High dead-live mismatch in richness of molluscan assemblages from carbonate tidal flats in the Persian (Arabian) Gulf

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1. Introduction

The quality of the fossil record as a reliable stock of biological information from deep time is an ongoing concern in paleontology when it comes to reconstructing past ecosystems, evolutionary and diversity trends over time, and extinction rates (Boucot, 1953; Kowalewski and Bambach, 2003; Patzkowsky and Holland, 2012). Tackling these questions implies quantification of paleobiological signals. This makes it crucial to assess the degree to which the composition of ancient living communities can be estimated from what is preserved in fossil assemblages (FAs). The formation of FAs involves a range of taphonomic biases that distort the structure of the original biological signals (Kidwell and Flessa, 1996; Kidwell, 2001a). To understand the effects and magnitude of these biases, an actualistic approach has been envisaged for decades by paleontologists, who paved the way to assessing the problem of fidelity of FAs by conducting so-called live-dead (LD) agreement studies in different marine and terrestrial habitats (Johnson, 1965; Peterson, 1976; Staff et al., 1986; Tietze and De Francesco, 2012; Albano, 2014; Zuschin and Ebner, 2015). LD studies evaluate how faithful modern death assemblages (DAs) of paleontologically relevant taxa (i.e., bearing potentially fossilizable, biomineralized hard parts) are to their counterpart living assemblages (LAs) in terms of community composition (measured by its species richness, relative abundance, and evenness) (Kowalewski et al., 2003; Kidwell, 2013). The most important trait of DAs lies in the fact that time-averaging is inherent to their formation, meaning DAs consist of temporal integration of the rank-order of species abundance (Kidwell, 2001b, 2002). The analysis of numerous datasets of molluscan assemblages, based on standardized metrics, has yielded encouraging results on the LD preservation of the rank-order of species abundance (Kidwell, 2001b, 2002).
are also important to address questions that involve temporal dynamics of ecological systems at decadal to millennial scales (Kidwell and Tomašových, 2013). The latter temporal framework escape any possible biodiversity survey at the human life-span scale. Stochastic demographic drifts and short-term habitat instability lead to turnover in dominance of species with different habitat optima, flattening the rank-order abundance curve and lengthening the rare species tail (McGill, 2003; Kidwell and Tomašových, 2013). Therefore, compared to LAs, DAs display an increase in alpha (site scale) and gamma (habitat scale) diversity and a decrease of beta diversity (or variation in community composition) (Tomašových & Kidwell, 2009). As a result, DAs capture a greater share of the regional species pool. This allows for less sampling effort in any survey aimed at inventoring the diversity of a study area (Albano and Sableti, 2011; Weber and Zuschin, 2013; Zuschin and Ebner, 2015). An important application of DAs lies in their potential use as a proxy for strong recent ecological shifts caused by anthropogenic impact. This is because DAs display taphonomic inertia, namely a lag of response in compositional turnover to changing environmental conditions (Kidwell, 2007, 2013; Korpanty and Kelley, 2014; Leshno et al., 2015; Albano et al., 2016): human-driven changes run at a higher rate than processes involved in the formation of DAs.

The current study addresses the compositional fidelity of molluscan DAs to LAs from tidal flats in a modern sub-tropical carbonate setting in the Persian (Arabian) Gulf (Indo-West Pacific province). Kidwell et al. (2005) found lower time-averaging in molluscan DAs from subtidal, tropical, carbonate environments, than in adjacent siliciclastic deposits. They found comparatively higher rates of shell loss in carbonate settings due to intense bioerosion and dissolution, which compositionally bias the resulting DAs due to taxonomic differences in shell durability. Therefore, carbonate environments are expected to display a higher temporal resolution than siliciclastic ones, but be compositionally more biased. A narrow window of time-averaging implies less time for environmental conditions in a habitat to change, and a decreasing probability of immigration of exotic species from the regional species pool into a habitat. Therefore, when comparing carbonate with siliciclastic settings, dead-live richness ratios are expected to be lower (D/L ~ 1) and the percentage of species in DAs represented in LAs is expected to be higher. Regarding rank-abundance in species composition, differential shell loss fosters lower fidelity, but higher rates of overall shell loss favor temporal autocorrelation (because DAs would be further dominated by shells of recently dead (identifiable) individuals (see Tomašových and Kidwell, 2011 for a detailed discussion on how temporal autocorrelation affects DAs)), therefore enhancing fidelity in rank-abundance. The primary goal of this study is to test whether these predictions hold in an intertidal carbonate environment.

Moreover, studying LD agreement in tidal flats is interesting because these sedimentary environments are frequently recorded throughout the Phanerozoic (Wanless, 1975; Pratt and James, 1986; Rameil, 2008). There are numerous examples from the Cenozoic of Europe (Lukeneder et al., 2011; Zuschin et al., 2011; Zuschin et al., 2014). Moreover, LD studies conducted in sub-tropical to tropical settings are scarce (Miller, 1988; Zuschin et al., 2000; Zuschin and Oliver, 2003b) and have focused on hard substrates or seagrass bottoms (Zuschin and Stachowitsch, 2007; Ferguson and Miller, 2007; Sørensen and Sørlby, 2013). The current paper stands as the only molluscan LD agreement study of tropical soft sediments in the Indo-West Pacific province – other than the study by Zuschin and Ebner (2015) in the Red Sea – and it is one of the few evaluating molluscan assemblages associated with mangrove ecosystems. Therefore, in this study, we specifically evaluate how faithfully molluscan DAs preserve the community composition of LAs, focusing on species richness, evenness, proportional abundance, beta diversity and feeding guild structure.

2. Materials and methods

2.1. Study area

The studied material comes from the localities of Umm al-Quwain (UAQ) and Al Rams (near Ras al-Khaimah (RAK)). Both localities lie on the southern coastline of the Persian (Arabian) Gulf, in the United Arab Emirates (Fig. 1A). The Gulf is a marginal epicontinental sea located in the Indo-West Pacific biogeographic province, with an average depth of 35 m. It is connected with the Indian Ocean through the 60-km-wide Strait of Hormuz, where it attains its maximum depth (100 m) (Purser and Seibold, 1973). This area is subject to subtropical, arid conditions leading to summer temperatures rising up to 50 °C (mean maximum temperature is 41 °C; Schneider, 1975), whereas winter temperatures seldom drop below 14 °C (Al-Farraj, 2005). These high temperatures coupled with partial isolation from the Indian Ocean foster evaporation and give rise to salinities up to 70 ‰ in lagoons (Purser and Seibold, 1973). The temperature of surface waters varies from 11.5
to 36 °C (Grandcourt, 2012). Mean annual precipitation reported for the Ras al-Khaimah area is 120 mm while mean spring tide ranges from 1.70 to 1.90 m (Goudie et al., 2000). At Ras al-Khaimah, waves higher than 2.44 m are highly unlikely to occur, most probably from December to March when the shimal winds blowing from the NW are most prevalent (Purser and Seibold, 1973; Goudie et al., 2000).

The studied localities are associated with carbonate barrier island-lagoon systems (Evans, 1970) (Fig. 1B). Carbonate mudflats with scattered shrubs of the mangrove Avicennia marina (Forsskål) Vierhapper, 1907 developed along a network of several tidal channels a few meters wide (Schneider, 1975; Al-Farraj, 2005; Rankey and Berkeley, 2012). We observed in the field that the sediment consists of poorly sorted carbonate mud with subsidiary fine- to coarse-grained bioclastic material. In the most proximal part of some channels, abundant individuals of the gastropod Cerithideopsis cingulata (Gmelin, 1791) crawl across the mudflats, while other molluscs are rare. Crabs and “Arencola-like” polychaetes are also frequent in the carbonate mudflats. Dead individuals of the venerid Pelecyora cf. ceylonica (Dunker, 1865) are often found articulated, forming clumps, and lying in a “butterfly” fashion on the sediment surface. Likewise, shell lags may form along the channel margins, while characteristic patches of the algae Chaetomorpha cover the bottom of the channels. These patches may act as a shelter for the gastropod Clypeomorpha bifasciata (G.B. Sowerby II, 1855), rare archaeogastropods, and bivalves. Towards the distal part of the channels, venerid bivalves become more frequent, some of which are alive. In contrast, Archaeogastropoda, C. bifasciata along with Pirella conica (Blainville, 1829) and C. cingulata prevail in the littoral and supralittoral zones. The channels have carved up older beach rock. In these hard substrates the gastropods Planaxis sulcatus (Born, 1778), C. bifasciata, Lunella coronata (Gmelin, 1791) and Osilinus kotschyi (Philippi, 1849) aggregate in small colonies several meters above the water line.

2.2. Fieldwork methods

Fieldwork was conducted during summer 2003. Six sampling sites were randomly selected in tidal flats at the locality of Al Rams (samples RAK1 to RAK5) and Umm al-Quwain (UAQ) (Table 1). The RAK site has been recently urbanized. A cylindrical frame of 25 cm in diameter was used to collect bulk samples of sediment to a depth of about 1 cm from the surface. Most of the living macroscopic individuals were identified, counted and released in the field. The bulk samples were screened through a 1 mm mesh. Since the sieved bulk samples were still very large, they were split into subsamples. For the DAs, subsamples were sorted to a minimum of 1000 body parts and counted, while for the LAs the whole bulk samples were sorted due to comparatively low numbers of individuals. Bivalve abundance was quantified by adding the abundance of articulate specimens to half the abundance of left plus right disarticulated valves.

Many specimens were affected by microbioerosion and abrasion to various degrees, therefore only specimens allowing identification were considered. To avoid fragmentation bias in identification, only specimens with more than 50% of the shell complete were considered (Albano and Sabelti, 2011). In particular, only bivalves preserving the umbonal area and gastropods preserving either the apex or the aperture were counted. Under these criteria, specimens were sorted to species level.

Taxonomic identification to species level was attempted whenever possible based on literature on molluscan faunas of the region (e.g., Bosch et al., 1995; Zuschin and Oliver, 2003a; Zuschin et al., 2009; Janssen et al., 2011); otherwise identification was left in open nomenclature.

3. Data analysis

Analyses were performed at two different scales of spatial resolution: at site and at habitat scales. For computation, site scale refers to a within-site comparison of DA and LA samples while habitat scale refers to a comparison of pooled DAs with pooled LAs samples (e.g., Tomášových and Kidwell, 2010b). To evaluate the influence of mixing due to post-mortem lateral transport on LD fidelity, we computed the proportions of shells of taxa attributed to intertidal and subtidal habitat types (inter-habitat shell mixing) (Fig. 2). Habitat preferences of taxa were largely gathered from literature on mollusks from the study area (e.g., Bosch et al., 1995; Janssen et al., 2011). Taxa that occur both in intertidal and subtidal habitats were coded as intertidal to prevent overestimation of out-of-habitat occurrences (therefore it is a conservative approach). In subsequent analyses, we report the results of LD comparisons 1) when DAs include both intertidal and subtidal shells, and 2) factoring out subtidal shells to check for an effect size.

LAs had smaller sample size than DAs. Therefore, in multivariate analyses, DAs were resampled without replacement (100 iterations) to the sample size of the corresponding LAs to avoid the inflation of dissimilarity related to unequal sample sizes (Lande, 1996; Tomášových and Kidwell, 2009). Sample-size standardization is also necessary to factor out the effect of excess richness from larger sample sizes (Kidwell, 2002; Olszewski, 2010), which might mask the effects of time-averaging on the diversity of DAs (Tomášových and Kidwell, 2009). Unless otherwise stated, the analyses are computed with 95% confidence intervals obtained through the percentile method (Kowalewski and Novack-Gottshall, 2010) around the mean of the 100 replicate values.

For the habitat-scale comparison of rarefaction curves, richness of the pooled LAs was extrapolated to the sample size of DAs following the method of Chao et al. (2014), with confidence intervals obtained by their bootstrapping method.

LD fidelity of diversity partitioned into alpha (within-sample), beta (between-sample) and gamma (sum of all samples) (Tomášových and Kidwell, 2009) components was addressed using Shannon entropy converted into its “numbers equivalents” by taking its exponent (Hill, 1973; Jost, 2006, 2007). Conversion of entropy to numbers equivalents provides the number of equally-frequent species (or communities) which would yield the same diversity value as the data. Numbers equivalents convey the combined effect of richness and evenness (Heip et al., 1998) and fulfill the “doubling” property because they are additive (further details in Jost, 2007; Olszewski, 2010; Tomášových and Kidwell, 2010b). Direct partitioning of Shannon entropy without such conversion can yield counterintuitive and misleading results (Jost et al., 2010).

Evenness at site scale was evaluated through the Probability of Interspecific Encounter (PIE = [N / (N − 1)](1 − Σpi)), where N = sample size, S = richness, pi = proportion of species (Hurlbert, 1971; Olszewski and Kidwell, 2007). PIE theoretically varies from ~0 to 1 (all species equally common) (Kidwell, 2008). Fidelity in evenness was measured as the difference between that of the DA and that of the corresponding LA (ΔPIE) per site and ranges between −1 (DA more even than LA) and +1 (DA more even than LA). PIE is insensitive to differences in sample size and number of stations/sites incorporated into

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Table 1: Facies where samples were retrieved.

<table>
<thead>
<tr>
<th>Samples/sites</th>
<th>Facies</th>
</tr>
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<tbody>
<tr>
<td>RAK1</td>
<td>Tidal flat in the upper intertidal (close to the algal mat zone) with Cerithideopsis cingulata.</td>
</tr>
<tr>
<td>RAK2</td>
<td>Tidal flat close to a channel; sample between pneumatophores of Avicennia.</td>
</tr>
<tr>
<td>RAK3</td>
<td>Tidal channel with archaeogastropods and hermit crabs.</td>
</tr>
<tr>
<td>RAK4</td>
<td>Outer tidal channel with venerid “butterflies”; tidal flat with many exposed, articulated Pelecyora cf. ceylonica.</td>
</tr>
<tr>
<td>RAK5</td>
<td>Macroalgae in the upper intertidal along the main tidal channel; sample close to the shoreline below beach rock.</td>
</tr>
<tr>
<td>UAQ</td>
<td>Tidal flat close to Avicennia; surface covered by algal patches.</td>
</tr>
</tbody>
</table>
the data set (Olszewski and Kidwell, 2007). To evaluate the relationship of evenness and richness at site scale, we cross-plotted evenness vs. differences in richness measured as $\Delta S = \log_{10} \text{(dead S)} - \log_{10} \text{(live S)}$ (Olszewski and Kidwell, 2007).

We also calculated the indices proposed by Kidwell and Bosence (1991): the percentage of species found in LAs occurring in DAs and the percentage of species found in DAs occurring in LAs, which we indicate by F1 and F2, respectively (following Ritter and Erthal (2013)).

LD differences in species composition were tested using nonparametric permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). A test of homogeneity of multivariate dispersions (PERMDISP) of the DAs and LAs was performed prior to PERMANOVA to account for potential heteroscedasticity (Anderson, 2001, 2006). The significance of the fitted model for multivariate dispersions was evaluated using 999 permutations (Oksanen et al., 2016). These analyses were conducted on proportional abundance to check the contribution to group differences of the most abundant species. Transformed proportions were progressively down-weighted (square-root, fourth-root and presence-absence) to evaluate dead-live differences produced by rare species (Clarke and Green, 1988; Clarke et al., 2014).

To further visualize the patterns of compositional similarity between LAs and DAs we used the Bray-Curtis distance measure and performed nonmetric multidimensional scaling (NMDS) as an ordination method. Fidelity of rank-abundance was tested using Spearman’s rho rank-order coefficients, after removing the double absences that might inflate the correlation (Kidwell, 2001b; Zuschin and Ebner, 2015). Temporal and spatial factors affect the patterns of richness, abundance and beta diversity in DAs (Kidwell, 2008; Tomašových and Kidwell, 2009). For example, pooling snapshot censuses of LAs over a time series simulates to some degree the effects of time-averaging on DAs (Peterson, 1977). Pooling temporal replicates of LAs therefore reduces LD mismatch in richness. For abundance, however, the pattern may be opposite. Lockwood and Chastant (2006) pooled temporal replicates of LAs encompassing a period of 20 years and found that rank-correlation decreased as the sampling-period of LAs was longer. This effect of higher fidelity of rank-abundance when DAs are compared to snapshot LAs might be explained by temporal autocorrelation (Tomašových and Kidwell, 2011). Similarly, pooling spatial replicates of LAs from sites scattered over a habitat simulates to some degree the effect of spatial mixing by time-averaging and post-mortem lateral transport naturally affecting DAs. This means that, since DAs capture the habitat composition at smaller spatial scales than LAs due to temporal drifts in community composition and lateral transport, a DA on a site might be expected to display higher fidelity to habitat (pooled spatial replicates) LAs. Therefore, we calculated rank-correlation between each spatial replicate of DAs and pooled spatial replicates of LAs to test whether the correlation was stronger than that of DAs vs. LAs at within-site level. We
consider a higher rank-order correlation of DAs vs. LAs at within-site level as a proxy for temporal autocorrelation.

Fidelity of feeding guild structure was assessed on square-root transformed proportional abundances using the Bray-Curtis distance measure in ordination space, whereas feeding guild rank-abundance was tested with Spearman’s rho coefficient. We use square-root transformation to de-emphasize possible inflation in fidelity by temporal autocorrelation. Feeding guild categories were adopted from Rueda et al. (2009), and information on feeding guild behavior of particular taxa was compiled mainly from Beesley et al. (1998) and Todd (2001). All statistical analyses were performed in the R statistical environment, version 3.3 (R Development Core Team, 2016).

4. Results

4.1. Abundance and richness

7193 mollusks were collected, representing 55 species of bivalves from 23 families, 77 species of gastropods from 38 families, and 1 scaphopod species. Out of 4369 gastropods, 25% of the individuals were found alive. For bivalves, out of 2821, 29.9% were alive, and the only 3 specimens of Scaphopoda belong to the DAs. Only two species were found exclusively in LAs: the muricid gastropod Semiricina cf. rissoti (Petit de la Saussaye, 1852) (1 specimen) and the pyramidalid gastropod Odostomia sp. 2 (3 specimens).

4.2. Spatial mixing at inter-habitat level

The proportion of subtidal (out-of-habitat) individuals in DAs increased from 3.1 to 9.5% at site scale, except for site RAK5 where the figure went up to a 38% of subtidal individuals in the DA. At habitat scale (total number of individuals for pooled samples), the proportion of subtidal individuals in DAs went up to a 38% of subtidal individuals in the DA. At habitat scale, out of 18 species present in LAs, only two are absent in DAs, and these represent a singleton and one species with 3 specimens (mean F1 ~83%) (Fig. 4A). When subtidal taxa were factored out, there were not remarkable changes. Regarding the F2 index, at site scale, the average values ranged from ~6 (RAK5) to 30% (UAQ) (grand mean = 21.5%) (Fig. 4B). At habitat scale, an average ~17% of DAs species were also found in LAs. Without subtidal taxa in DAs, F2 ranged from ~8 (RAK5) to ~47% (UAQ) (grand mean = 27.8%), and an average 24.4% at habitat scale.

4.3. Fidelity of richness and diversity partitioning

DAs displayed higher richness than LAs at both site and habitat scales. Individual rarefaction curves at habitat scale showed a rapidly flattening curve for LAs, while the curve for DAs was still rising (Fig. 3A). At habitat scale (total number of individuals for pooled LAs = 1938) (Fig. 3A), DAs were nearly five times richer than LAs (D/L = 4.27). At site scale (Fig. 3B), rarefaction showed that species richness in DAs was over four times higher than in LAs on average (mean D/L = 5.52), with a median value of approximately four (see boxplot of Fig. 3B). Mean DL richness ratio at site scale decreased a 20% (30% at habitat scale) when factoring out subtidal taxa.

As regards diversity partitioning, alpha and gamma numbers equivalents displayed higher diversity in DAs than in LAs (Fig. 3C). We found that alpha diversity was about four times bigger in DAs than in LAs (D/L = 4.27), while gamma was ~2.6 times more diverse in DAs than in LAs. For beta diversity, however, LAs were only 1.53 times more diverse than DAs (beta diversity is reduced a ~34% when comparing LAs to DAs). After factoring out subtidal taxa in DAs, the D/L ratio decreased a 22% for alpha, a 29% for gamma, and beta diversity displayed a ~41% reduction from LAs to DAs.

F1 index values ranged from ~79 (RAK5) to 94% (RAK2) (grand mean = 86.94%, for the 100 size-standardized replicate datasets). At habitat scale, out of 18 species present in LAs, only two are absent in DAs, and these represent a singleton and one species with 3 specimens (mean F1 ~83%) (Fig. 4A). When subtidal taxa were factored out, there were not remarkable changes. Regarding the F2 index, at site scale, the average values ranged from ~6 (RAK5) to 30% (UAQ) (grand mean = 21.5%) (Fig. 4B). At habitat scale, an average ~17% of DAs species were also found in LAs. Without subtidal taxa in DAs, F2 ranged from ~8 (RAK5) to ~47% (UAQ) (grand mean = 27.8%), and an average 24.4% at habitat scale.

4.4. Fidelity of evenness

Comparison of PIE of DAs and LAs (Fig. 5A) showed that DAs were more even than LAs both at site and at habitat scale. Dispersion of evenness values in DAs was relatively narrow (varying from 0.81 to 0.94), whereas it was more heterogeneous in LAs (0.10 to 0.83). Cross-plots of live-dead differences in evenness versus richness (ΔPIE vs. ΔS) fell in the upper right quadrant (Fig. 5B). We did not find relevant changes in these patterns by factoring out subtidal shells. It is apparent in our dataset that differences in evenness increased as differences between richness in DAs and LAs became larger, both variables displaying a strong positive linear correlation (r = 0.86, df = 4, p = 0.03). Rank-abundance curves summarize the differences in richness and show how the long tail of rare species in DAs increases their evenness (McGill, 2003) (Fig. 6).

4.5. Differences in species composition

For location of group centroids the PERMANOVA test yields different results: in contrast to the proportions matrix, subsequently transformed proportion matrix is significantly different (see Table 2), with a LD mismatch of ~45% for presence-absence matrix. LD fidelity improved an average ~19% by factoring out subtidal taxa. NMDS ordination shows that, except for the LAs at sites RAK2 and RAK5, dispersion of the groups is...
relatively similar, and although both groups plot clearly separated, they display very close location (Fig. 7).

Spearman’s rho coefficients were all positive and significant at site and at habitat scales, except for sites RAK2 and RAK5. At site scale, the mean value of Spearman’s rho for the six sites was 0.40 (Fig. 8). Spearman’s rho coefficients of DAs at site scale vs. pooled LAs were lower than those for within-site rank correlation, except for the two outliers in LAs (RAK2 and RAK5 sites) (Fig. 8). For habitat scale in both assemblages, rank-order Spearman correlation was lower (rho = 0.37) than at site scale except for the two outliers (RAK2 and RAK5) (Fig. 8). Exclusion of subtidal taxa improved fidelity a 22% on average.

4.6. Fidelity of feeding guild structure

The Spearman rank-order correlation coefficient attained a high value (rho = 0.89, p < 0.001) for pooled samples when comparing DAs vs. LAs based on 10 feeding guild categories (Fig. 9A). Microalgae herbivores, deposit feeders, filter feeders and symbiont-bearing species were the most abundant groups in both LAs and DAs. For these four categories, all but deposit feeders shared the same rank in both assemblages. NMDS ordination of feeding guilds shows that similarity among sites was also greater in DAs than in LAs (Fig. 9B). Even though DAs and LAs displayed different dispersion in the ordination space (PERMDISP: F = 8.354, p = 0.002), the point clouds overlapped (Fig. 9B).

5. Discussion

5.1. Fidelity of richness

In our study, DAs are, on average, over five times richer than LAs at site scale, and nearly five times at habitat scale. These ratios are considerably higher than those reported by Weber and Zuschin (2013) for an inner and outer tidal flat in a siliciclastic, temperate environment in the Adriatic Sea (range 1.06–2.77), and those from a subtropical, mixed carbonate-siliciclastic tidal flat in the northern Red Sea (range 1–2.36) (Zuschin and Ebner, 2015). These results contradict the expectation of a high fidelity in D/L richness ratios for carbonate environments. An important factor contributing to notably high D/L ratios is a large window for time-averaging (Kidwell, 2002). The window may be larger with 1) a high degree of shell mixing by post-mortem lateral transport, because of the possible input of shells older than the oldest shell of the previous deposit; moreover, mixing processes increase richness (Finnegan and Droser, 2008; Kidwell, 2008); 2) low sedimentation rates because the lower the sedimentation rates, the more pervasive the mixture of young and old cohorts of dead shells; 3) high bioturbation intensity, which may lead to vertical advection of shells, enhancing the mixture
and sequestering shells from the taphonomically active zone (TAZ) (Tomašových et al., 2014); 4) low rates of shell loss to bioerosion and dissolution (Kidwell et al., 2005); 5) early diagenetic cementation fostering durability of shells in DAs (Tomašových and Zuschin, 2009).

Other factors for high D/L ratios include high patchiness of LAs. This is because at a given spatial scale, since DAs are homogenized to some degree, sites with few species in the LA may produce a high D/L ratio. Another factor is undersampling of LAs (Kidwell and Bosence, 1991), which can be spatial (non-captured patches) or temporal (snapshot censuses do not capture temporal variability in community composition), and, finally, anthropogenic impact affecting the diversity of living communities (decreasing their richness and evenness structure) (Kidwell, 2007; Johnston and Roberts, 2009). The following chapters address individually the above factors in our study.

5.1.1. Influence of post-mortem transport on fidelity of richness

Marine DAs reflect the product of shell mixture resulting from 1) post-mortem lateral transport, 2) bioturbation, and 3) time-related processes (e.g., temporal variability of LAs, lateral drift of subenvironments and/or microhabitats during time). The former two processes are also enhanced by time, which provides a window of opportunity for them to operate on DAs (Tomašových and Kidwell, 2009). We mention time-related processes separately to highlight that, in the absence of transport and bioturbation, DAs will still record an increase in richness with respect to LAs (on average by a factor of 2.1 each 1000 years) (Tomašových and Kidwell, 2010b). The effects of time-averaging alone on composition of DAs, however, will be relatively homogeneous (i.e., small variability of DA distances-to-centroid in multivariate space; increasing time-averaging would make each site to locate closer and closer to the compositional centroid) (Tomašových and Kidwell, 2011). On the contrary, the mixing effects of post-mortem lateral transport may be heterogeneous when there are within-habitat differences in the intensity of tractive processes (e.g., a tidal channel vs. a sheltered mudflat). Therefore, in such habitats, and all else being equal among sites (i.e., in situ hard part input from dead organisms and vertical advection intensity) the LD mismatch in richness is expected to be higher for subenvironments subject to a greater intensity of within- and out-of-habitat transport (Dominici and Zuschin, 2005; Zuschin et al., 2005). If, on top of that, the counterpart LA is patchy (i.e., representing a specific microhabitat that harbors a small fraction of the diversity of the habitat), the LD mismatch will be maximal at scale. Site RAK5, located near the main tidal channel, serves as an example. The DA at this site contains about 40% of out-of-habitat individuals (Fig. 2), producing a D/L richness ratio of ~14 (D/L = 11 factoring out subtidal taxa). This is most likely the reason why the DA of this site is located further away from DAs centroids in NMDS plots (Fig. 7).

5.1.2. Early cementation

Small and fragile taxa might be differentially more vulnerable to loss due to taphonomic processes, which might affect the LD fidelity regarding both richness and relative abundance patterns (Korpanty and Kelley, 2014). We found that frequent small and delicate shells (e.g., Jitlada arsinoensis and Tornatina spp.) in the DAs were cemented, as is to be expected in an area characterized by carbonate supersaturation (Kendall and Alsharhan, 2011). Cementation, which takes less than 1000 years in this area (Shinn, 1969), might counteract to some degree the effects of microbioerosion and abrasion (Tomašových and Zuschin, 2009).

5.1.3. Patchiness in LAs

The observed decrease of D/L richness from site to habitat scale together with the wide range in F2 values (Fig. 4B) points to a high patchiness in LAs. As an example, RAK2 was sampled below Avicennia pneumatophores near a channel. Only P. conica and Assiminea sp. were found in the LA (which conforms to the reports of Feulner and Hornby (2006) on P. conica sometimes climbing Avicennia pneumatophores and Assiminea seeking shelter in saltbushes) while the rarefied DA contained ten species out of which eight are exotic to this microhabitat. An F2 value of 17% at habitat scale represents an extremely low figure in comparison to those of snapshot censuses found by Kidwell and Bosence (1991), Zuschin and Oliver (2003b) and Lockwood and Chastant (2006). The only study with comparable results (F2 ~20%) is that of Ritter and Erthal (2013) for lagoons in southern Brazil. In our study, the F2 value at habitat scale is explained by the patchiness of the LA in RAK2 and the high degree of shell mixture from lateral transport in RAK5 (Fig. 4B).

5.2. Fidelity of diversity partitioning

We found that alpha and gamma components of diversity are larger in DAs than in LAs, while for beta it was the opposite (beta was larger in LAs than in DAs), which is consistent with the meta-analytical results by Tomašových and Kidwell (2009). It is worth highlighting that our dead/live ratio for alpha (D/L > 4) is larger than the largest reported value while for gamma the ratio we found fell within the upper part of the reported range (Tomašových and Kidwell, 2009). After correcting for subtidal (out-of-habitat) shells, we found that post-mortem transport inflated alpha and gamma by 28 and 42%, respectively. The tractive processes that transported the subtidal shells out into intertidal environments operate also within-habitat, thereby influencing the DL.

Table 2

Differences in composition between DAs and LAs (group dispersion and group centroid location) in Bray-Curtis dissimilarity space. It is computed for proportions and transformations that progressively down-weight the influence of the most abundant species. R² provides the effect size regarding how much variability in overall compositional difference is explained by differences between the groups (DAs and LAs). These results show that the highest fidelity is attained considering the most abundant species (proportions), and the highest mismatch regarding species presence-absence. The last four rows are computed for DAs with subtidal taxa factored out (LD mismatch is reduced on average a 19%).

<table>
<thead>
<tr>
<th>Tests</th>
<th>Group dispersion</th>
<th>Group centroid location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameters</td>
<td>PERMDISP</td>
<td>PERMANOVA</td>
</tr>
<tr>
<td>Proportions</td>
<td>df F p</td>
<td>df F R² p</td>
</tr>
<tr>
<td>1</td>
<td>4.602 0.060</td>
<td>1.385 0.122 0.173</td>
</tr>
<tr>
<td>Square-root proportions</td>
<td>2.826 0.130</td>
<td>2.802 0.219 0.001</td>
</tr>
<tr>
<td>Fourth-root proportions</td>
<td>1.407 0.259</td>
<td>5.150 0.340 0.003</td>
</tr>
<tr>
<td>Presence-absence</td>
<td>0.378 0.643</td>
<td>8.136 0.449 0.002</td>
</tr>
<tr>
<td>Proportions</td>
<td>6.437 0.0134</td>
<td>1.106 0.100 0.379</td>
</tr>
<tr>
<td>Square-root proportions</td>
<td>3.863 0.073</td>
<td>1.979 0.165 0.018</td>
</tr>
<tr>
<td>Fourth-root proportions</td>
<td>2.014 0.170</td>
<td>3.796 0.275 0.004</td>
</tr>
<tr>
<td>Presence-absence</td>
<td>0.622 0.536</td>
<td>5.410 0.391 0.001</td>
</tr>
</tbody>
</table>
mismatch in diversity. As for beta diversity, it was underestimated by a 34% in DAs with respect to LAs (a 41% factoring out subtidal shells). This leads to the conclusion that within-habitat differential transport increases beta diversity in DAs. Our results suggest strong underestimation of beta diversity in DAs (Tomašových and Kidwell, 2009).

5.3. Fidelity of proportional abundance

The most abundant species in LAs were also the most abundant in DAs, as was observed in other studies (Kidwell, 2001b; Kowalewski et al., 2003; Weber and Zuschin, 2013; Zuschin and Ebner, 2015). At site scale, Spearman’s rho values for DAs vs. LAs were positive and relatively high (range from 0.08–0.60; grand mean = 0.41) (Fig. 8). At habitat scale the Spearman rank-correlation attains a significant rho value of 0.37, which lies below the lower limit of the range reported by Kidwell (2001b) for the same substrate and habitat types. This is consistent with a higher compositional bias in carbonate environments (Kidwell et al., 2005).

These values roughly compare to those reported by Weber and Zuschin (2013) and Zuschin and Ebner (2015), representing soft siliciclastic substrate–temperate climate and soft mixed siliciclastic-carbonate substrate–subtropical climate, respectively. As found here, these studies found a lower rank-correlation at habitat than at site scale. Their Spearman’s rho values are similar to those found by Lockwood and Chastant (2006) for pooled LAs encompassing a period of 20 years. This observation suggests that DAs in our study area are time-averaged to a degree that produces lower rho values.

The high fidelity of DAs to LAs regarding dominant species is supported by a PERMANOVA test performed on untransformed proportional abundances. When compared with the outcome of transformations that increasingly dampen the contribution of the abundant species, the centroids of the groups increasingly and significantly fall apart (Table 2). Therefore, DAs reflect palimpsests of richness, and snapshots of abundance (Kidwell, 2002).

Together with the PERMANOVA results, the higher Spearman’s rho values at site than at habitat scale suggest temporal and spatial autocorrelation exerted by younger dead cohorts of patchy communities (Kosnik et al., 2007; Kidwell, 2007; Albano and Sabelli, 2011; Zuschin and Ebner, 2015; Leshno et al., 2015). This interpretation is further supported by higher Spearman’s rho values for within-site DAs vs. LAs over DA site vs. habitat LA level (Fig. 8). In particular, the largest differences are for sites RAK1 and RAK4, which we interpret to be more temporally autocorrelated (Fig. 8). The opposite pattern is observed for RAK2 and RAK5, which we attribute to the factors discussed in Sections 5.1.1 and 5.1.3.

5.3.1. Influence of shell loss on temporal autocorrelation

Frequent examples of intense microbioerosion affecting living shells of dominant species (e.g., C. cingulata) were observed in this study, which is consistent with high taphonomic alteration rates in carbonate environments reported by Kidwell et al. (2005). This observation underlines how fast severe taphonomic alteration develops in our study area, considering the 4-year life-span of this gastropod (Bagarinao and Lantin-Olaguer, 2000). Assuming a constant rate of microbioerosion, a larger time-frame implies that many shells become unidentifiable if exposed in the TAZ (Davies et al., 1989), fostering temporal autocorrelation.

5.3.2. Influence of bioturbation and sedimentation rates on temporal autocorrelation

Vertical advection (i.e., due to burrowing) may sequester shells from the TAZ (Tomašových et al., 2014), decreasing the correlation between age and taphonomic alteration profile (Flessa, 1993; Martin et al., 1996). The proportion of such sequestered shells depends on habitat-specific sedimentary and biogenic processes. For example, Kidwell et al. (2005) argued that easy re-suspension of organic-rich flocculants in siliciclastic settings hampers the colonization and survival of foulers.
other than microbes, enhancing the preservation potential of dead shells. A significant proportion of sequestered shells might counteract the effects of temporal autocorrelation to some degree. On the Trucial Coast (i.e., southern coasts of the Gulf), lagoonal sediments are subjected to homogenization by bioturbation of abundant infaunal organisms (Wright and Burchette, 1996 and observation by the authors); hence, a notable proportion of shells might be expected to be sequestered from the TAZ in this area.

High sedimentation rates might increase fidelity in embayments such as lagoons and estuaries, because the re-equilibration rate between DAs and LAs positively correlates with sedimentation rates (Kidwell, 2007). In addition, this re-equilibration rate operates through temporal autocorrelation, because the oldest cohorts remain in the TAZ for a shorter time in a high sedimentation rate scenario (Kidwell, 2002). On the Trucial Coast, however, the sedimentation rate is estimated to be 0.5 mm/year (Kinsman, 1969), which is a moderate value. We conclude that temporal autocorrelation is involved to some degree in the formation of DAs in our study area, but high levels of bioturbation and moderate sedimentation rates here suggest that many shells are potentially sequestered from the TAZ.

5.3.3. Anthropogenic impact

Tidal carbonate mudflats with mangroves at RAK and UAQ were reported to have been affected by pollutants before 2003 (stranded oil from spills, industrial and municipal wastewater polluting discharges, heavy metals) (Shriadah, 1998; Shriadah and Al-Ghais, 1999). A good match in rank-order of species abundance does not mean that the area has not been impacted (especially in estuaries and lagoons, which act as sediment traps), because re-equilibration after taphonomic inertia can occur in a time-lapse of a decade or less (Kidwell, 2007; Feser and Miller, 2014). The high F1 value (Fig. 4A) is not suggestive of anthropic impact because there are only two “live-only” species which are numerically unimportant. To explain such high D/L richness ratios, the decrease in richness produced by an impact has to be very strong, but this might notably change proportional abundance as well (Kidwell, 2007). The PERMANOVA test, however, does not detect a significant difference (Table 2).

5.4. Fidelity of evenness

LAs were ~39% less even than DAs on average. This average difference reflects the large unevenness of LAs at sites RAK2 and RAK5 (with differences in evenness of ~86% and 90% with respect to DAs) (Fig. 5A). The smaller range in DA evenness among sites (compared with that of LAs) is explained by homogenization of DAs. This suggests the influence of time-averaging operating on their formation. The LD differences in richness and evenness of the outliers (sites RAK2 and RAK5) (Figs. 5A and B) explain the high alpha and gamma diversity D/L ratios with number equivalents (Fig. 3C).

ΔPIE vs. ΔS cross-plot (Fig. 5B) showed that all of the samples fell within the upper-right quadrant. This pattern is consistent with the DAs having been formed in a framework of long time-averaging, increasing the chances of incorporation of exotic species into the DAs (non-ergodic mixing of Olszewski and Kidwell, 2007). At habitat scale, fidelity of evenness is greater (only site UAQ displays higher evenness), falling between 0.8 and 1.0. RAD curves visualize the DL differences in richness and evenness, as expected in time-averaged DAs (Tomašových and Kidwell, 2010a) (Fig. 6).

5.5. Fidelity of feeding guild structure

Our study points to a high fidelity of trophic structure between DAs and LAs for carbonate tidal flats. Similar conclusions have been reached for terrestrial vertebrate DAs (e.g., Miller et al., 2014). The rank correlation of feeding guild categories yielded a significant high Spearman correlation (ρ = 0.92) for pooled samples (Fig. 9A). NMDS ordination shows overlapping point clouds, but there are different dispersions, DAs being more compositionally homogeneous (Fig. 9B). This feature is to be expected with time-averaging. Rank-abundance is dominated by primary consumers (e.g., filter feeders, grazers, detritivores) (Palmqvist, 1993) over secondary consumers (predators, scavengers and parasites; i.e. carnivores). In a LD molluscan meta-analytical study, Palmqvist (1993) argued that primary consumers had a higher potential of preservation due to their higher abundance in marine ecosystems related to their food requirements. Higher abundances enhance chances of incorporation into fossil assemblages because of the large number of taphonomic filters the shells in DAS have to go through. Molluscan secondary consumers are usually small, motile, and have delicate shells (Palmqvist, 1993), making their shells more easily underrepresented in the fossil record due to taphonomic factors. In our study, for the secondary consumers, only egg and spawn feeders attain higher abundances in LAs than in DAs. Frequent small shells of carnivore taxa such as Odostomia spp. and Tornatina spp. were found cemented in DAs. This is consistent with the higher proportional abundance of these taxa in DAs. Factoring out subtidal shells from the dataset did not change the observed patterns.
6. Conclusions

Detailed investigation of dead and live molluscan assemblages in carbonate tidal flats from the Persian (Arabian) Gulf suggests that substantial time-averaging can occur in intertidal carbonate settings. It is evidenced primarily by very high D/L richness ratios compared to those in other studies. This is probably because rapid cementation plays a role in preserving small, delicate shells that would display lower preservation potential in other environments. Although the analysis suggested temporal autocorrelation operating on DA formation, intense bioturbation might sequester a significant proportion of shells from the TAZ, and moderate sedimentation rates may foster lateral mixing by tidal currents and storms. The degree of lateral mixing by post-mortem transport varies at site scale according to the particular features of the sampled subenvironments. This is evidenced by the proportion of subtidal (out-of-habitat) shells found in the DA at each sampling site. A high degree of post-mortem transport increases the odds of reworking and exhuming old cohorts into surficial layer DAs, expanding the window of time represented in surficial layer DAs. Another effect of differential lateral mixing by post-mortem transport is a 10% increase of beta diversity in DAs. Fidelity of evenness is generally high at site and habitat scales (mismatch is only high at sites with patchy LAs); therefore the large difference in diversity is driven by differences in richness. Rank-abundance Spearman correlation is very high for feeding guild structure, and in general secondary consumers are well represented in DAs when compared to LAs. The input of out-of-habitat shells into DAs did not affect the high LD fidelity of feeding guild structure.

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