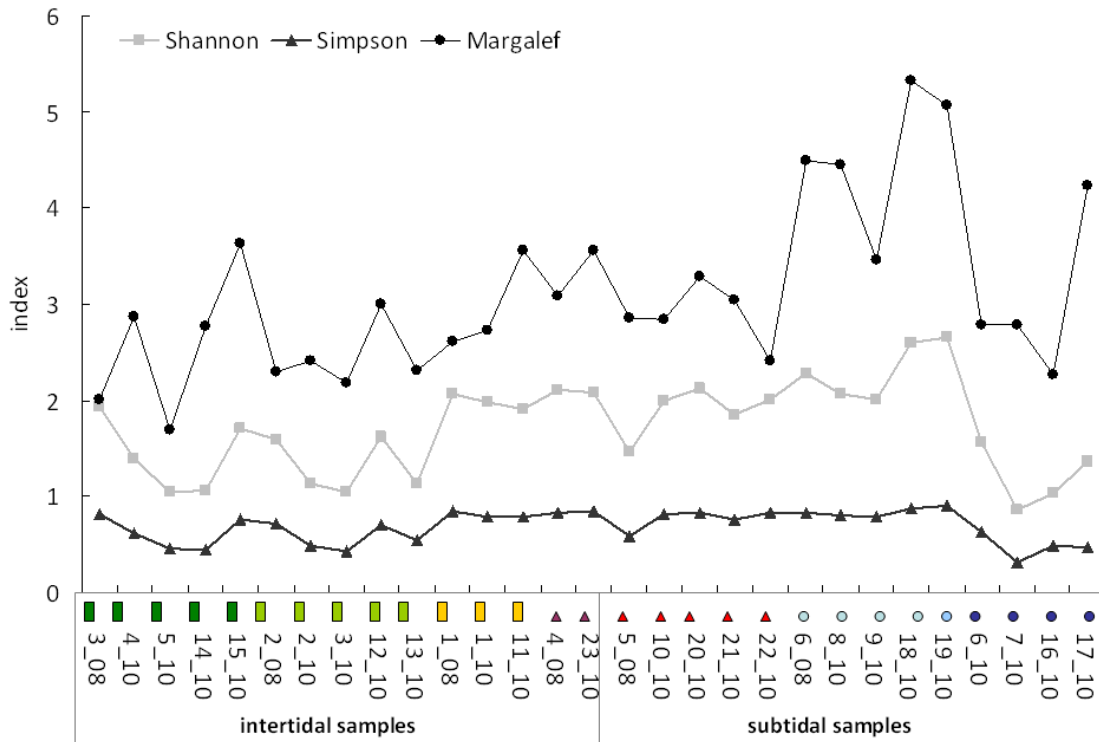


Figure 12. Shannon-, Simpson- and Margalef- index of the total of shells in all samples. Diversity is higher in the subtidal than in the intertidal samples. Simpson (1-D) index shows high dominance of few species in the outer (dark green) and inner (bright green) tidal flat and in the delta sand (dark blue). Sampling zones are illustrated in the x-axis with colours of the maps in Fig. 2 and Fig. 3.

3.4.2. Diversity of the living assemblage

3.4.2.1. Environments

Diversity indices for the seven environments were calculated for the living shells and show that the molluscan fauna in the outer flat sandbar and channel have high evenness in contrast to the inner flat, shallow subtidal, delta seagrass and delta sand (Fig. 13), which were dominated by few species (Fig. 14).

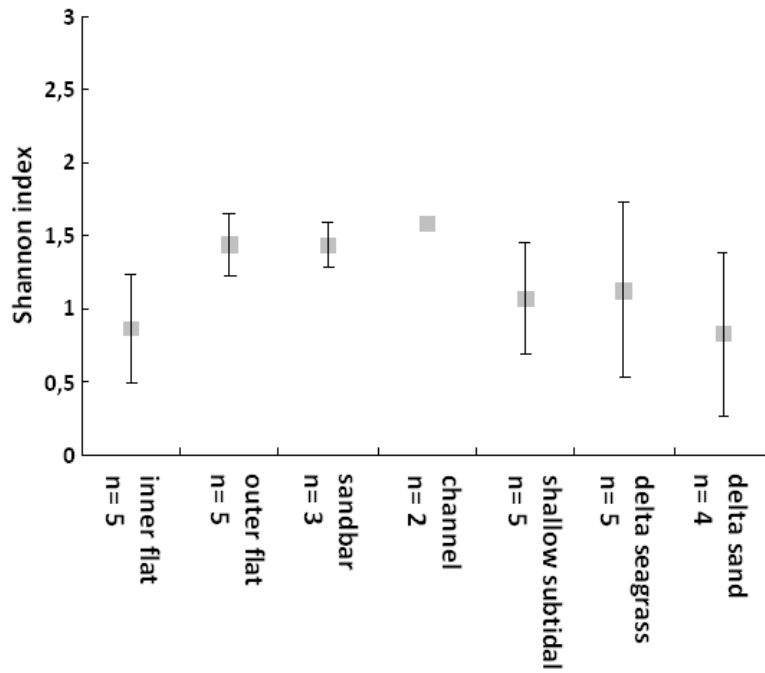


Figure 13. Shannon diversity and 95% confidence intervals for the living shells in the different environments. Molluscan fauna shows highest diversity in the outer flat, the sandbar and the channel.

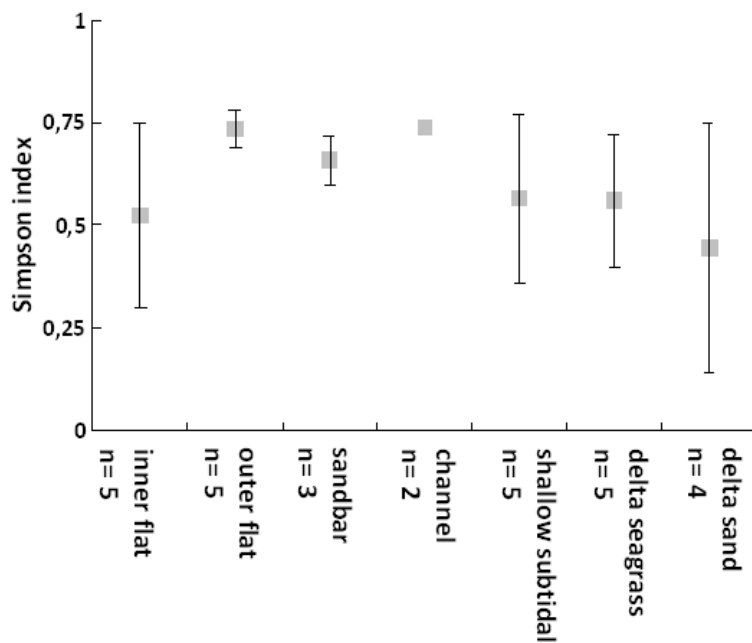


Figure 14. Simpson diversity ($D-1$) and 95% confidence intervals for the seven environments (living shells). Outer flat, sandbar and channel have lower dominance than the other environments. Note the wide confidence intervals, which indicate that differences between environments are largely not statistically significant.

3.4.2.2. Samples

Number of species found alive in the samples ranges between 1 and 12 (Fig. 15). Highest number of individuals per samples was 515, but in most of the samples the number of individuals is less than 100.

Highest number of species was found in one delta seagrass sample and on the sandbar. Number of living individuals was highest in a delta sand sample, which contained high amounts of the small bivalve *L. mediterraneum*.

The diversity indices are not constant, neither in the intertidal nor in the subtidal zones (Fig, 16). In general, the indices of the inner tidal flat and the delta sand samples are lowest.

Highest diversity can be found in the delta seagrass samples, in the sandbar samples and in one channel sample. Diversity of the inner flat, the shallow subtidal and the delta sand are dominated by few species.

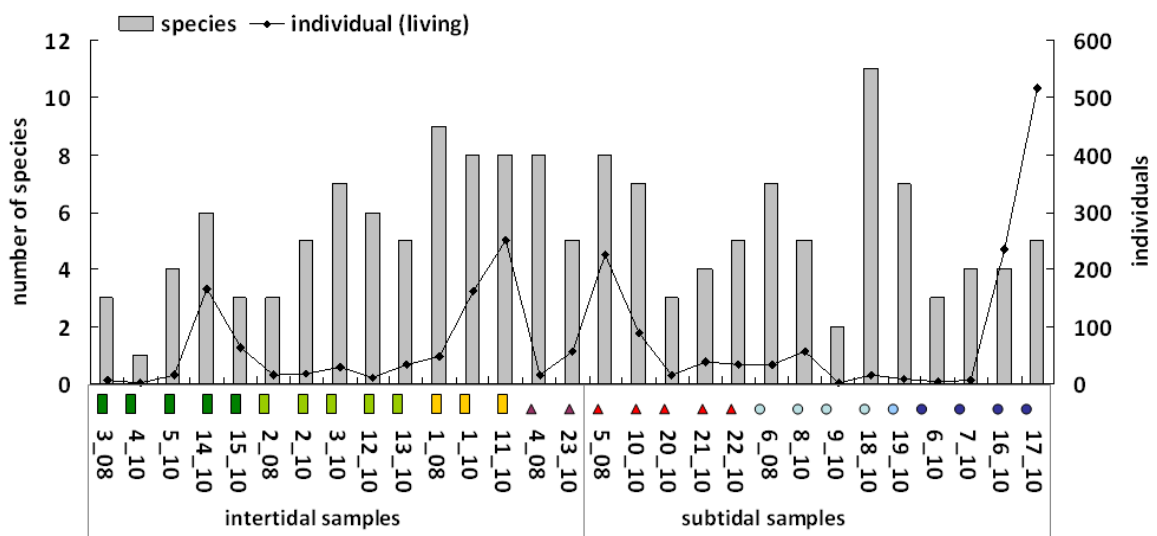


Figure 15. Overview of the diversity in living bivalves and gastropods. Number of species compared to the number of individuals per sample. Low number of individuals paired with high number of species suggests high diversity. Number of species and individuals is variable within the sampling zones. Some samples of the delta seagrass (bright blue) show highest species richness. Sampling zones are illustrated in the x-axis with colours of the maps in Fig. 2 and Fig. 3.

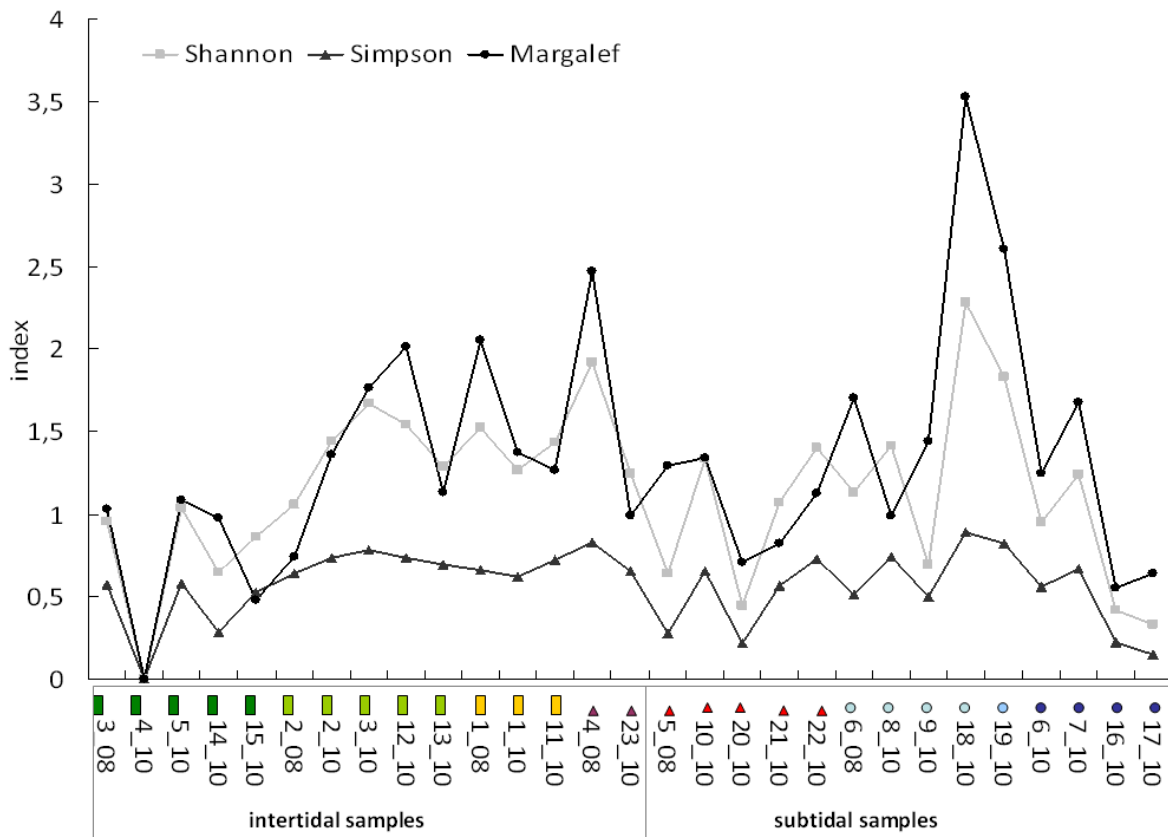


Figure 16. Shannon-, Simpson-, and Margalef indices of the living molluscs. All indices show low diversity in the inner tidal (dark green). High diversity is found in the delta seagrass samples (bright blue) and some of the outer tidal (bright green) and sandbar samples (yellow). Sampling zones are illustrated in the x-axis with colours of the maps in Fig. 2 and Fig. 3.

3.4.3. Diversity of the dead shells

3.4.3.1. Environments

Diversity indices for the seven environments were calculated for the dead shells and show that the molluscan fauna in the inner flat, outer flat and delta sand have low evenness in contrast to remaining samples (Fig. 17), which were dominated by few species (Fig. 18).

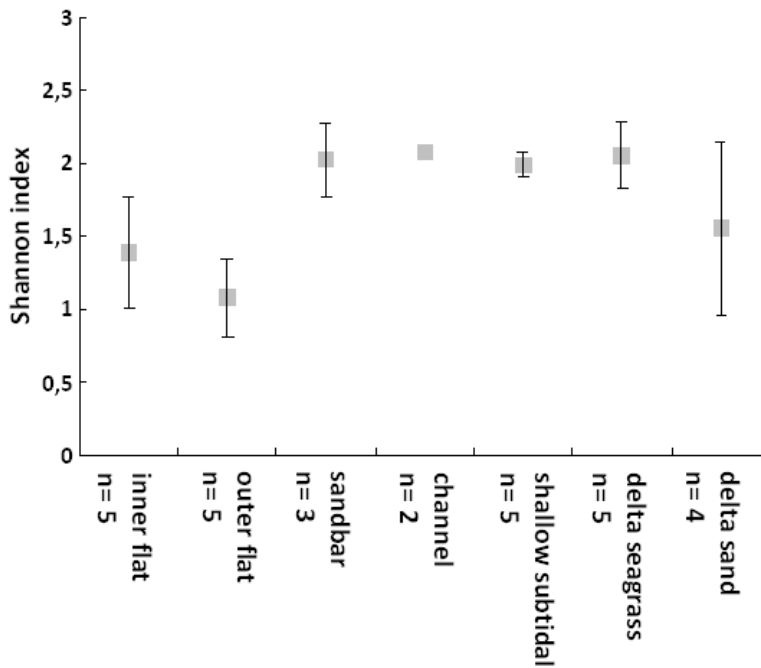


Figure 17. Shannon diversity and 95% confidence intervals for the dead shells in the different environments. Molluscan fauna in the inner and outer flat and in the delta sand shows lowest diversity

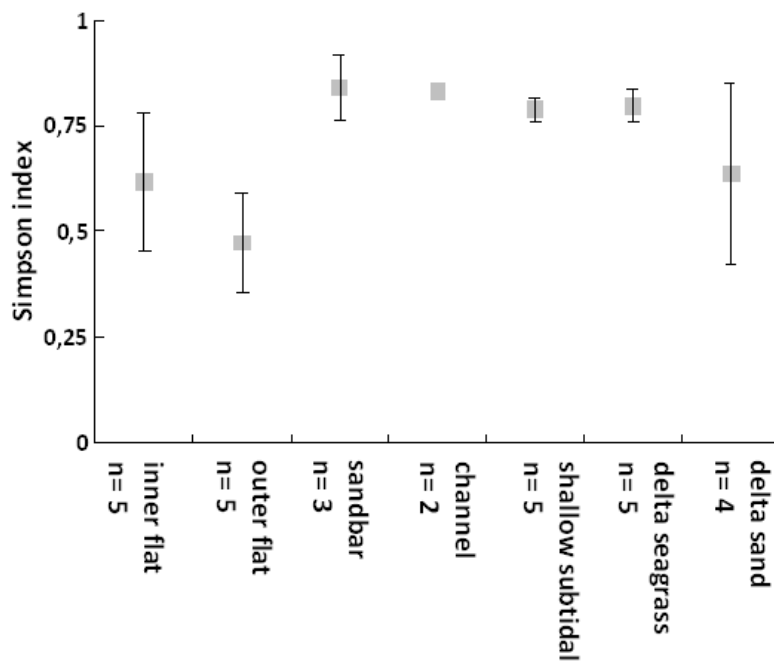


Figure 18. Simpson diversity ($D-1$) and 95% confidence intervals for the seven environments (dead shells). Inner and outer flat and delta sand are dominated by few species.

3.4.3.2. Samples

Low number of individuals paired with high number of species suggests high diversity in the subtidal and lower diversity in the intertidal samples (Fig. 19) and resembles diversity of the total of shells (compare Fig. 11). This is similar to diversity indices (Fig. 20, compare Fig. 12), with exception of the Simpson index, which remains rather constant in all samples.

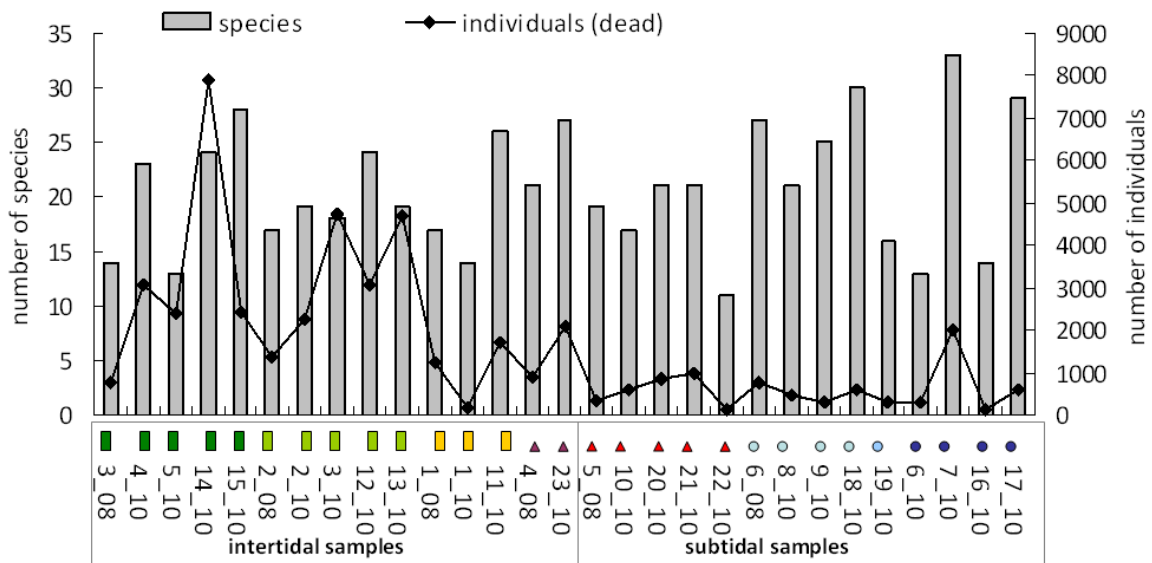


Figure 19. Overview of the diversity in dead bivalves and gastropods. Low number of individuals paired with high number of species suggests high diversity in the subtidal and lower diversity in the intertidal samples. Sampling zones are illustrated in the x-axis with colours of the maps in Fig. 2 and Fig. 3.

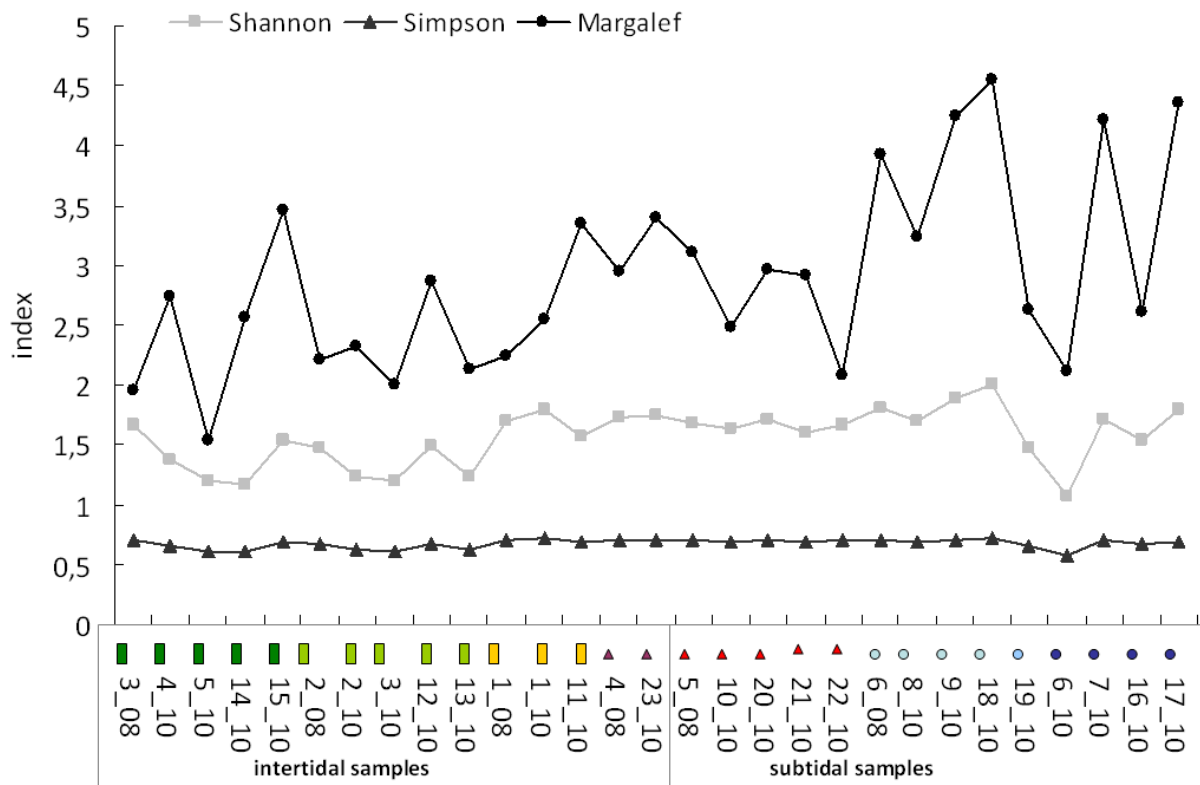


Figure 20. Diversity indices of the dead shells. Shannon and Margalef indices resemble the diagram of the total of shells (see Fig. 12), but the Simpson index is rather constant in all samples. Sampling zones are illustrated in the x-axis with colours of the maps in Fig. 2 and Fig. 3.

3.5. Rarefaction curves

3.5.1. Rarefaction curves (total)

Figure 21 shows the rarefaction curves of the total of shells. Delta sample curves (bright and dark blue) have a steep slope, indicating a diverse community in which a large fraction of the species diversity remains to be discovered. Curves of the tidal flat (dark and bright green) have a shallower slope, suggesting that diversity is low, but a reasonable number of species were already sampled. Curves of the channel (purple) and the sandbar (yellow) are steeper than the tidal flat samples, but flatter than the subtidal samples curves. Similar to the latter more intense sampling is likely to yield additional species.

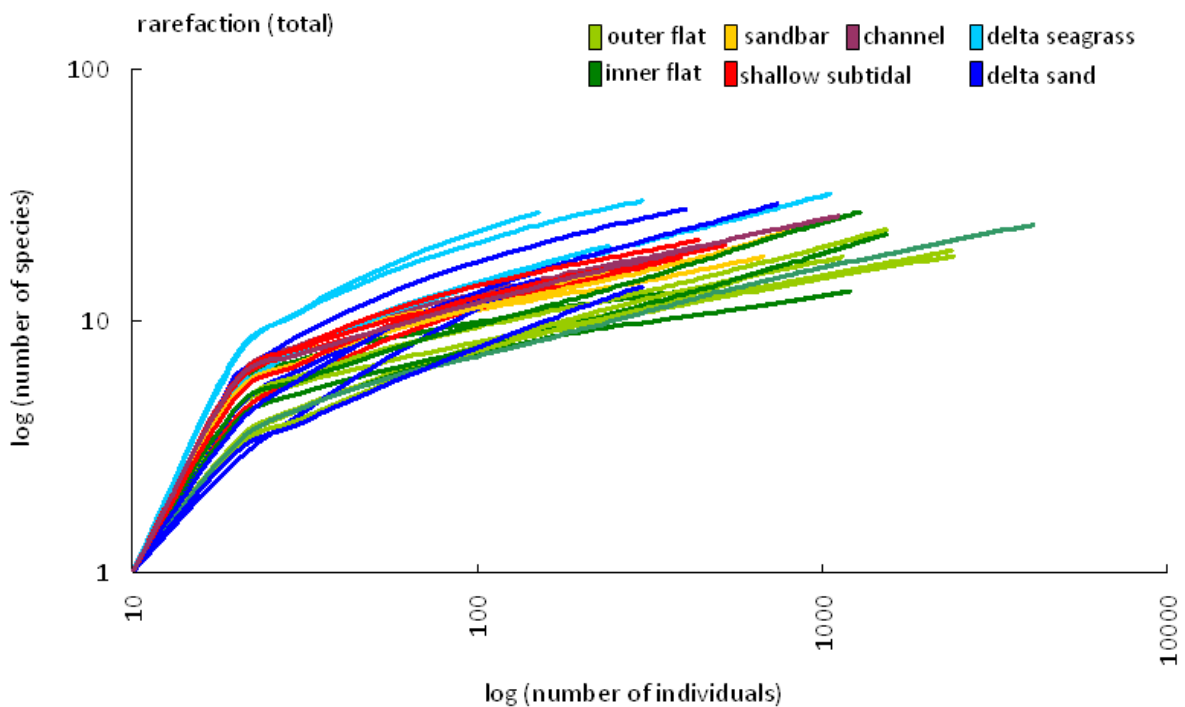


Figure 21. Rarefaction curves of the total of shells. Delta samples (bright and dark blue lines) have the steepest slopes, whereas tidal flat samples have the shallowest slopes (dark and bright green lines). Samples of the sandbar (yellow) and the shallow subtidal (red) are intermediate.

3.5.2. Rarefaction curves (living)

Figure 22 shows the rarefaction curves of the living shells. It is important to consider the low number of living individuals in the samples, compared to the total of shells. Diversity is low in the channel (purple), in the shallow subtidal (red) and on the sand bar (yellow). Some of the delta samples (dark and bright blue) level off, whereas one delta sand and one delta seagrass sample generate the steepest curves in the figure. Strikingly, only one of the intertidal samples (dark and bright green) is flat, but all others are steep and suggest that species diversity in this area is higher than suggested by the number of living shells sampled.

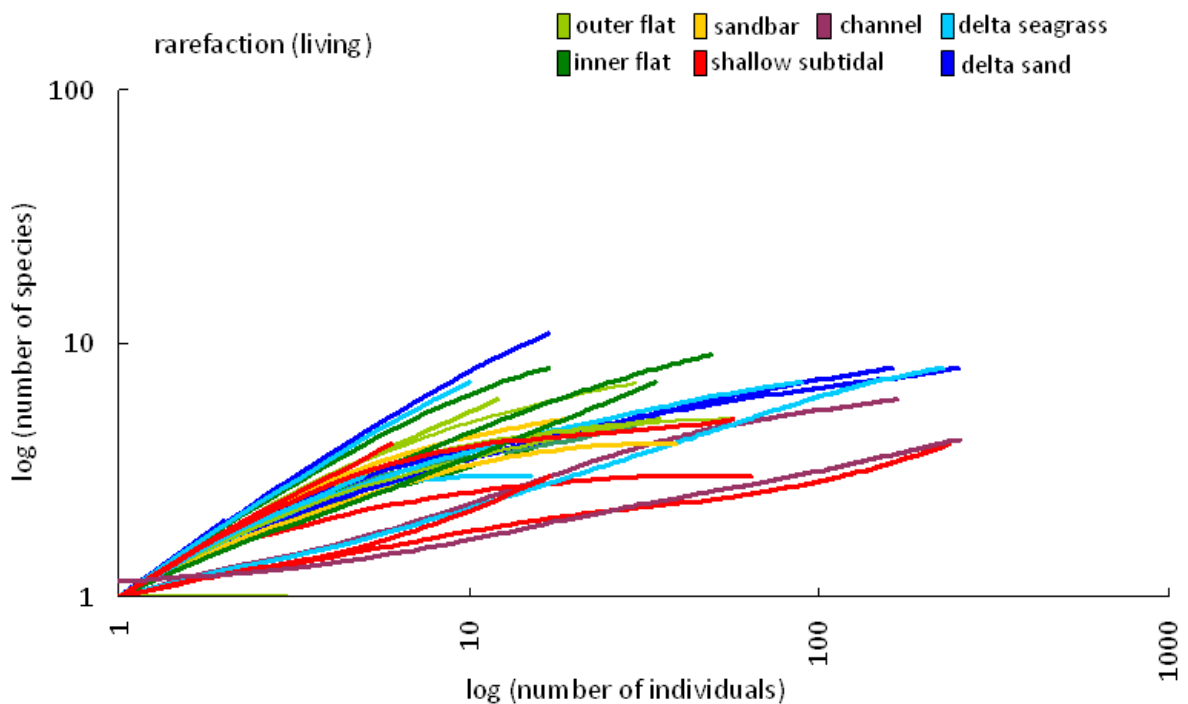


Figure 22. Rarefaction curves of the living shells. Some of the delta samples (dark and bright blue) have shallow slopes, whereas other samples from this area have the steepest curves in the figure. The shallowest slopes are from samples of the channel (purple) and the shallow subtidal (red) but also sandbar samples. None of curves from the intertidal samples (dark and bright green) levels off, and most of them are quite steep.

3.5.3. Rarefaction curves (dead)

Rarefaction curves of the dead shells (Fig. 23) are similar to the rarefaction curves of the total of shells (see above).

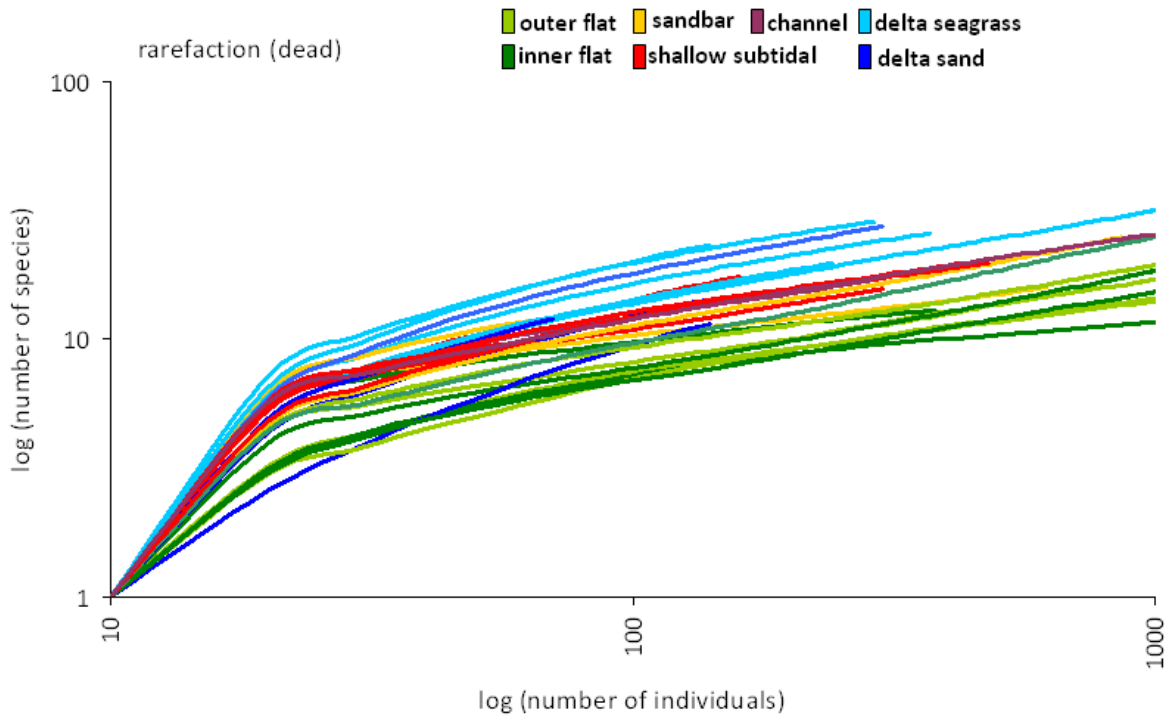


Figure 23. Rarefaction curves of dead shells. Delta curves are steep, whereas tidal flat curves are shallow and level off, slopes of the sandbar, channel and shallow subtidal are intermediate.

3.6. Clusteranalysis

3.6.1. Clusteranalysis (total)

Concerning the total of shells, two major clusters are present at a similarity level of 0.5 (Fig. 24). Samples of the sandbar, the channel, the shallow subtidal in front of the tidal flat and the delta seagrass zone fuse to one cluster. All inner and outer tidal flat samples have high similarity with each other and both areas form distinct site groups within the second cluster. However, the four samples collected in the delta sand are heterogeneous, because they do not link together until quite low levels of between-group similarities are reached.

3.6.2. Clusteranalysis (living)

The dendrogram of the living shells (Fig. 25) contains four clusters at a similarity level of 0.25. The largest cluster is dominated by subtidal samples. It combines all sandbar, channel and shallow subtidal samples, four of five delta seagrass samples and also one outer tidal flat sample. Within the cluster, however, the sandbar and shallow subtidal samples show higher levels of similarity than the delta seagrass samples. The second cluster combines all inner and all the rest of the outer tidal flat samples. The outer tidal flat samples form a distinct site within this cluster. The samples of the delta sand and also one of the delta seagrass samples are outstanding, forming two discrete clusters.

3.6.3. Clusteranalysis (dead)

The cluster analysis of the dead shells (Fig. 26) is very similar to that of the total of shells. At the similarity level of 0.5 the samples of the tidal flat build one cluster; inner tidal samples seem to have the highest similarity. Samples of the sandbar, channel, shallow subtidal, delta seagrass and one of delta sand are combined in a large cluster. Remaining samples of the delta sand and one sample of the delta seagrass are quite distinct.

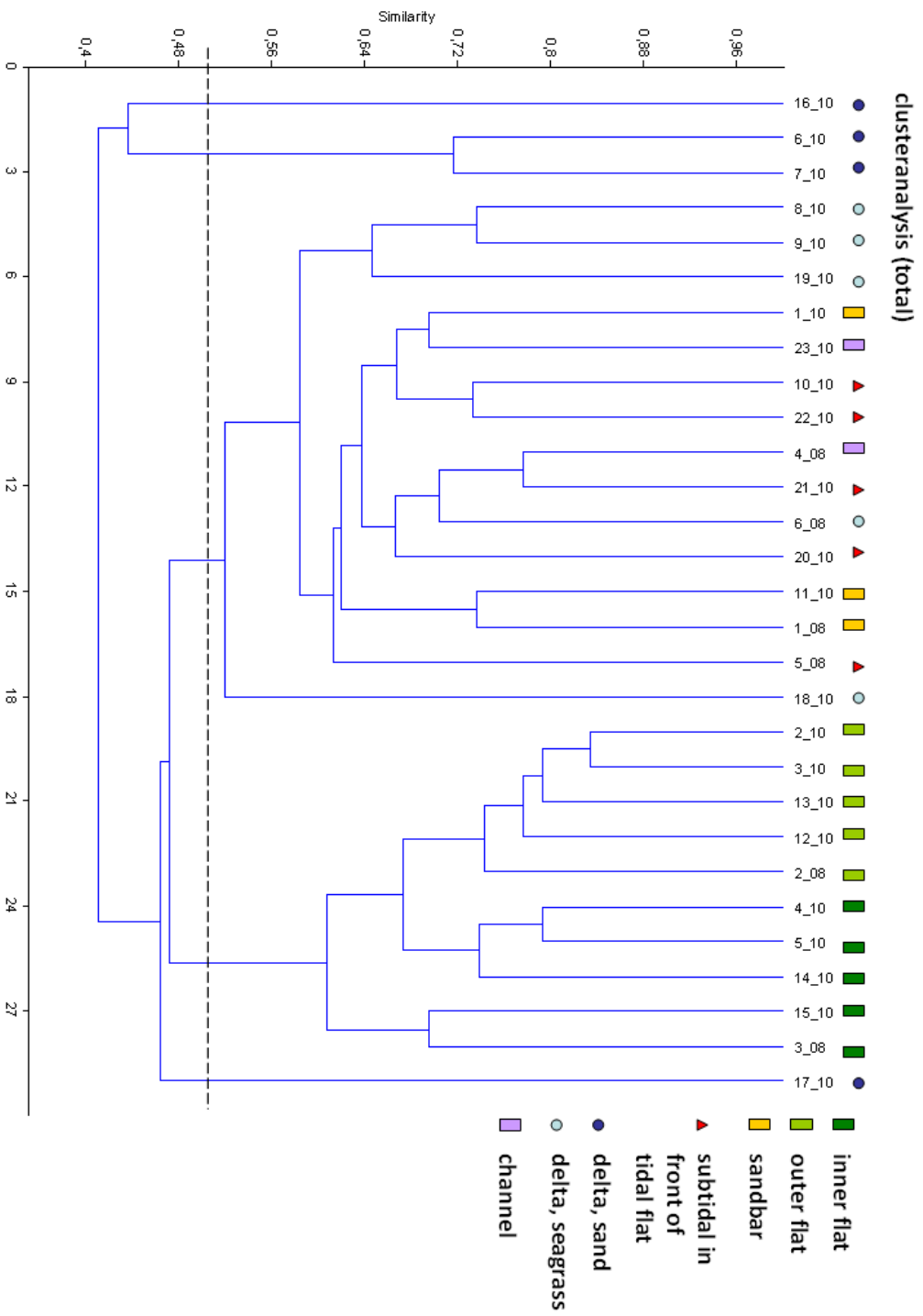


Figure 24. Cluster analysis of the total number of shells based on the Bray-Curtis similarity index. The x-axis represents the set of samples and the y-axis the similarity level. At a level of 0.5 the dendrogram contains two main clusters and a few outliers. Sandbar, channel, shallow subtidal and delta seagrass samples fuse to a large cluster. The inner and outer tidal flats plot together, whereas the delta sand samples do not link together until low similarity levels.

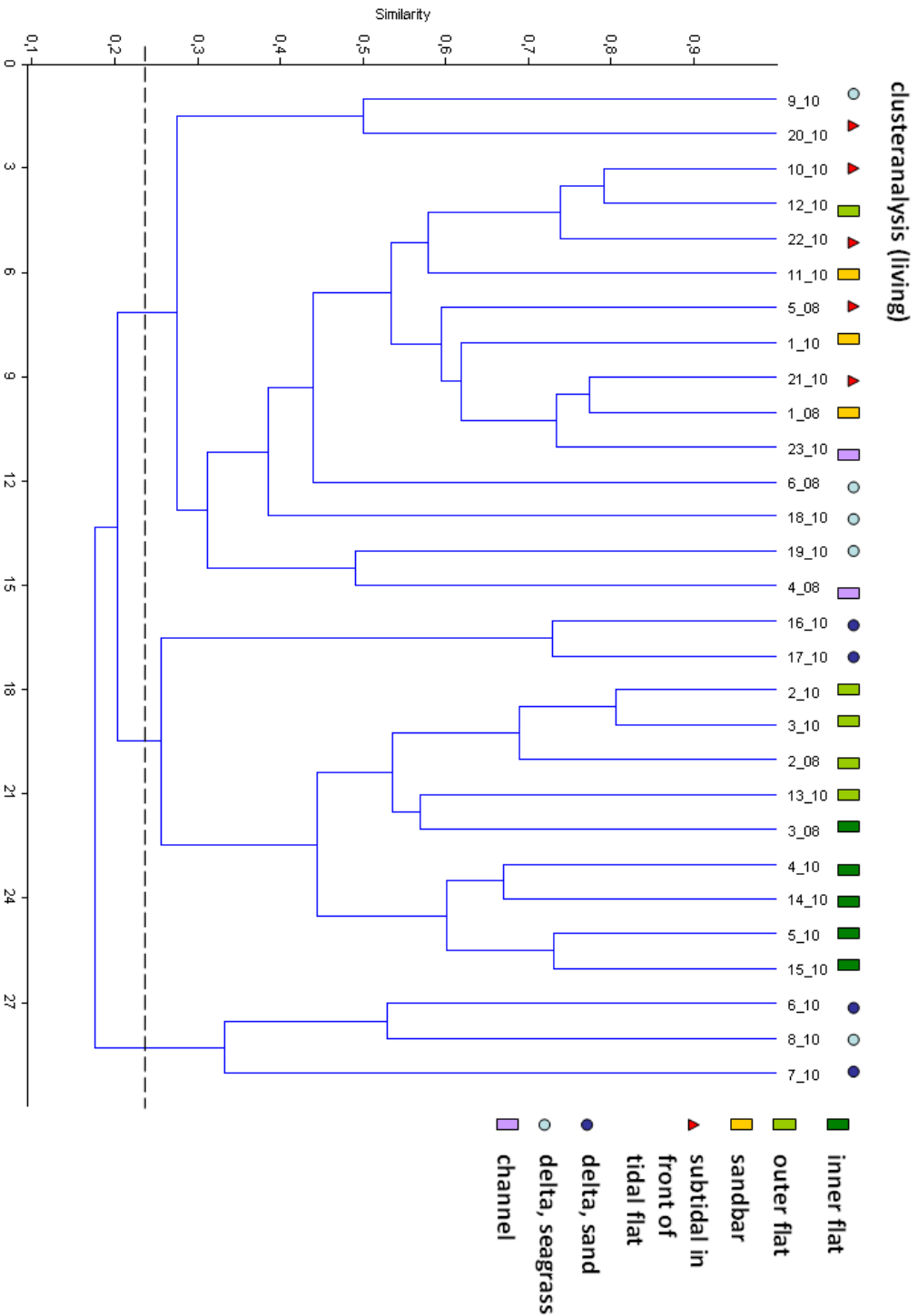


Figure 25. Cluster analysis of living shells based on the Bray-Curtis similarity index. Three clusters are formed at the similarity level of 0.25. One cluster contains nine out of ten inner and outer tidal flat samples. Another big cluster contains all sandbar-, channel and shallow subtidal samples. Delta sand samples are found in two different clusters.

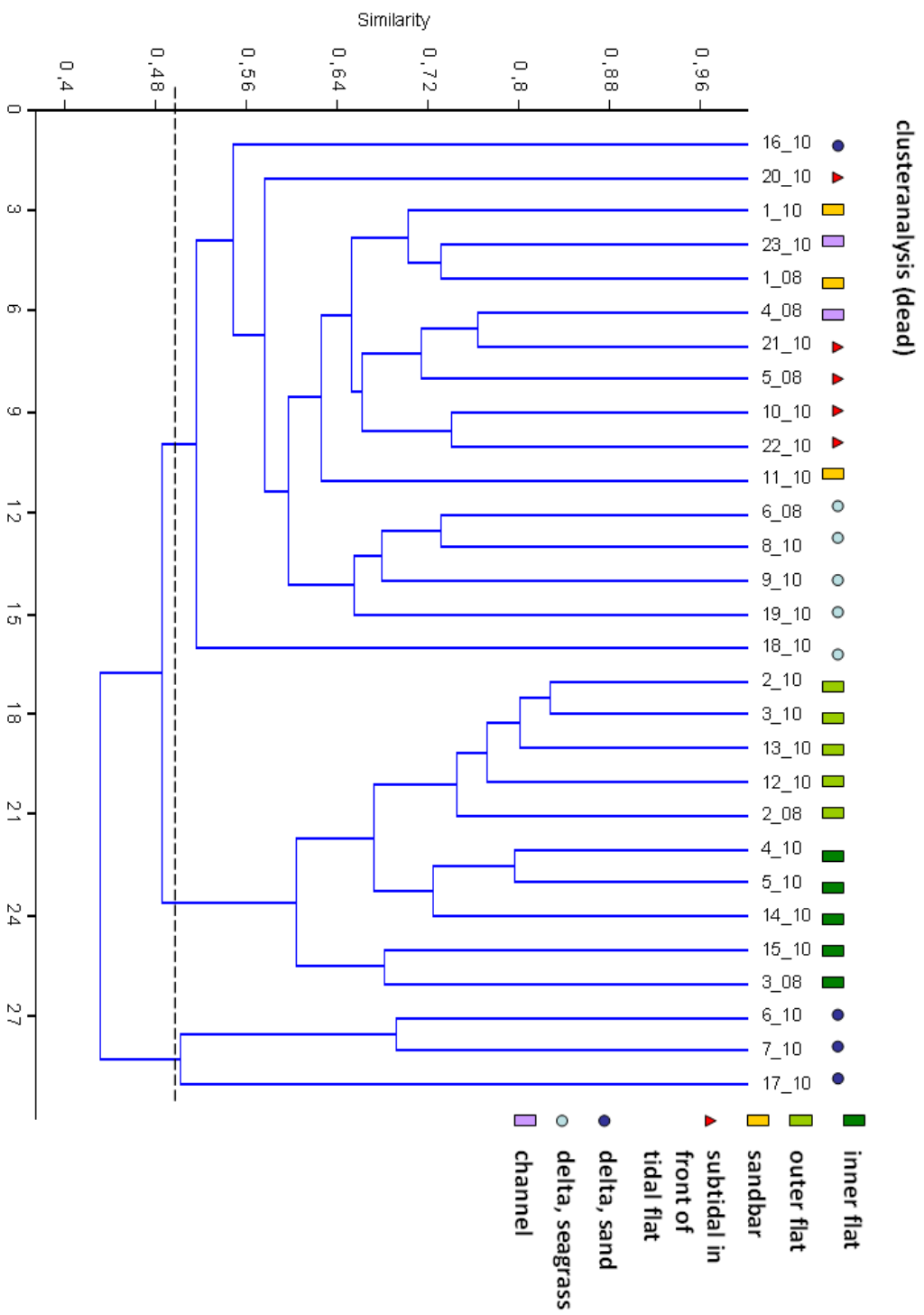


Figure 26. Cluster analysis of dead shells. At the similarity level of 0.5 the samples of the inner and outer tidal flat build one cluster. Samples of the sandbar, the channel, the shallow subtidal, delta seagrass and one of delta sand form the largest cluster. Remaining samples of the delta sand and one of the delta seagrass samples are separated.

3.7. Non-metric multidimensional scaling (nMDS)

3.7.1. nMDS (total)

The ordination of the total assemblage plots inner tidal, outer tidal and delta seagrass substrates as distinct groups, while samples from sandbar and shallow subtidal plot together, near to the delta seagrass samples (Fig. 27). Delta sand samples are widely dispersed in the ordination caused by heterogeneous molluscan compositions, which are different from all other samples. Stress value is 0.1588 and therefore the scaling still gives a potentially usefully picture, though for values of the upper end of this range too much reliance should not be placed on the detail of the plot (Clarke and Warwick, 2001).

3.7.2. nMDS (living)

nMDS of the living shells also plotted all samples of the inner tidal and of the outer tidal close to each other (Fig. 28). This indicates high similarity of the species composition in both areas. The samples of the shallow subtidal and the sandbar are close in the ordination and therefore have similar species composition. Samples of the delta sand show high similarity among each other, but there is also close similarity to one of the channel samples. Two of the delta sand samples are very similar, whereas the remaining two and one of the shallow subtidal samples are distant. The stress level is 0.2083 and should therefore be treated with some scepticism (Clarke and Warwick, 2001).

3.7.3. nMDS (dead)

nMDS of the dead shells calculated a stress level of 0.1611, indicating a reliable ordination (Fig. 29). Inner and outer tidal flat samples are plotted in close distance, indicating high similarity within the samples of each area. Samples of the delta seagrass show high similarity, with exception of sample 18_10. Samples of the sandbar, the channel and the shallow subtidal are plotted in the centre of the scaling. Delta sand samples are widely dispersed.

In general, the samples of the inner tidal, the outer tidal and the delta seagrass showed high similarity of species composition in total, living and dead shells, whereas delta sand samples were always distinct. The samples of the sandbar, the channel and the shallow subtidal plotted together in all categories, but also always in close distance to the outer tidal and the subtidal seagrass samples.

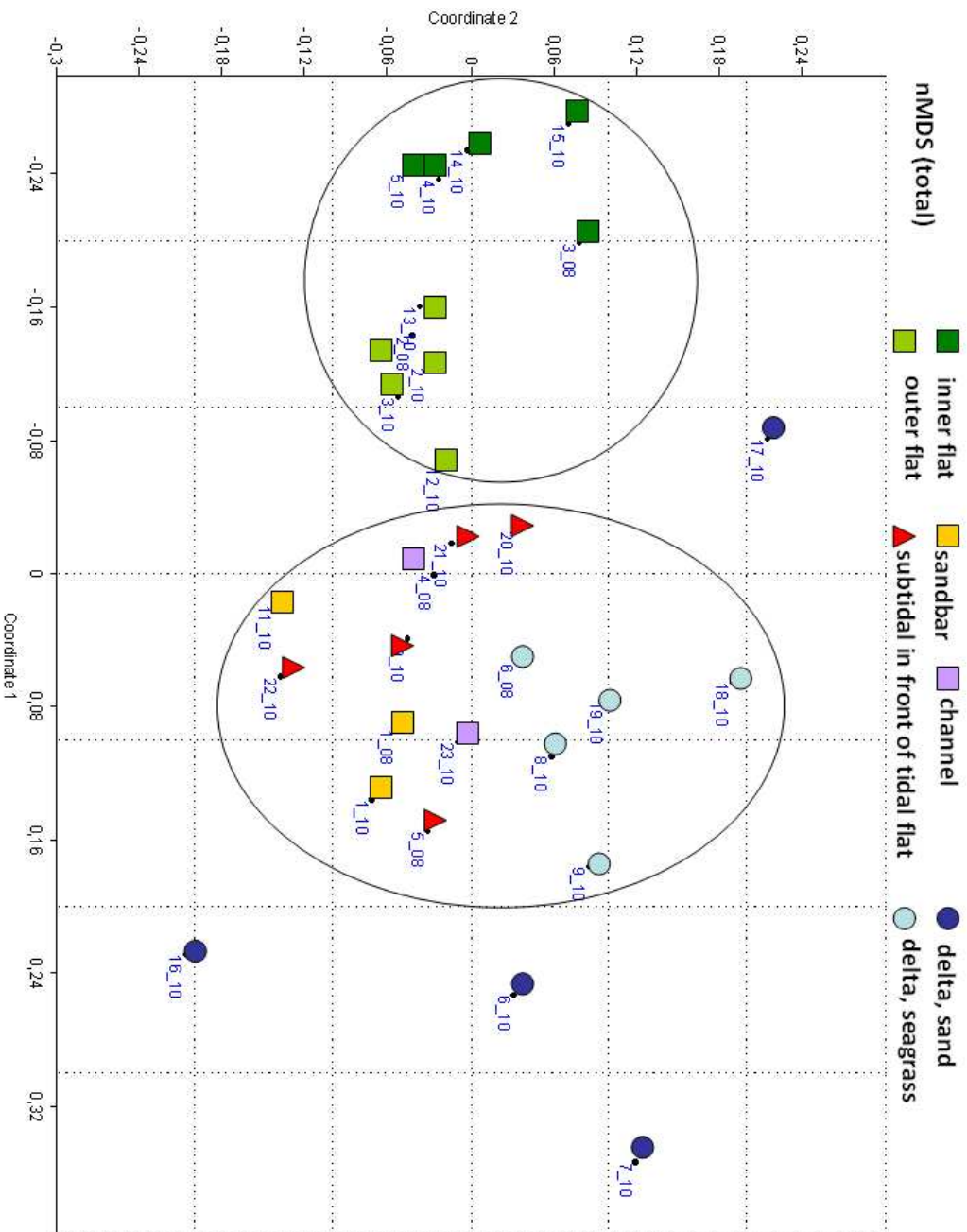


Figure 27. nMDS of the total of shells (stress 0.1588). Clusters formed in the clustering from Bray-Curtis similarities at the level of 0.5 are superimposed as ellipses. Symbols represent the sampling area together with the sample number. Inner and outer tidal flat and delta seagrass samples are plotted in distinct groups, whereas shallow subtidal, channel and sandbar samples are mixed. Delta sand samples are widespread.

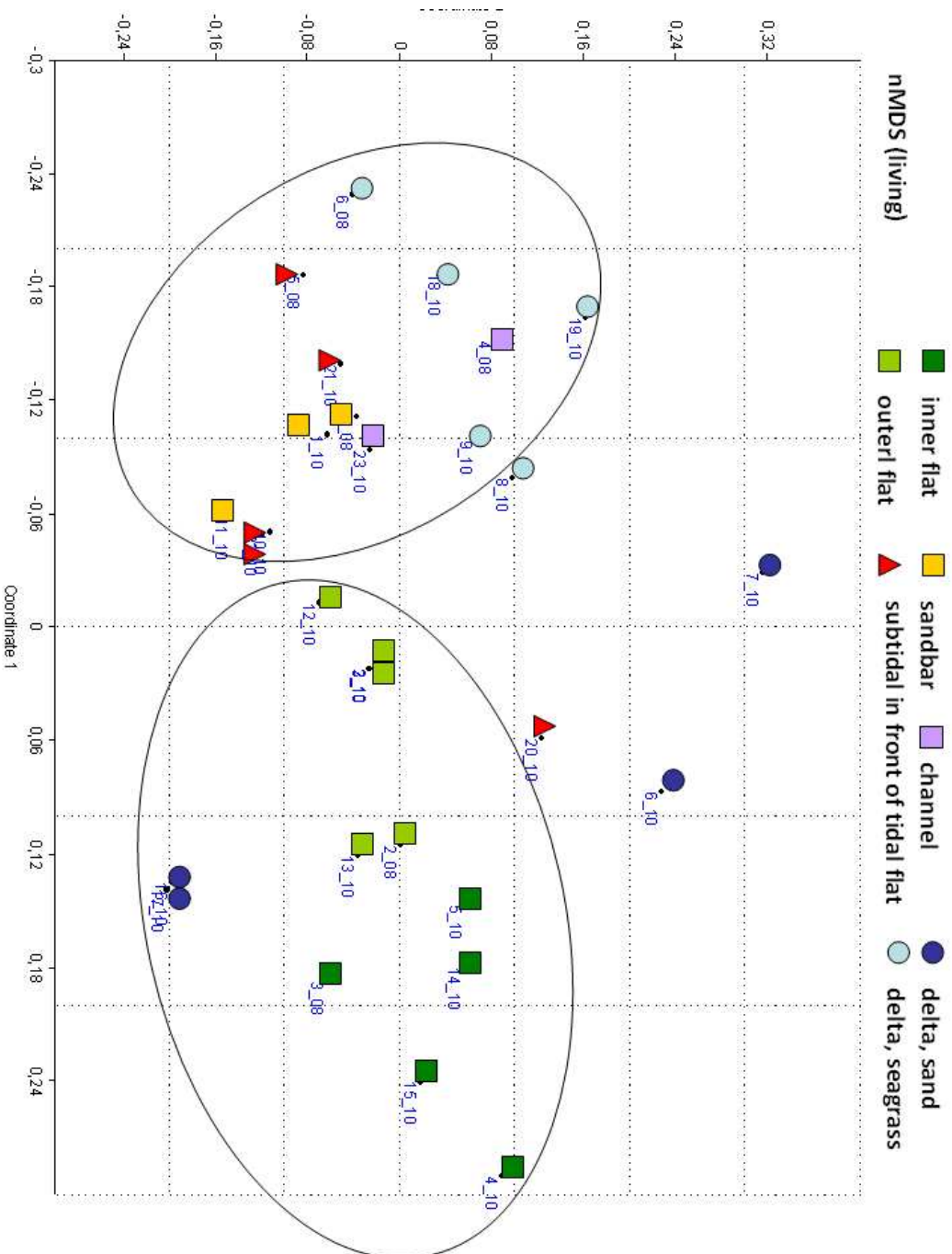


Figure 28. nMDS of the living molluscs (stress 0.2083). Symbols represent the sampling area together with the sample number. Clusters formed in the clustering from Bray-Curtis similarities at the level of 0.5 are superimposed as ellipses. Inner and outer tidal flat and two of the delta sand samples are plotted in close distance, indicating high similarity. Sandbar, shallow subtidal and seagrass samples are similar to each other with exception of 20_10 and 8_10. Some delta sand samples show lowest similarity to any other sample.

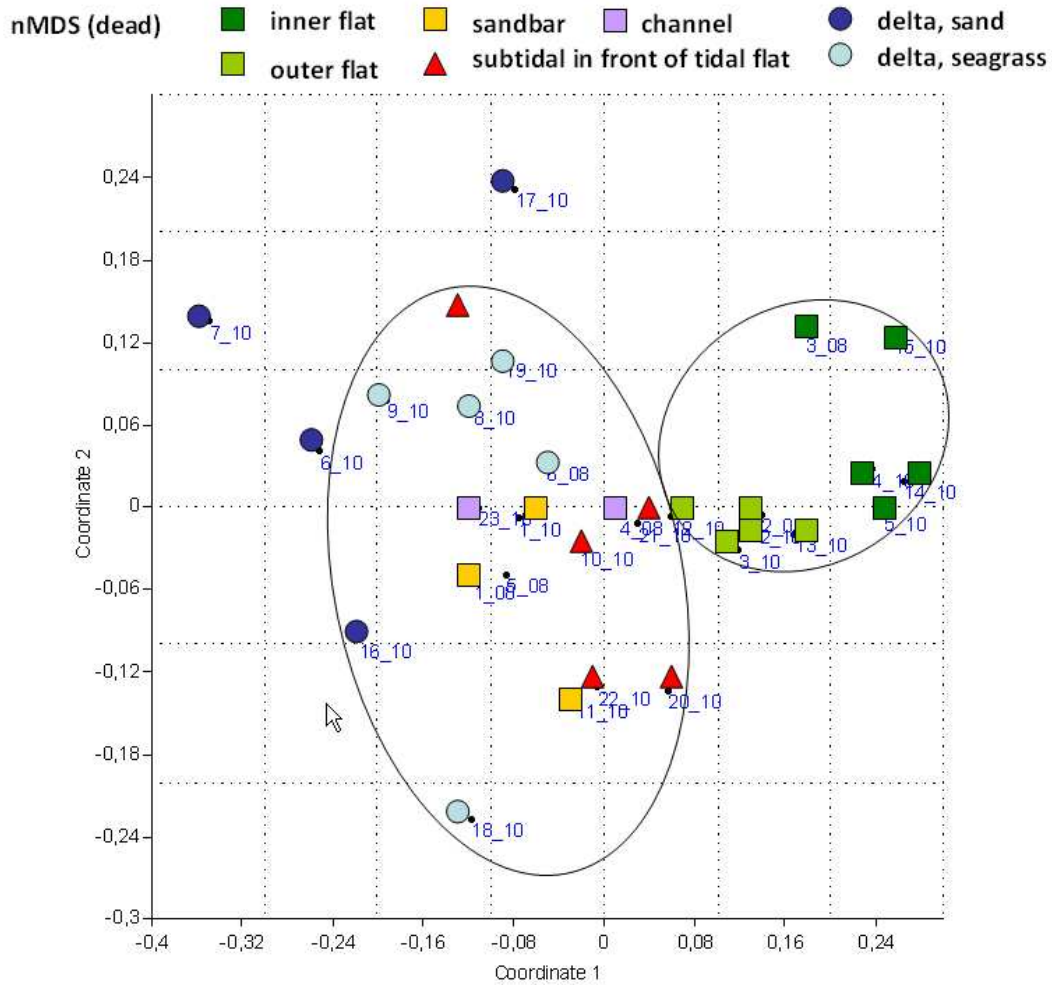


Figure 29. nMDS of the dead shells (stress 0.1611). Symbols represent the sampling area together with the sample number. Clusters formed in the clustering from Bray-Curtis similarities at the level of 0.5 are superimposed as ellipses. Inner and outer tidal flat samples are plotted in close distance and within a circle, indicating high similarity within the samples of the area. The samples of delta seagrass, sandbar, channel and shallow subtidal show also high similarity. Delta sand samples are widely dispersed, but one is within the ellipse of the subtidal samples.

3.8. Abundance and size frequency distribution of living and dead shells

The size distribution of living and dead shells was compared in samples which contained both living and dead individuals of a species. In fourteen out of thirty size comparison, significant differences between the shell-size of living and dead molluscs were found.

C. glaucum was the species with the highest number of individuals collected alive in all environments. The proportion of living shells, however, was very low in the delta seagrass and in the channel (Tab. 1). Highest number of living shells was found on the sandbar (Fig. 30, 11_10), alike the number of dead shells (185) was striking there. Size of most individuals, both living and dead, was less than 10 mm, bigger shells were rare. Further sandbar samples contained fewer living individuals (Tab. 2a). In the outer tidal flat (Fig. 30, 12_10, 13_10 and Tab. 2a) mostly dead and only very few living individuals of *C. glaucum* were collected. In both samples living individuals of more than 20 mm were rare and also most dead shells were smaller than 10 mm. In the inner tidal flat the living individuals of *C. glaucum* were rare (Tab. 2a), but fell into all size classes from less than 5 mm up to 25 mm (Fig. 31, 14_10, 15_10). Highest percentages of dead individuals of this species with size over 15 mm were found in the inner flat. In sample 14_10 the dead shells are significantly bigger than the living shells (Tab. 3). In two of four delta sand samples more living than dead individuals of *C. glaucum* were found (Tab. 2b). The size ranged from less than 5 mm up to 10 mm (Fig. 31, 16_10, 17_10). Sample 17_10 contained living and dead shells of the same size classes, whereas in sample 16_10 dead shells were significantly bigger than living ones (Tab. 3). In the shallow subtidal (Fig. 32, 22_10) only few living *C. glaucum* were found. All of them were smaller than 10 mm. Dead shells there were not bigger than 5 mm. In the channel sample living shells ranged between <5 and 10 mm, whereas dead shells of all size classes were found (Fig. 32, 23_10).

Living individuals of *C. gallina* were frequent on the sandbar, the shallow subtidal and in the seagrass covered delta, whereas dead shells were found in all environments (Tab. 1). Living shells in the sandbar sample (Fig. 33, 11_10) were of all size classes, but they were significantly bigger than the dead shells of this species (Tab. 3). The sample of the outer tidal flat contained mostly dead shells of less than 5 mm size (Fig. 33, 12_10). Living *C. gallina* were rare in this environment (Tab. 2a), but ranged between 5-10 mm and were thus significantly larger than the dead (Tab. 3). In the shallow subtidal samples *C. gallina* was frequent (Tab. 2b). Samples contained both living and dead shells in nearly all categories, only the size class from 10-15 mm does not have any living individuals (Fig. 34; 21_10 and 22_10). Again in 21_10 the living were significantly larger than the dead bivalves (Tab. 3). The total number of *C. gallina* was only 13 in sample 22_10. Sample 23_10 (Fig. 34) was taken in the channel and contained mostly dead shells smaller than 10 mm. Most living individuals in this sample were larger than 15 mm. This size difference was significant (Tab. 3).

Living shells of *T. tenuis* were found frequently on the sandbar, the shallow subtidal, in the channel and also in the outer flat, but dead shells were also found in all other environments (Tab. 1). Sizes on the sandbar ranged from less than 5 mm up to 10 mm (Fig. 35, 11_10). Dead shells were significantly larger (Tab. 3) and ranged mainly from 5 mm to 15 mm. In the shallow subtidal (Fig. 35; 21_10 and 22_10) the living shells ranged between <5 and 15 mm and dead shells between 5 and 15 mm. In sample 21_10 the living *T. tenuis* were significantly smaller than the dead shells of this species (Tab. 3). Numbers of dead *T. tenuis* was highest in the channel (Tab. 1). The sample 23_10 contained high percentages of dead shells bigger than 10 mm, but living shells were all smaller than 15 mm and most of them ranged between 5-10 mm (Fig 35; 23_10). Accordingly, the size difference between living and dead shells was significant (Tab. 3).

Living *S. plana* were found exclusively on the tidal flat (Tab. 1). The outer tidal flat contained only few individuals (Tab. 2a). The size distribution of living and dead shell was balanced (Fig. 36, 13_10). In contrast, in the inner tidal (Fig. 36, 14_10, 15_10) living and dead individuals of up to 10 mm were frequent. Although shell-sizes of more than 10 mm were rarely found, the living *S. plana* of 14_10 were significantly larger than the dead individuals in this sample (Tab. 3).

Living individuals of *L. mediterraneum* were found in high abundances in the delta sand (Tab. 1); there this species occurred in masses of more than 400 individuals per sample (Tab. 2b). Size of living individuals was always less than 5 mm (Fig. 37; 16_10 and 17_10). The rare dead shells also were significantly smaller than the living shells in sample 16_10 (Tab. 3). Few living individuals of 5-10 mm were found in the channel. Dead shells there ranged from <5 to 10 mm.

L. lacteus was found alive in all environments, except the delta sand (Tab. 1), but was not highly abundant in any sample (Tab. 2a and 2b). Size of the dead *L. lacteus* in the shallow subtidal (Fig. 38; 20_10) ranged from < 5 to 20 mm, but shells of the largest category were rare. Living individuals were all smaller than 10 mm. The channel samples (Fig. 39; 23_10) contained many more dead than living shells. Most dead shells ranged between 5 and 15 mm. Living individuals size distribution was balanced in the first three size classes and no significant differences were found (Tab. 3).

The gastropod *B. reticulatum* was found in all environments (Tab. 1), but was most abundant on the tidal flat samples (Tab. 2a). Living individuals were detected in two tidal flats only (Tab. 4). Three living *B. reticulatum* of 10- 15 mm were found in the outer tidal flat (Fig. 39; 13_10a). Dead shells ranged from 5 to 15 mm. In the inner flat (Fig. 39; 14_10a) there were most living individuals of this species. Living shells were significantly smaller than the dead shells (Tab. 3), which were abundant in the first three size classes but rarely bigger than 15 mm.

Living *Tapes philipinarium* were exclusively found in the inner flat and one single living individual in the delta sand (Tab. 1). Only dead shells, but rarely, were found in the other samples (Tab. 2a and 2b). In the sample of the inner flat (Fig. 40) the ratio of living and dead shells was balanced, but the

living individuals reached sizes up to 10 mm and were significantly bigger than dead individuals (Tab. 3).

Living *Lucinella divaricata* were found exclusively in subtidally influenced environments (Tab. 1) and were rather frequent in the delta seagrass (Tab. 2a). Both living and dead shells ranged from <5 to 10 mm (Fig. 41), but the size differences were not significant (Tab. 3).

Hydrobia sp. were found living only in the inner tidal, whereas dead shells were even detected in the delta areas (Tab.1). All shells in the inner flat sample 15_10 were smaller than 5 mm (Fig. 42). The ratio of living and dead individuals was balanced and size differences were not significant (Tab. 3).

Living individuals of *Gregariella petagnae* were found in the delta sand exclusively (Tab. 1). Although all shells were smaller than 5 mm, the living shells were significantly smaller than the dead shells (Fig. 43). The size difference between the median of the living and dead shells, however, is 0.3 mm only (Tab. 3).

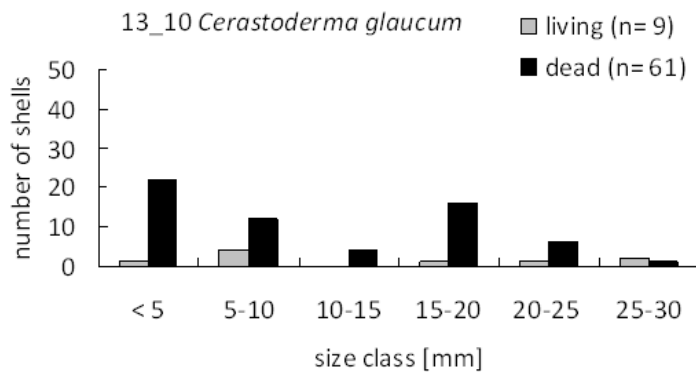
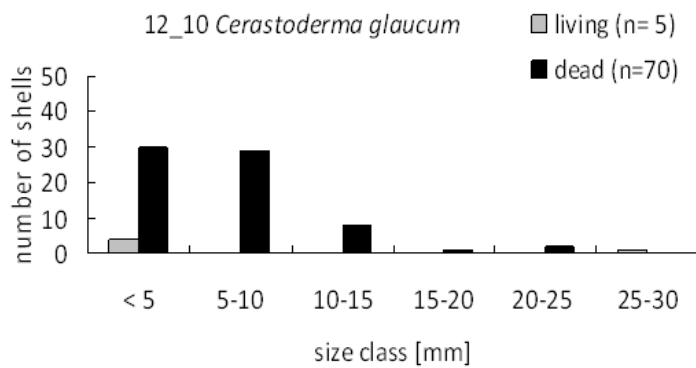
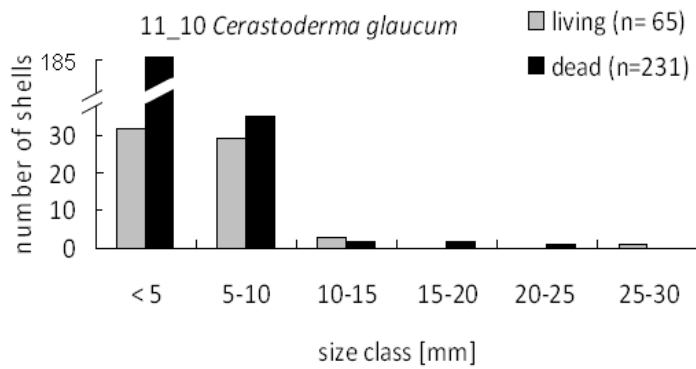


Figure 30. Comparison of size-distribution of living and dead shells of *C. glaucum*. Highest number of living *C. glaucum* was found on the sandbar (11_10), where also the number of dead shells was striking (185). Most individuals, both living and dead, were of less than 10 mm size. The outer flat (12_10, 13_10) contained mostly dead and only few living individuals. In both samples living individuals bigger than 20 mm were rare and also most dead shells were smaller than 10 mm.

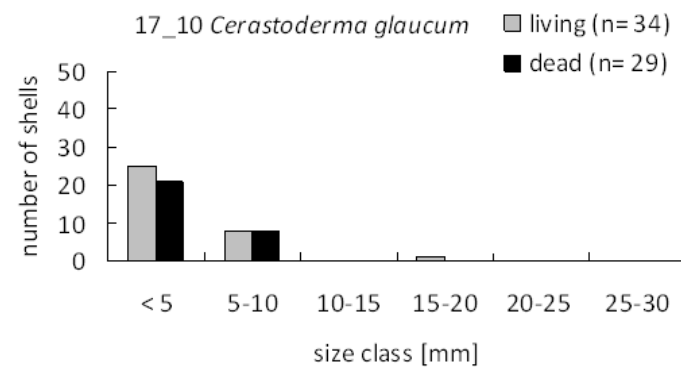
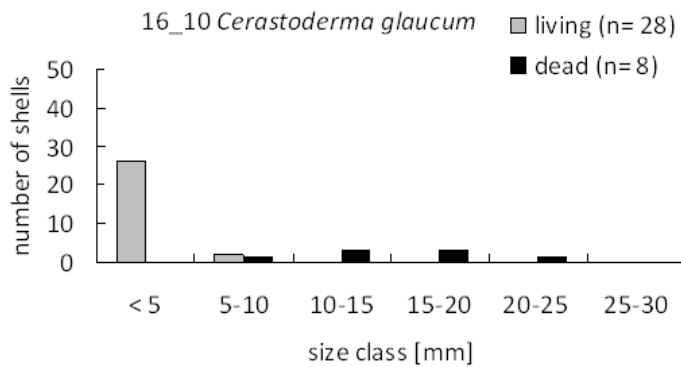
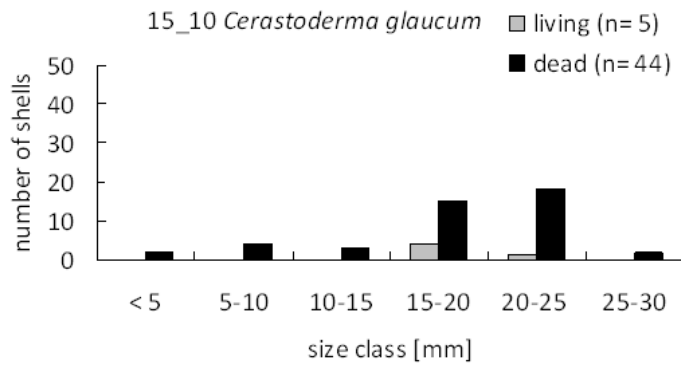
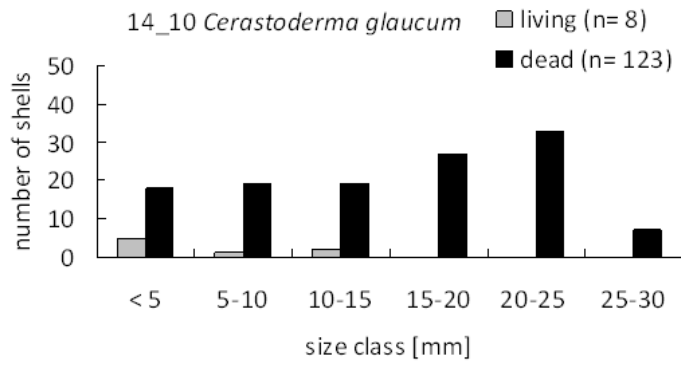


Figure 31. The rare living individuals of *C. glaucum* in the inner tidal flat (14_10, 15_10) fell to all size classes from less than 5 mm up to 25 mm. Dead individuals were mostly bigger than 15 mm, but also smaller individuals were found. Living individuals of *C. glaucum* were also found in the delta sand (16_10, 17_10), with size ranging from less than 5 mm up to 10 mm. Sample 17_10 contained also dead shells of the same size classes, whereas in sample 16_10 they were exclusively larger than 10 mm.

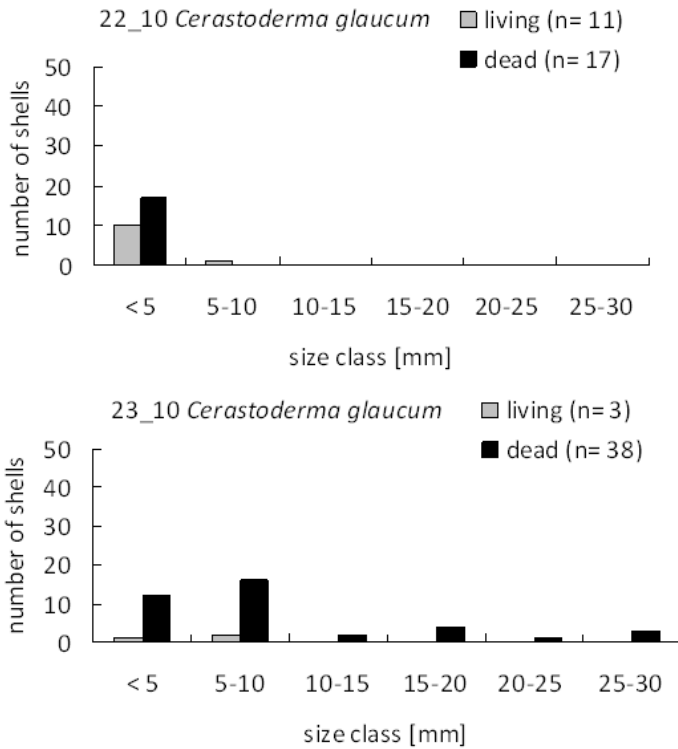


Figure 32. The shallow subtidal sample 22_10 contained few *C. glaucum*. All of them were smaller than 10 mm. In the channel (23_10) dead shells of all sizes were found whereas living individuals were all smaller than 10 mm.

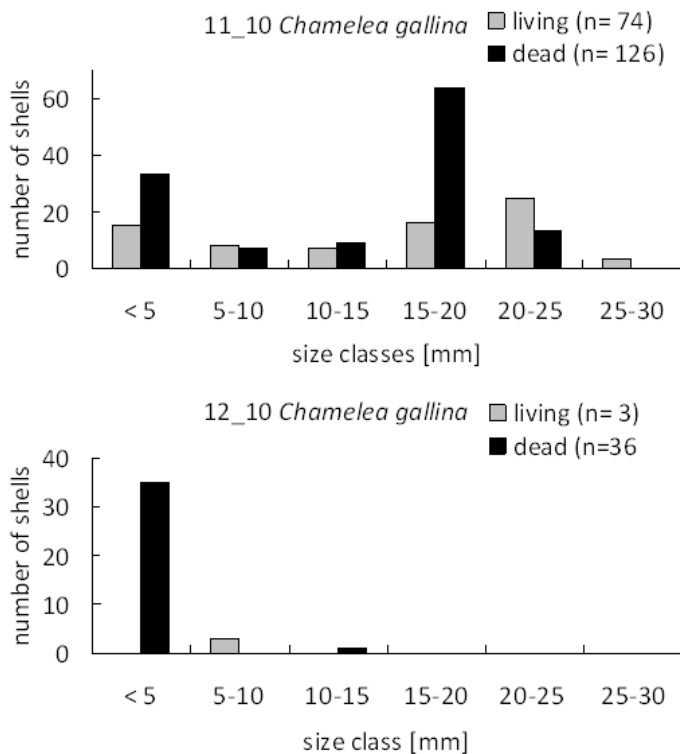


Figure 33. Comparison of size-distribution of living and dead shells of *C. gallina*. In the sandbar sample (11_10, y-axis maximum 70) there are living individuals of all size classes. Dead shells were mostly smaller than 5 mm and not bigger than 25 mm. The sample of the outer tidal flat (12_10) contained mostly dead shells of less than 5 mm size, whereas only few living individuals were found.

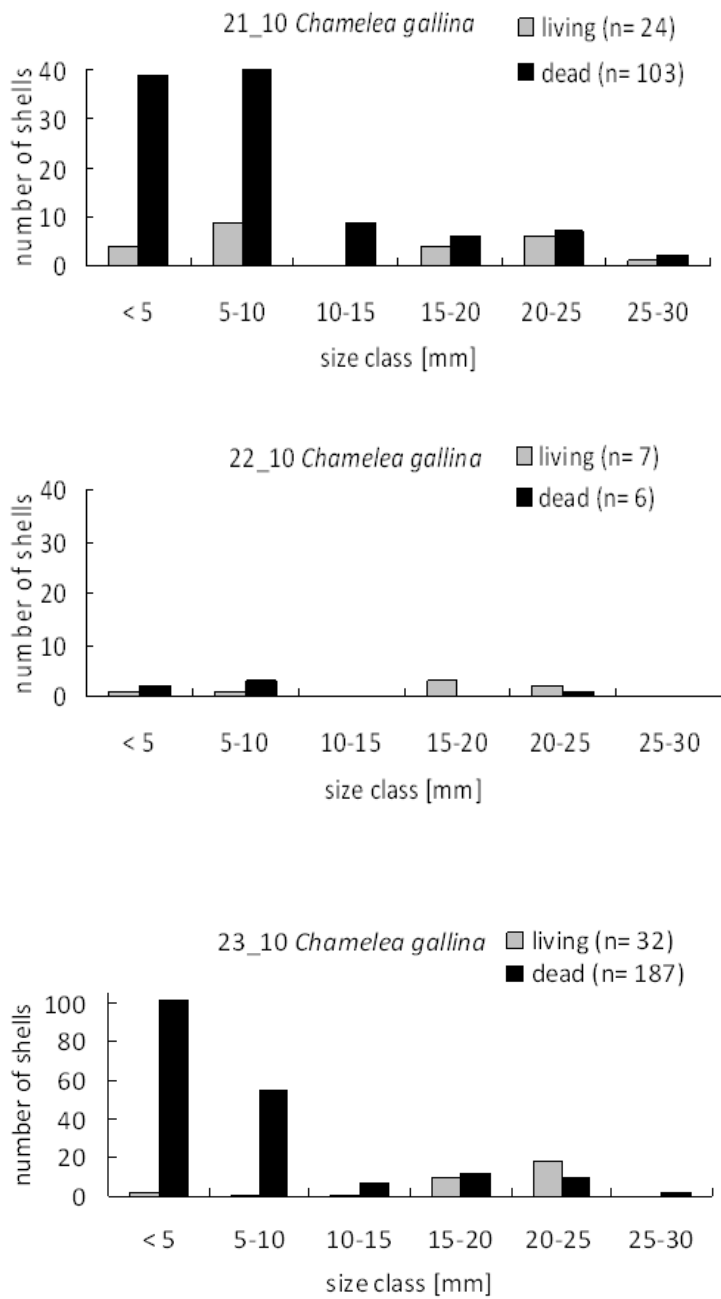


Figure 34. Comparison of size-distribution of living and dead shells of *C. gallina*. Samples 21_10 and 22_10 were both taken in the shallow subtidal. Both samples contain living and dead shells in nearly all categories, only the size class from 10-15 mm does not have any living individuals. The total number of *C. gallina* is only 13 in sample 22_10. Sample 23_10 (y-axis maximum 100) was taken in the channel and contained mostly dead shells smaller than 10 mm. Most living individuals were bigger than 15 mm.

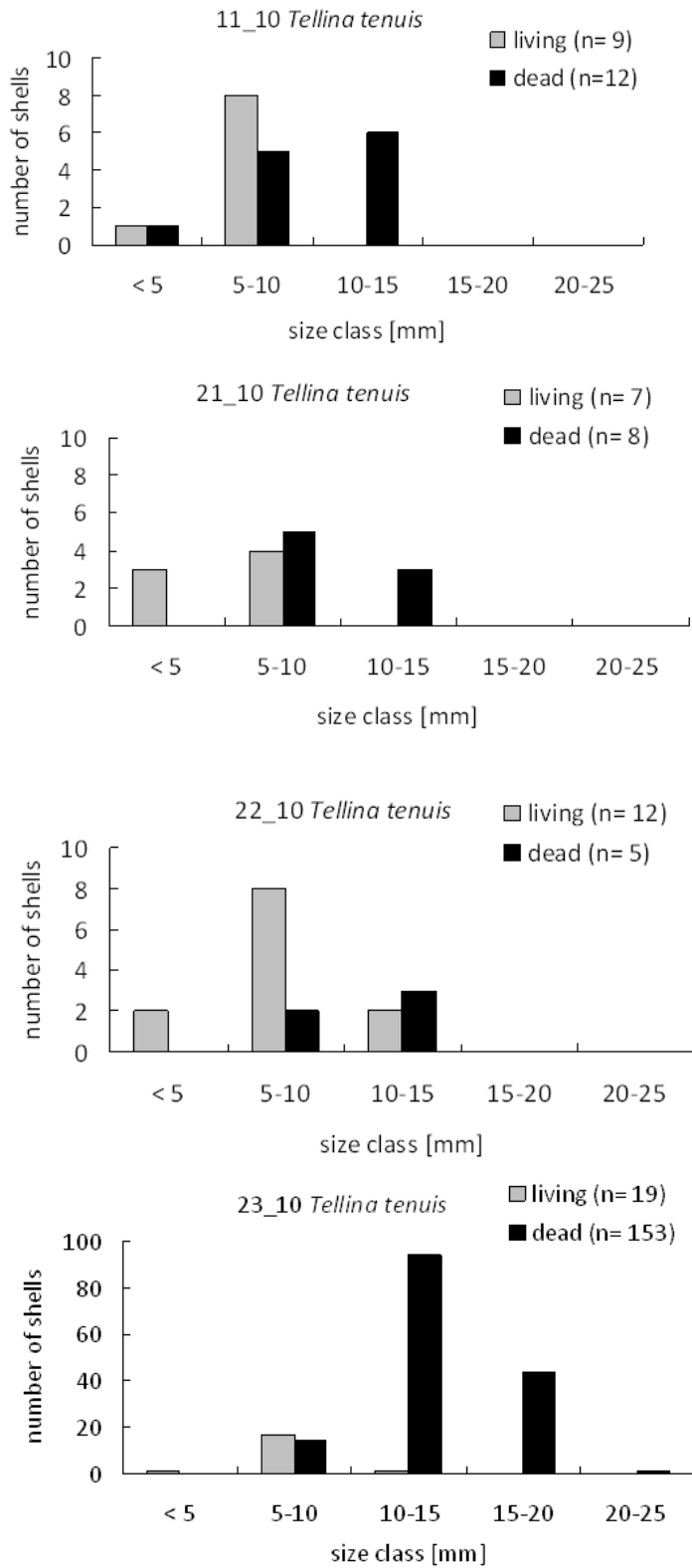


Figure 35. Living *T. tenuis* were found on the sandbar (11_10) only in the size of less than 5 mm up to 10 mm. Dead shells there ranged mainly from 5 mm to 15 mm. In the shallow subtidal (21_10 and 22_10) living shells were frequent, but generally smaller than the dead shells. Numbers of *T.tenuis* in the channel (23_10) were high, therefore scale of hundred was chosen. The sample contained many dead shells bigger than 10 mm. Living shells were all smaller than 15 mm and most ranged between 5-10 mm.

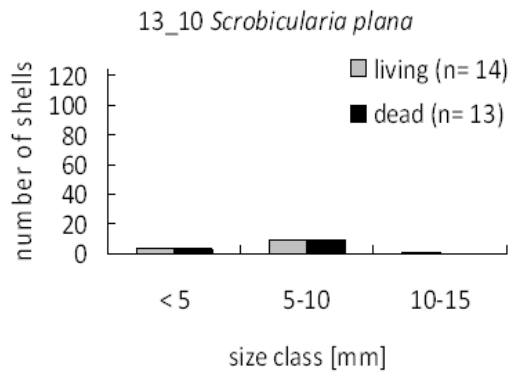
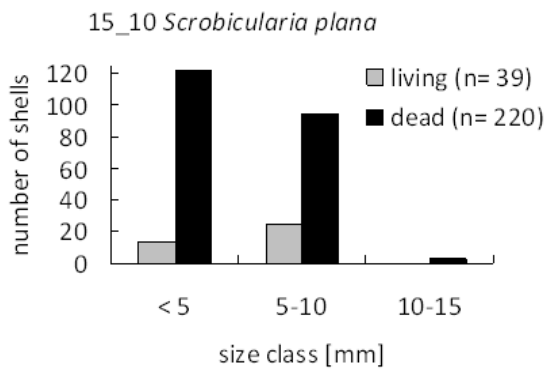
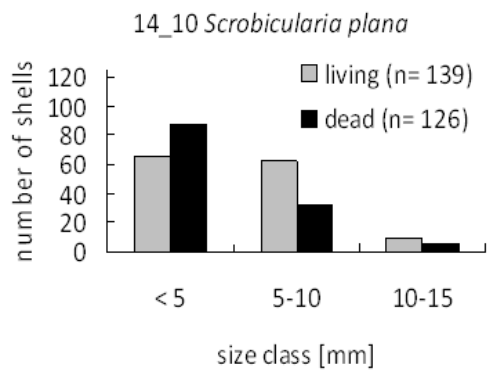


Figure 36. Living *S. plana* were found exclusively on the tidal flat. The outer tidal flat (13_10) contained only few individuals, both living and dead. In the inner tidal (14_10, 15_10) living and dead individuals of up to 10 mm were frequent. Shell-sizes of more than 10 mm were rarely found.



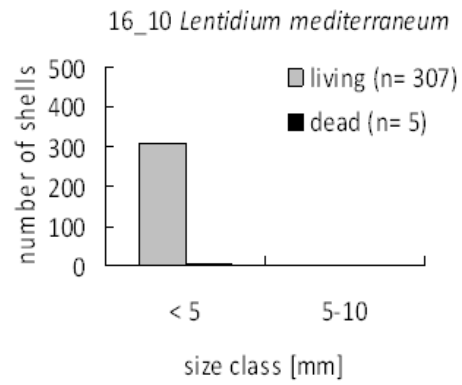
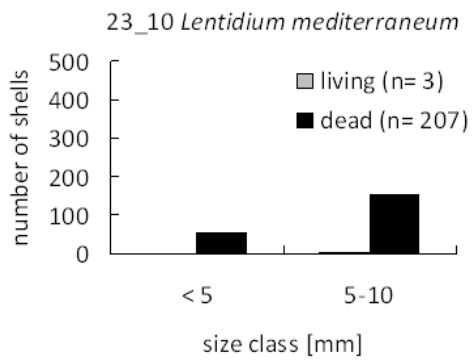
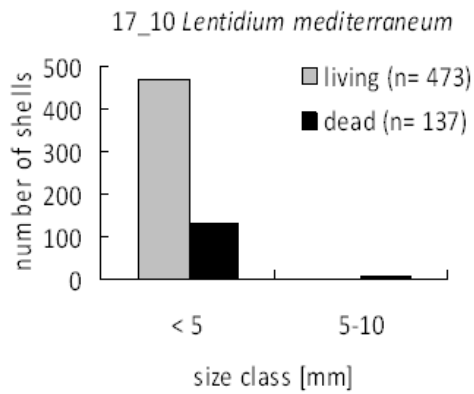


Figure 37. Living individuals of *L. mediterraneum* were found in masses in the delta sand. Size of living individuals was always less than 5 mm. The rare dead shells also were mostly smaller than 5 mm, only few were larger. Three living individuals of 5-10 mm were found in the channel (23_10), dead shells ranged from less than 5 mm up to 10 mm.



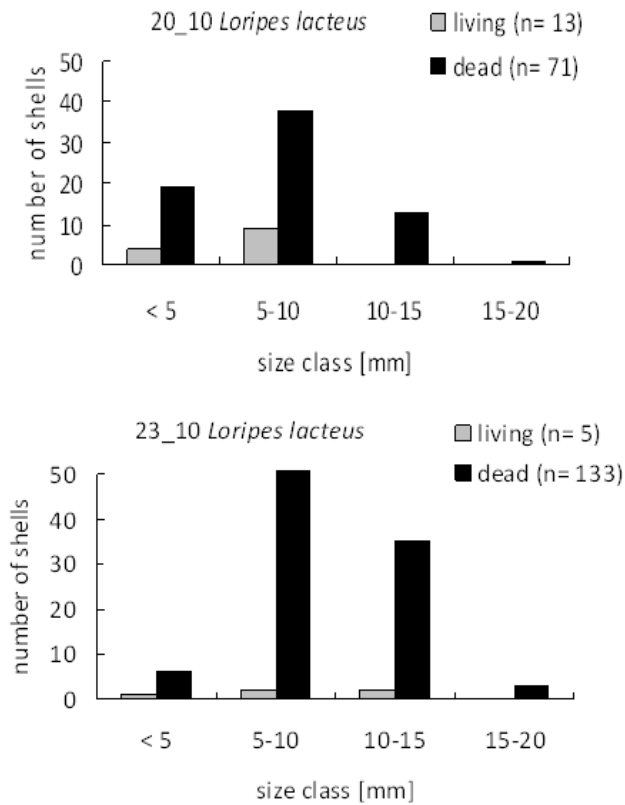


Figure 38. Size of the dead *L. lacteus* in the shallow subtidal (20_10) ranged from < 5 to 20 mm, although shells of the largest category were rare. Living individuals were all smaller than 10 mm. The channel samples (23_10) contained many more dead than living shells. Most dead shells ranged between 5 and 15 mm. Living individuals size distribution was balanced in the first three size classes.

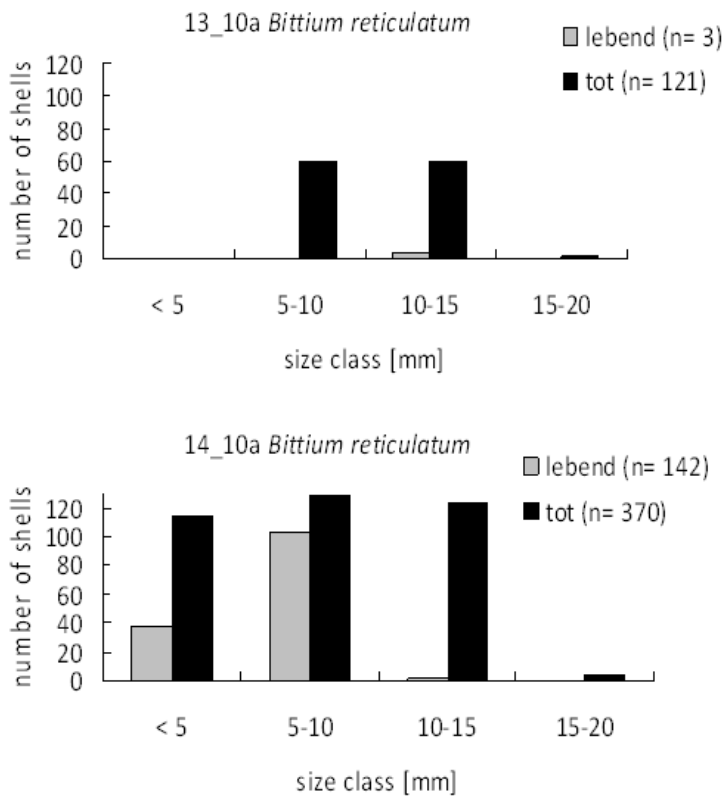


Figure 39. Three living *B. reticulatum* of 10- 15 mm were found in the outer tidal (13_10a). Dead shells there ranged from 5 to 15 mm. In the inner tidal (14_10a) there were many more living individuals. Most of them were smaller than 20 mm. Dead shells were abundant in the first three size classes but only few were larger than 15 mm.

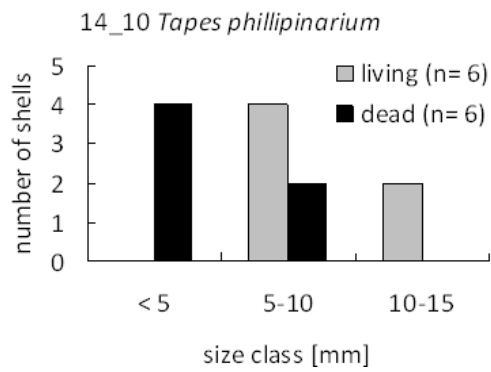


Figure 40. Living *T. philipinarium* were exclusively found in a sample of the inner flat. Ratio of living and dead shells was balanced, but the living individuals reached sizes up to 10 mm, whereas dead individuals measured up to 15 mm.

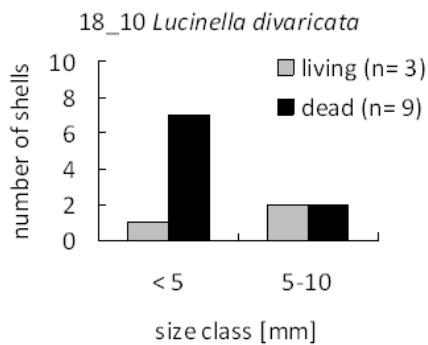


Figure 41. Living individuals of *L. divaricata* were exclusively found in the delta seagrass. Both living and dead shells ranged from <5 up to 10 mm.

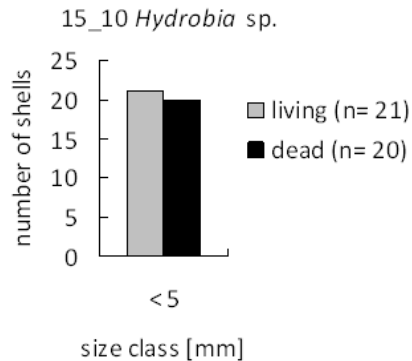


Figure 42. Living individuals of *Hydrobia* sp. were found only in the inner tidal. All shells were smaller than 5 mm; the ratio of living and dead individuals was balanced.

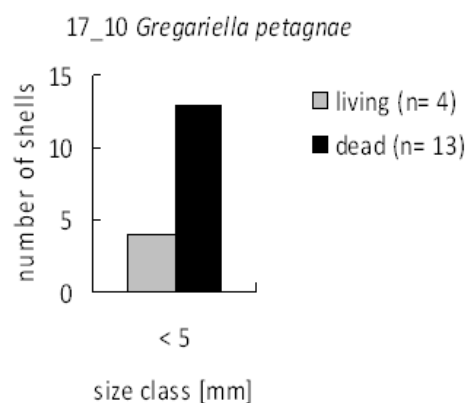


Figure 43. Living individuals of *G. petagnae* were found in the delta sand. All shells were smaller than 5 mm.

Table 1. Abundances of living and dead shells of the most common living species in the investigated environments. In this data set *B. reticulatum* and *R. labiosa* were not differentiated in categories and therefore counted as dead.

environment	category	<i>Cerastoderma glaucum</i>	<i>Chamelea gallina</i>	<i>Tellina tenuis</i>	<i>Scrobicularia plana</i>	<i>Loripes lacteus</i>	<i>Lentidium mediterraneum</i>	<i>Bitium reticulatum</i>	<i>Tapes philippinarum</i>	<i>Lucinella divaricata</i>	<i>Hydrobia</i> sp.	<i>Gregariella petagnae</i>	<i>Rissoa labiosa</i>
inner flat	living	18	0	0	194	14	0	-	7	0	21	0	-
	dead	454	16	1	789	57	7	5268	8	0	250	3	1038
outer flat	living	34	5	12	23	20	1	-	0	0	0	0	-
	dead	369	75	77	40	412	277	5154	4	12	2	0	1417
sandbar	living	73	143	103	0	8	2	-	0	17	0	0	-
	dead	354	183	41	1	131	190	481	2	14	0	0	13
channel	living	3	29	21	0	10	5	-	0	0	0	0	-
	dead	52	265	221	15	174	258	318	2	10	0	0	90
shallow subtidal	living	59	241	53	0	19	2	-	0	2	0	1	-
	dead	77	248	55	3	45	66	513	0	16	0	0	222
delta seagrass	living	1	40	2	0	12	20	-	0	12	0	0	-
	dead	77	472	36	39	59	493	338	3	47	13	1	91
delta sand	living	62	0	0	1	0	686	-	1	2	0	4	-
	dead	63	35	7	15	28	350	39	2	8	9	25	22

Table 2a. Abundances of living and dead shells of the most common species are displayed for all tidal flat samples. In this data set *B. reticulatum* and *R. labiosa* were not differentiated in categories and therefore counted as dead.

environment	sample	category	<i>Cerastoderma glaucum</i>	<i>Chamelea gallina</i>	<i>Tellina tenuis</i>	<i>Scrobicularia plana</i>	<i>Lentidium mediterraneum</i>	<i>Loripes lacteus</i>	<i>Bitium reticulatum</i>	<i>Tapes philippinarum</i>	<i>Lucinella divaricata</i>	<i>Hydrobia</i> sp.	<i>Gregariella petagnae</i>	<i>Rissoa labiosa</i>	
inner flat	3_08	living	4	0	0	2	0	0	-	1	0	0	0	-	
		dead	60	0	0	114	3	28	82	2	0	20	0	43	
	4_10	living	0	0	0	3	0	0	-	0	0	0	0	-	
		dead	130	3	0	204	0	10	894	0	0	0	0	176	
	5_10	living	1	0	0	9	0	5	-	0	0	1	0	-	
		dead	75	0	0	47	0	14	875	0	0	0	0	127	
	14_10	living	8	0	0	139	0	9	-	6	0	0	0	-	
		dead	123	12	1	126	2	1	2995	6	0	200	0	353	
	15_10	living	5	0	0	39	0	0	-	0	0	21	0	-	
		dead	44	1	0	220	2	4	422	0	0	20	3	339	
	outer flat	2_08	living	6	0	0	3	0	6	-	0	0	0	0	-
			dead	86	6	0	11	9	91	323	1	0	0	0	117
2_10		living	5	1	7	2	0	4	-	0	0	0	0	-	
		dead	35	4	9	1	6	89	804	1	6	1	0	149	
3_10		living	9	1	4	4	0	9	-	0	0	0	0	-	
		dead	98	19	38	4	58	79	1769	0	3	0	0	260	
12_10		living	5	3	1	1	1	0	-	0	0	0	0	-	
		dead	70	36	28	7	178	111	771	2	3	0	0	270	
13_10		living	9	0	0	14	0	1	-	0	0	0	0	-	
		dead	61	10	2	13	26	42	1487	0	0	1	0	621	
sandbar		1_08	living	2	27	5	0	2	4	-	0	0	0	0	0
			dead	106	85	24	0	140	90	116	0	6	0	0	0
	1_10	living	6	41	89	0	0	3	-	0	17	0	0	-	
		dead	5	6	4	0	16	12	15	0	2	0	0	13	
	11_10	living	65	74	9	0	0	1	-	0	0	0	0	0	
		dead	231	126	12	1	34	29	350	2	6	0	0	0	
channel	4_08	living	0	2	2	0	2	5	-	0	0	0	0	-	
		dead	15	77	40	2	34	24	150	0	0	0	0	64	
	23_10	living	3	27	19	0	3	5	-	0	0	0	0	-	
		dead	38	188	153	13	207	133	168	2	10	0	0	26	

Table 2b. Abundances of living and dead shells of the most common species are displayed for all subtidal samples. In this data set *B. reticulatum* and *R. labiosa* were dot differentiated into the categories living/dead and therefore counted as dead.

environment	sample	category	<i>Cerastoderma glaucum</i>	<i>Chamelea gallina</i>	<i>Tellina tenuis</i>	<i>Scrobicularia plana</i>	<i>Lentidium mediterraneum</i>	<i>Loripes lacteus</i>	<i>Bitium reticulatum</i>	<i>Tapes philippinarum</i>	<i>Lucinella divaricata</i>	<i>Hydrobia</i> sp.	<i>Gregariella petagnae</i>	<i>Rissoa labiosa</i>
shallow subtidal	5_08	living	0	191	21	0	0	1	-	0	2	0	0	0
		dead	10	49	13	1	9	6	52	0	2	0	0	0
	10_10	living	47	19	13	0	2	0	-	0	0	0	0	-
		dead	20	47	19	0	29	20	131	0	3	0	0	26
	20_10	living	1	0	0	0	0	13	-	0	0	0	0	-
		dead	17	43	8	0	14	71	115	0	5	0	0	108
	21_10	living	0	24	7	0	0	3	-	0	0	0	0	-
		dead	13	103	8	2	10	15	200	0	6	0	0	83
	22_10	living	11	7	12	0	0	0	-	0	0	0	1	-
		dead	17	6	5	0	4	4	15	0	0	0	0	5
delta seagrass	6_08	living	0	23	0	0	2	0	-	0	0	0	0	-
		dead	12	54	14	3	68	11	122	1	4	0	0	17
	8_10	living	1	14	0	0	17	8	-	0	17	0	0	-
		dead	40	272	7	5	317	24	133	0	18	11	1	52
	9_10	living	0	1	0	0	0	1	-	0	0	0	0	-
		dead	11	85	3	13	64	11	10	0	8	1	0	2
	18_10	living	0	1	2	0	1	2	-	0	3	0	0	-
		dead	9	10	1	2	6	6	30	0	9	0	0	1
	19_10	living	0	1	0	0	0	1	-	0	3	0	0	-
		dead	5	51	11	16	38	7	43	2	9	1	0	19
delta sand	6_10	living	0	0	0	1	3	0	-	0	1	0	0	0
		dead	17	19	0	2	85	3	6	2	3	0	0	0
	7_10	living	0	0	0	0	3	0	-	1	0	0	0	0
		dead	3	7	0	1	123	1	2	0	1	0	2	0
	16_10	living	28	0	0	0	307	0	-	0	1	0	0	-
		dead	8	8	0	1	5	8	2	0	1	0	0	2
	17_10	living	34	0	0	0	473	0	-	0	0	0	4	-
		dead	29	1	7	11	137	16	29	0	3	9	13	20

Table 3. Comparison of the shell sizes of living and dead molluscs. Significant differences are marked with an asterisk.

species	sample	median	median	p-value	significance
		living	dead		
<i>Cerastoderma glaucum</i>	11_10	5.00	4.82	0.1708	
	12_10	2.83	5.93	0.1181	
	13_10	9.08	7.52	0.1228	
	14_10	4.52	17.21	0.0003	*
	15_10	18.81	19.63	0.8559	
	16_10	3.17	14.84	< 0.0001	*
	17_10	3.29	3.10	0.3086	
	22_10	3.98	3.52	0.09033	
	23_10	6.24	6.58	0.5981	
<i>Chamelea gallina</i>	11_10	18.20	11.64	0.0007	*
	12_10	6.99	2.55	0.0082	*
	21_10	8.84	5.78	0.0034	*
	22_10	19.12	5.58	0.1747	
	23_10	20.26	4.43	<0.0001	*
<i>Tellina tenuis</i>	11_10	6.77	10.21	0.0062	*
	21_10	5.05	8.37	0.0031	*
	22_10	6.36	10.14	0.1547	
	23_10	6.19	13.84	<0.0001	*
<i>Scrobicularia plana</i>	13_10	6.00	5.85	0.8353	
	14_10	5.83	4.04	<0.0001	*
	15_10	5.63	5.48	0.7826	
<i>Lentidium mediterraneum</i>	16_10	3.57	2.60	0.0034	*
	17_10	3.57	3.48	0.7346	
	23_10	6.92	6.13	0.5334	
<i>Loripes lacteus</i>	20_10	5.35	7.15	0.0830	
	23_10	9.12	8.39	0.9820	
<i>Bittium reticulatum</i>	13_10	11.19	9.99	0.6001	
	14_10	5.53	7.56	<0.0001	*
<i>Tapes philippinarium</i>	14_10	9.01	4.37	0.0051	*
<i>Lucinella divaricata</i>	18_20	5.32	4.61	0.0644	
<i>Hydrobia</i> sp.	15_10	2.84	2.96	0.1404	
<i>Gregariella petagna</i>	17_10	2.28	2.58	0.0077	*

Table 4. Abundances of living and dead shells of the gastropod *Bittium reticulatum* in the extra samples taken on the tidal flat. Highest abundances of both, living and dead shells were found in one inner flat sample.

environment	sample	category	<i>n</i>
sandbar	11_10a	living	0
		dead	8
outer flat	12_10a	living	0
		dead	35
	13_10a	living	3
		dead	121
inner flat	14_10a	living	142
		dead	370
	15_10a	living	0
		dead	32

4. Discussion

As expected, the Isonzo tidal flat and the delta were characterized by highly variable physical conditions. The input of freshwater of the Isonzo River caused stratification with dense seawater in the deeper layers of the water body. Incoming tides transported sea water up the river and this influence was measurable even some kilometres upstream. Conversely, the upper layers of freshwater were still present in the delta. Seawater with a salinity of less than 28 psu is considered as brackish water (Nybakken and Bertness, 2005). The only environment with marine salinity in our study was therefore the delta seagrass.

Low temperatures on the tidal flat were mainly caused by the cool night temperatures, as measurements were taken at sunrise. Due to shallow water depth, both temperature and salinity on the flat must be highly influenced by short-term weather conditions and are much more extreme than the conditions in the subtidal environments. Oxygen content on the flat was very low, due to the high microbial oxygen consumption in the tidal flat sediments (Nybakken and Bertness, 2005).

More than 80% of the collected individuals were dead shells when *Rissoa* and *Bittium*, for which living and dead shells were not distinguished in the main samples are not included. The percentage is much higher when these species are only counted as dead shells (95 %). For those extra samples where *Bittium* was investigated for living and dead shells, the average proportion of living individuals is 23 % (range in individual samples is from 0 to 38 %).

Are there differences in the abundances of common species in different zones of the intertidal and the subtidal?

The tidal and subtidal regions differed in the composition of the most abundant species.

In the **inner tidal** flat the abundance of *B. reticulatum*, a member of the Cerithiidae, was striking. Cerithiidae inhabit variety of substrata, generally in shallow water and are micro- algal feeders. They show remarkable adaptive radiations within a variety of marine and estuarine habitats (Poppe and Goto, 1991). The gastropod *B. reticulatum* is often found together with *Zostera* spp. therefore the tidal flats offer optimal living conditions for this species. Also very common was *R. labiosa*. The genus Rissoidea occurs worldwide in shallow seas especially in the mid to lower littoral zones, few species occur in brackish water. They feed on diatomaceous films covering macroalgae or on foraminiferans or are selective deposit feeders (Beesley et al., 1996). Another abundant species on the inner tidal flat was the bivalve *S. plana*, a member of the Semelidae, which are infaunal inhabitants of muddy bays and can burrow deeply in the sediment. *C. glaucum* of the genus Cardiidae, are shallow burrowers in soft substrata ranging from muds to coarse sands (Beesley et al., 1996). The species *C. glaucum* prefers estuarine conditions (Poppe and Goto, 1993) and mostly dead shells were frequent in the inner flat.

The **outer tidal** flat had similar common species, with the exception that also *L. lacteus* was common. also most of the individuals were found dead. This species belongs to the family Lucinidae which live infaunal in sandy silts in the intertidal or in the shallow benthos. They live in symbiosis with sulphide-oxidizing bacteria and are therefore able to inhabit anoxic environments with high levels of sulphide, like the tidal flat (Beesley et al., 1996).

In general the tidal flat was characterized by few common species, but these occurred in very high numbers. This supports the thesis, that these environments with extreme physical condition can be settled by few adapted species only.

The environmental conditions are special in the **channel**. The channel is the run-off and inflow of the tidal flat and may therefore also transport and accumulate shells. Accordingly, there is constant water flow, but in opposite directions during high and low tide. Hence species composition in the channel samples was heterogeneous. There were high numbers of individuals, but with low numbers of living shells. Abundant species were similar to the tidal flat and sandbar samples but the high amount of supplementary species points to transport of species from the subtidal zones into this setting.

The **sandbar** is an unvegetated elevation that falls dry only at low tides. The most abundant species there was *C. gallina*, a venerid bivalve. 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., 1996). Also very common was the bivalve *T. tenuis*. Tellinids are infaunal and live at depths up to several times their shell length. If uncovered, they can reburrow rapidly up to 400 mm deep. Another species found there

living was *Lucinella divaricata*, a lucinid bivalve which lives in fine sand or mud just below the low tide line to a depth of 60 m (Poppe and Goto, 1993).

Lentidium mediterraneum was frequently found dead in some flat samples, but very abundant on the sandbar. It belongs to the Corbulidae, a genus of ciliary suspension feeders with cosmopolitan distribution. Their foot is compressed and grooved and may be 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, sand-muddy or muddy substrata in subtidal settings. They are common in estuaries and embayments, usually at depths greater than 4 m (Beesley et al., 1996). *Lentidium mediterraneum* is typical in intertidal to shallow water environments of the Mediterranean (Poppe and Goto 1993). To sum up, the composition of abundant species on the sandbar was heterogeneous and contained many intertidal and also marine species, what reflects the position at the seaside of the tidal flat.

The shallow subtidal was covered with dense seagrass meadows. Physical conditions there are much more stable than on the tidal flat. Abundant species there were similar to the sandbar which is explained with the very close spatial distance of these two areas to each other.

The composition of abundant species was completely different in the **delta seagrass** samples than on the inner and outer tidal flat. *V. rhomboids*, for example, is an infaunal filter-feeder that lives in shallow marine and occasionally estuarine habitats and was amongst the sixth most abundant species only in the delta samples. The presence of more stenohaline species is consequential (Lange, 1970), since the delta seagrass location was the only sample site with marine salinity conditions.

Delta sand samples contained species compositions similar to the sandbar and the shallow waters in front of the tidal flat. The location of the delta sand sampling sites was right in front of the Isonzo River mouth. The strong current generated sand ripples. It is assumed that only small and burrowing individuals like *L. mediterraneum* can live there. Abundance of this species was striking, whereas other species were rather rare.

Were there differences in the diversity of the zones of the intertidal and the subtidal?

Diversity was differentiated for the seven monitored environments. In general, the evenness was low in the inner flat, outer flat and delta sand and these environments were always dominated by few species. In contrast diversity was always high on the sandbar, in the channel, the shallow subtidal and the delta seagrass. This trend is apparent in the total of shells, as well as in the separately analyzed living and dead mollusc percentages. Only the outer tidal flat is much more diverse in the living shells than in the other categories. This may be due to the low individual numbers per sample. Reason for the low diversity in the inner and outer flat samples were single specially adapted species like the gastropods *B. reticulatum* and *R. labiosa* which reached extraordinarily high abundances.

Other, less intertidal-specialised species like *Gibbula* sp. were rare and may be accumulated by wave action. Contrarily, the more stable environmental conditions in the subtidal regions enabled various species to settle.

The diversity indices of the total of shells and the dead shells were quite similar, caused by the low abundances of living molluscs. The percentage of living shells was only 5% of the total of shells; this low numbers possibly influenced the calculation of the diversity indices. But there were also exceptions. Two of four delta sand samples contained up to 500 living individuals. Possible explanation for that might be some patchiness of the sediment in the delta sand zone, as these two samples consisted muddy sand. Living individuals there were all of the species *L. mediterraneum* (see chapter above), therefore the Simpson index shows high dominance of a single species and Shannon index low diversity.

The considerably higher number of species found only as dead individuals over most parts of the tidal flat suggest intensive time averaging (Fürsich und Flessa, 1991a). Time-averaging" is the process by which organic remains from different time intervals come to be preserved together (Kidwell, 1997). Diversity of the living fauna was relatively low. Fluctuations in larval settling as well as environmental fluctuations may have caused changes in the composition of the benthic molluscan fauna through time and this leads to an increase of faunal diversity within the taphocoenoses over time (Fürsich and Flessa, 1991a). It is likely, however, that continued sampling for living shells over years would lead to stronger similarities in diversity between living and dead faunas. If adequate sampling size for living shells is used, species that are numerically dominant in a census of the live fauna tend to be among the most abundant dead, and species that are rare or absent alive are usually rare among the dead (Kidwell, 2001).

Interestingly diversity of living molluscs was highest on the sandbar. Although located at the border of the tidal flat and therefore running dry at low spring tides, it showed similarity in the diversity with the subtidal samples. Close spatial distance to the spring tide line seems to cause a more important marine than intertidal influence on the sandbar, as is also indicated by the presence of diverse species composition (see above).

Rarefaction curves of the total of shells resulted in expected curves. Diversity was highest in the delta seagrass, since seagrasses in general contain large numbers of organisms. The diversity of organisms within seagrass beds is much higher than in unvegetated surrounding areas like the delta sand (Nybakken and Bertness, 2005). Low species richness in the intertidal curves results again from the extreme living condition on the tidal flat, as outlined above.

Interestingly the rarefaction pattern of the living shells is reverse to the total of shells. Intertidal samples result in flat curves in the rarefaction of the total of shells, but show steep curves in the rarefaction of living shells. More detailed comparisons revealed that in subtidal samples the number

of living individuals was low, whereas the number of species was high. In contrary, the intertidal samples contained more living individuals, but few species. This discrepancy between intertidal and subtidal samples leads to a misleading rarefaction result. Consequently it is essential to gain higher numbers of living individuals by continued sampling (Kidwell 2001).

Do the dead shells reflect distribution patterns of living molluscs, or is there drifting by wave action?

Two main compositions in molluscan assemblages are evident: one characterizes the intertidal, and the other one the subtidal, with exception of the delta sand, whose molluscan composition is rather unique. Obviously the molluscan fauna of the Isonzo tidal flat is not randomly distributed, but individual species have their peak distribution in particular environments.

Both Cluster and nMDS display a common pattern: adjacent samples tend to cluster together, as they tend to have a similar faunal composition. In the living fauna this results from similar habitat preferences. In the analysis of the shelly remains, both original habitat preferences and common response to taphonomic processes cause the close association of nearby samples, as was outlined by Fürsich and Flessa (1991b).

The samples of the inner and the outer tidal flat showed high similarity in their faunal composition. On the other hand, samples of the sandbar, the channel, the shallow subtidal and the delta seagrass were similar to each other. It is important to emphasize that with respect to molluscan composition the sandbar and the channels are more similar to the subtidal than to the tidal flat.

In the nMDS the samples of the sandbar, the channel and the shallow subtidal always plot together with the delta seagrass samples. This indicates that the sandbar, the shallow subtidal and the channel are somehow a transitional zone from the intertidal to the deeper subtidal environments. The outstanding positions of the delta sand may be caused by the high current energy of this environment; due to the instable sediment and the lack of vegetation this environment is completely different to all other investigated environments.

The pattern was similar in the living and in the dead shells. In general the good match is evidence, that post-mortem processes do not redistribute shelly remains (Fürsich and Flessa, 1991b). The molluscan fauna can therefore be used to define the environments of the subtidal (seagrass, shallow subtidal, sandbar, channel) and the tidal flat (inner flat, outer flat).

Are there differences in the distribution of living and dead shells, concerning abundances and shell size?

Because live individuals of most species were rare, live- dead shell-size comparisons had to be restricted to a few common species. In nearly half of the investigated cases, the size differences were

significant. In most cases, the living shells were smaller, than the dead ones, like in *C. glaucum*, *T. tenuis*, *L. mediterraneum*, *B. reticulatum* and *G. petagnae*.

C. glaucum was the species with the most living shells and was found alive in all sampled zones with exception of delta seagrass. Its distribution seems to be not related to any environmental gradients as they occur from subtidal to high intertidal areas. By trend the living shells were smaller and therefore younger than the dead shells. Anyway, only in two out of nine samples this difference was significant. *C. glaucum* can reach shells size up to 35 mm (Poppe and Goto, 1993), hence living individuals were mainly juveniles.

T. tenuis was found alive in all samples, except in the inner tidal and on the delta sand, where also dead shells were rather rare. The size differences were significant in three out of four samples, which were taken on the sandbar, in the shallow subtidal and in the channel. This species can reach shell-sizes of 30 mm; therefore individuals were rather young as most of them did not measure more than 10 mm.

L. mediterraneum was abundant as dead shells in nearly all environments, except in the inner flat. Small shell size may lead to drifting; anyway live individuals were only frequent in the delta sand. Adult individuals reach 10 mm, hence the found shells must have been juveniles (Poppe and Goto, 1993). As nearly all shells were smaller than 5 mm, this may be a hint to a contemporary colonization event.

Similarly *B. reticulatum* were wide spread, as shells were found in all environments. Living individuals appeared only in the inner flat. The dead shells there were of all size classes, but living shells were smaller than 10 mm, indicating that they were young and of nearly the same age.

G. petagnae lived only in the delta sand. Dead individuals were rarely detected; maybe due to the quite fragile shells. In general the shells were all rather small, as adults reach shell-sizes of 8-18 mm (Poppe and Goto, 1993).

But there were also few living ones that were larger than the dead, like *C. gallina*, *S. plana*, *Tapes philippinarium*. The living individuals of *C. gallina* were found in all environments, except the inner flat and the delta sand and had maximal abundances on the sandbar and in the shallow subtidal. Living shells were significantly larger in three out of four samples, which were all of subtidal provenience. As this species can reach 25 to 50 mm (Poppe and Goto, 1993) the living individuals found were mostly adult.

Living *S. plana* was mainly abundant in the inner and outer flat, dead shells were drifted into the adjacent environments. Adult individuals can reach 30- 65 mm in length (Poppe and Goto, 1993). Living individuals of this species were therefore all juveniles.

Also *T. philippinarium*, which appeared sparsely in the inner flat, were all young individuals, as adults reach 25-57mm (Poppe and Goto, 1993).

5. Conclusion

- (1) Mollusc species on the Isonzo tidal flat exhibit a zonation from the shallow subtidal to the intertidal zone and physical factors force this zonation.
- (2) There are many more dead than living shells.
- (3) Characteristic species on the tidal flat are *Bittium reticulatum*, *Rissoa labiosa* and *Scrobicularia plana*. Characteristic species in the subtidal are *C. gallina* and *L. mediterraneum*.
- (4) Diversity was lowest in the inner and outer tidal flat and highest in the delta seagrass.
- (5) More samples would be necessary to analyse diversity of living shells. But dead shells seem to reflect molluscan fauna very well. Limited distortion is caused by drifting and time-averaging of dead shells on the flat.
- (6) Two main species compositions were found in the molluscan assemblages: one characterizes the intertidal, and the other the subtidal, the delta sand is quite unique.
- (7) In nearly half of the investigated cases, the shell-size differences of living and dead individuals were significant. In most cases, the living individuals were smaller and therefore younger than the dead shells.

6. Danksagung

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8. Appendix

8.1. Abstract

This work investigates the distribution and abundance of bivalve and gastropod species on the tidal flat and delta zone of the Isonzo River in the Gulf of Trieste (Northern Adriatic Sea), to provide a dataset for comparison with fossil examples from Austria. A total of 24,922 molluscs from fifteen tidal flat and fourteen sublittoral sites were analysed for species composition and shell-size distribution of living and dead molluscs. The mollusc species exhibited a zonation from the intertidal to the shallow subtidal zone. Physical factors as aerial exposure, salinity, temperature and pH forced this zonation, as living conditions on the tidal flat are extreme. Characteristic species on the tidal flat were *Bittium reticulatum*, *Rissoa labiosa* and *Scorbicularia plana* and in the subtidal *Chamelea gallina* and *Lentidium mediterraneum*. There were many more dead than living shells and more samples would be necessary to analyse diversity of living molluscs. The diversity was lowest in the inner and outer tidal flat and highest in the delta seagrass. Two main species compositions were found: one characterizes the intertidal and the other one the subtidal, with exception of the delta sand. In many cases the distribution of dead shells corresponds to that of live shells and dead shells seem to reflect the living molluscan fauna very well. Limited distortion is caused by drifting and time-averaging of dead shells on the flat. In nearly half of the investigated cases, the shell-size differences of living and dead individuals were significant. In most cases, the living individuals were smaller and therefore ontogenetically younger than the dead shells.

8.2. Zusammenfassung

In dieser Arbeit werden die Verteilungsmuster und Häufigkeiten von Bivalven- und Gastropoden-Arten im Watt und Deltabereich des Isonzo im Golf von Triest (Nord Adria) untersucht, um einen Vergleichs-Datensatz für fossile Proben aus Österreich zu erhalten. Eine Gesamtanzahl von 24 922 Mollusken von fünfzehn Watt- und vierzehn subtidalen Proben wurden auf ihre Artenzusammensetzung und die Verteilung der Schalengrößen von lebenden und toten Individuen untersucht. Die Molluskenarten wiesen eine Zonierung von den intertidalen Wattflächen zum flachen sublittoralen Bereich auf. Physikalische Faktoren wie das Trockenfallen bei Niedrigwasser, Salinität, Temperatur und pH sind für diese Zonierung verantwortlich, da die extremen Lebensbedingungen auf dem Watt nur von wenigen Arten toleriert werden. Charakteristische Spezies auf der Wattfläche waren *Bittium reticulatum*, *Rissoa labiosa* und *Scorbicularia plana* und in den subtidalen Bereichen *Chamelea gallina* und *Lentidium mediterraneum*. Generell wurden mehr tote als lebende Schalen gefunden und weitere Beprobungen wären notwendig um die Diversität der lebenden Mollusken zu erfassen. Am geringsten war die Diversität im inneren und äußeren Watt, am höchsten dagegen in den seegrassbewachsenen Bereichen des Deltas. Zwei große Artengemeinschaften wurden anhand ihrem Vorkommen unterschieden: die erste besiedelte die intertidalen Flächen, während die andere auf allen subtidal beeinflussten Flächen, mit Ausnahme des Delta-Sand-Bereichs, gefunden wurde. In den meisten Fällen entsprach die Verteilung der toten Schalen denen der lebenden und die toten Schalen scheinen die lebende Molluskenfauna relativ gut zu repräsentieren. Geringfügige Veränderungen wurden durch Verdriftung toter Schalen und Vermischung unterschiedlich alter Molluskengesellschaften verursacht. In nahezu der Hälfte aller untersuchten Proben waren die Unterschiede in der Schalengröße zwischen lebenden und toten Individuen signifikant. In den meisten Fällen waren die lebenden Mollusken kleiner als die toten Schalen und damit ontogenetisch jünger.

8.3. Lebenslauf

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