

**Explaining high-diversity death assemblages: Undersampling of the living community, out-of-habitat transport, time-averaging of rare taxa, and local extinction**

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## Abstract

Molluscan benthic assemblages provide unique opportunities for understanding both spatial and temporal patterns of biodiversity. Species richness in the shell remains found at a site (i.e. the death assemblage) is typically several times higher than in the counterpart living assemblage, reflecting a complex history of settlement, dissemination and decomposition post-mortem. We used high-density temporal and spatial sampling (>37'000 individuals representing 196 taxa) of a shallow (5-8 m) nearshore sandy habitat off the coast of south-east Sardinia (Italy, Mediterranean Sea) to study the factors responsible for differences in the relative diversity of living and death assemblages. We found that death assemblages at all sites were considerably more diverse than living communities (1.5-3.5x more dead than living taxa after sample-size standardization), with 78% of all taxa solely recovered as empty shells, resulting in low live-dead agreement. By carefully filtering the raw data and combining them with habitat information extracted from the literature, we disentangled the major causes of this discordance and quantified their individual effects. Increased dead diversities could not be attributed to undersampling of the living community, but instead resulted from three phenomena of decreasing importance: the post-mortem, out-of-habitat transport of non-indigenous taxa (57% of dead-only taxa were allochthonous), the time-averaged presence of rare indigenous taxa (40% of dead-only taxa), and the likely local extirpation of a small number of species (3% of dead-only taxa). Our approach demonstrates how ecological inferences based on death assemblages can be improved by restricting analyses to demonstrably indigenous taxa, and highlights how mollusc shell remains can be used to provide information over both ecological and evolutionary timescales.

## 1. Introduction

Molluscan benthic assemblages provide unique opportunities to compare contemporary biodiversity with time-averaged data from the dead record of shell remains. Hard-shelled molluscs are among the most durable taxonomic groups in aquatic ecosystems (Kidwell & Flessa, 1995, Jablonski et al., 2003, Kidwell, 2005, Valentine et al., 2006), and the comparison of molluscan living and death assemblages offers a promising model to study how processes of settlement, dissemination and decomposition after death influence the long-term preservation of species in the fossil record (Warne, 1969, Staff et al., 1986, Kidwell & Bosence, 1991, Kidwell, 2001a, Kidwell, 2001b, Tomašových & Kidwell, 2011). As death assemblages preserve and accumulate specimens over considerable timespans, they often yield species lists more complete than lists obtained from surveys of living communities, even if living communities are repeatedly sampled (Bouchet et al., 2002, Warwick & Light, 2002, Warwick & Turk, 2002, Zuschin & Oliver, 2005, Albano & Sabelli, 2011, Kidwell & Tomasovych, 2013). Comparisons between living and death assemblages can be used to identify recent ecological shifts in benthic communities that occurred, for instance, as a consequence of anthropogenic eutrophication and other human activities (Kidwell, 2007, Kidwell, 2009, Kowalewski, 2009, Kidwell, 2013, Weber & Zuschin, 2013, Kidwell & Tomasovych, 2013). Death assemblages act as unique intermediate stages between living communities and fossil records, and are therefore of great value for understanding spatial and temporal patterns of biodiversity.

Species richness in a death assemblage is typically many times higher than in the corresponding living community (e.g., Carthew & Bosence, 1986, Cummins et al., 1986a, Kidwell, 2001a, Kidwell, 2002b, Kidwell, 2007, Olszewski & Kidwell, 2007, Tomašových & Kidwell, 2009).

67 Increased dead diversities often persist even after correcting for differences in the number of  
68 living and dead specimens recovered in a census (Kidwell, 2001a, Kidwell, 2002b, Kidwell,  
69 2007, Olszewski & Kidwell, 2007, Kidwell, 2009, Tomašových & Kidwell, 2009) and despite the  
70 likelihood of species sampled alive leaving a local sedimentary record (Kidwell & Bosence,  
71 1991, Kidwell, 2001a, Kidwell, 2001b, Kidwell, 2002a). The apparent ‘excess’ or surplus of  
72 species found in the death assemblage compared to the living community is most pronounced  
73 when assessed within a sample (i.e. in alpha diversity), but typically also persists at higher spatial  
74 scales (i.e. gamma diversity) (Carthew & Bosence, 1986, Tomašových & Kidwell, 2009, Kidwell  
75 & Tomasovych, 2013). The ultimate causes of high dead diversities in molluscan benthic  
76 assemblages are multifarious (Kidwell, 2001a, Kidwell, 2009) and systematically addressing  
77 potential confounding factors is essential in order to use these records for the assessment of local  
78 biodiversity.

79 Increased diversity in the dead record can arise artificially if living communities are sampled less  
80 exhaustively than dead communities (Kidwell, 2001a, Kidwell, 2002b, Kidwell, 2009). Many  
81 studies of living and dead communities in marine soft-bottom habitats are based on single  
82 censuses and thus likely provide a rather conservative estimate of contemporary diversity  
83 (Carthew & Bosence, 1986, Kidwell, 2001a, Kidwell, 2001b, Kidwell, 2002a, Kidwell, 2002b,  
84 Kidwell, 2007, Kidwell & Rothfus, 2010). Pooling data from replicate censuses of living  
85 molluscan communities has been shown to improve live-dead agreement (Peterson, 1976,  
86 Carthew & Bosence, 1986, (calculations by Kidwell & Bosence, 1991), Knight, 1988, Staff &  
87 Powell, 1988), and the extent to which communities are undersampled can be quantified by  
88 comparing the observed and estimated species richness of a census. Apart from extrapolating a  
89 species accumulation curve to its asymptote (Gotelli & Colwell, 2011), the true number of

species can also be estimated using nonparametric estimators (Chao et al., 2009). If the degree of sampling completeness in living and death assemblages is similar, high dead diversity may reflect a true taphonomic bias requiring closer examination (Kidwell, 2001a).

Apparent mismatches between living and dead molluscan communities may reflect a variety of biological and physical processes, such as the transport of empty shells of non-indigenous species to the study site post-mortem (Carthew & Bosence, 1986, Henderson & Frey, 1986, Kidwell & Bosence, 1991, Kidwell, 2001a, Kidwell, 2002b). The probability that death assemblages are enriched by allochthonous (non-indigenous) species increases when sampling in heterogeneous habitats, as, for example, when sampling marine soft-bottom habitats in close proximity to rocky shores (Carthew & Bosence, 1986, Kidwell & Bosence, 1991, Kidwell, 2001a). Shells of species indigenous to a location, here defined as species living in the same habitat in which their shells are present in the dead record, can be distinguished from shells of species not likely to occur alive at the study site by compiling habitat information from the literature. If a species has been found alive in similar habitats in previous studies of a region, the species may be part of the indigenous community. In this way species can be classified as either indigenous or allochthonous. The reliability of such classifications can be evaluated by quantifying the proportion of the living community correctly identified as indigenous based on literature sources.

A third hypothesis to explain high numbers of dead-only species after correcting for geographic origin is that these species may be naturally rare, and thus unlikely to be recovered alive without extensive sampling effort (Kidwell, 2002b, Kidwell, 2009). In most studies, dead species richness is heavily influenced by the presence of rare species, which can be recovered in the time-averaged dead record, even if extremely rare (Kidwell & Bosence, 1991, Zuschin et al., 2000,

Kidwell, 2001a, Bouchet et al., 2002, Kidwell, 2002b, Zuschin & Oliver, 2005, Kidwell & Tomasovych, 2013). The concepts of rarity and sampling completeness are closely linked, as high numbers of rare species are one of the hallmarks of undersampled communities (Chao et al., 2009). A large number of rare indigenous dead-only species may characterize living communities substantially dominated by seasonal, patchily distributed, ephemeral, or truly numerically rare species (Kidwell, 2001a, Kidwell, 2002b).

Finally, death assemblages can be enriched with relict shells of species that are no longer present at a site (Kidwell, 2001a, Kidwell, 2002b, Kidwell, 2009, Kidwell & Tomasovych, 2013). Finding locally extinct species in dead records is more likely when time-averaging is strong, when deeper sediment layers become exhumed, or after recent environmental change (Kidwell, 2001a, Kidwell, 2009). While the absence of a comparatively abundant indigenous species from the living community does not prove that it is locally extinct, a few predictors can be used to estimate the probability of recent extirpation. If repeated censuses fail to recover a species expected to be locally abundant despite the regular occurrence of this species in the dead record, this provides a strong indication of local extinction. Furthermore, good candidates for local extinction should be distinctive, and have living individuals that are difficult to confound with dead specimens. The application of stringent criteria can help to reveal dynamic changes in the composition of local molluscan communities, information that is highly valuable both ecologically and in a conservation context.

We used temporal and spatial sampling of diverse nearshore molluscan communities in south-east Sardinia, Italy (flat, subtidal sandy bottoms in 5-8 m depth), to assess the agreement of species diversity in living and death assemblages over space and time, using a dataset of more

134 than 37'000 living and dead molluscs representing 196 taxa. We show how live-dead agreement  
135 of both species abundance and species richness are affected by the presence of large numbers of  
136 dead-only taxa, examine potential causes of live-dead disagreement in turn, and quantify their  
137 relative impact on the surplus of taxa in death compared to living assemblages. Our study shows  
138 how the careful analysis of molluscan living and death assemblages can reveal the underlying  
139 causes of this disagreement, and provide a unique window into the processes contributing to  
140 changes in local biodiversity over space and time.

141

## **2. Materials and Methods**

### **2.1 Sampling sites**

Twelve censuses of living and dead molluscs were carried out at six sites in south-east Sardinia, Italy, between 2008 and 2009 (Figure 1). Sampling sites were extensive, flat, subtidal sandy bottoms in 5-8 m water depth in front of sandy beaches, located at a minimum distance to rocky shores of several hundred meters. Although this part of Sardinia's coastline is not densely populated, all sampling sites show low to moderate degrees of settlement, agriculture, and aquaculture. Two sites, Tortoli (To) and Geremeas (Ge) were sampled in 2009, while four sites, Porto Corallo (PC), Feraxi (Fe), Cala Sinzias (CS) and Solanas (So) were surveyed in both years, providing information on interannual variation in community structure. In addition, PC and Fe were surveyed twice in 2009, providing information on short-term within-season variation in community composition (Table 1).



**Figure 1**

Geographic location of the six sampling sites in south-east Sardinia (Italy). This map was generated in GMT5 (Wessel et al., 2013).



158 **Table 1**

159 Geographical coordinates of the sampling sites, and names, dates and sampling depths of mollusc  
160 censuses.

Site	Geographical coordinates	2008			2009		
		Census name	Date	Depth [m]	Census name	Date	Depth [m]
Cala Sinzias	39° 11' 34.7"N, 9° 34' 3.0" E	CS08	11/09/08	8.1	CS09	02/09/09	8.6
Feraxi a	39° 19' 48.9"N, 9° 36' 16.1" E	Fe08	09/09/08	7.6	Fe09a	27/08/09	8.6
Feraxi b	39° 19' 41.1"N, 9° 36' 21.3" E	-			Fe09b	13/09/09	8.9
Geremeas	39° 9' 19.3"N, 9° 23' 32.3" E	-			Ge09	18/09/09	7.1
Porto Corallo a	39° 25' 30.6"N, 9° 37' 59.1" E	PC08	05/09/08	7.3	PC09a	30/08/09	8.8
Porto Corallo b	39° 25' 23.8"N, 9° 37' 56.5" E	-			PC09b	10/09/09	8.5
Solanas	39° 7' 49.4"N, 9° 25' 50.1" E	So08	04/09/08	5.0	So09	08/09/09	7.2
Tortoli	39° 57' 31.3"N, 9° 41' 23.4"E	-			To09	21/09/09	8.0

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## 2.2 Sampling and taxonomy

Sampling was done by SCUBA at an average depth ( $\pm$  SD) of  $7.8 \pm 1.1$  m on sandy ground (Table 1). For each census, ten separate quadrats of  $1 \text{ m}^2$  were marked using a plastic cord, and the topmost 5–10 cm of sediment were sieved under water using a sieve of 1.3 mm mesh width. Shells, living molluscs and other animals remaining in the mesh were collected into flasks and brought ashore, where samples from separate quadrats were pooled. All living molluscs were identified and counted in Sardinia and released back to the sea. Empty shells were brought to Switzerland for identification.

Goto & Poppe (1991, 1993), Huber (2010), and the internet platform CLEMAM – Check List of European Marine Mollusca (Le Renard, 2015) were used as taxonomic references. In the case of taxonomic disagreements, priority was given to Huber (2010) concerning bivalves and to CLEMAM (Le Renard, 2015) for all other taxa. Identifications of all dead individuals identified in 2008 were reconfirmed after the 2009 survey to prevent potential identification bias. 171 specimens (100 bivalves, 71 gastropods) could not be identified and were excluded from subsequent analyses. These unidentified specimens constituted a negligible fraction of dead individuals (0.5%), were mostly small ( $<5$  mm), often damaged, discolored or bleached, and were never recovered alive. As these unidentified specimens may represent additional taxa and were only recovered in the dead record, our estimates of taxa richness in death assemblages are thus conservative.

The inclusion of broken shells in the dataset was dependent on the extent of the damage: Bivalves were included if the umbo was still present, while gastropods required a complete apex (Cummins et al., 1986b, Kidwell, 2009). These criteria were used to prevent the double counting

of fragmented individuals. Yet, even among undamaged bivalve shells a large proportion of shells were disarticulated, raising the question of how often a census included both valves of a single individual. According to Gilinsky & Bennington (1994), the true number of bivalve individuals of a given taxon in a death assemblage depends on the size of the “sampling domain”, the number of individuals of that species potentially available to be sampled. We performed simulations to estimate the number of unique individuals in each sample of the dead record of bivalves, assuming sampling domains three times the size of an observed collection (1000 iterations per observed sample size) (Gilinsky & Bennington, 1994). The inferred size of the sampling domain is based on two facts: (1) only the uppermost sediment layer was sampled, with additional unsampled shell layers present in the underlying sediment (at least to a depth of 30 cm (A. Bürkli, personal observation), i.e. three times the depth sampled here), and (2) sampling sites showed evidence of considerable disturbance, as suggested by the large proportion of allochthonous individuals in death assemblages (see results). We used corrected abundances in all analyses.

All measures of live-dead agreement were also calculated using both the minimum number of bivalve individuals, assuming that both valves of all individuals were represented in the sample (the “MNI approach”), and the maximum number of bivalve individuals, assuming that each valve represented a unique individual (the “XNI approach”, Gilinsky & Bennington, 1994). All three approaches yielded qualitatively similar results - see Supplementary Tables 1-4 for comparisons between the three methods of bivalve quantification. Minimum and maximum sample abundances of dead bivalves are also provided in Table 2 along with the corrected values. The complete dataset is available at the Dryad doi: XXX. All simulations and statistical analyses were performed using R version 3.0.1 (R Core Team, 2013).

207 **Table 2**

208 Numbers of living and dead taxa and individuals for each census. Taxon numbers reflect the true  
 209 number of independent taxa sampled at each site, and are not standardized by census size. Dead  
 210 individual numbers are corrected for disarticulated valves of single bivalve individuals following  
 211 Gilinsky & Bennington (1994) – all analyses were performed using corrected values. Minimum  
 212 (MNI) and maximum (XNI) dead abundances are provided in the last columns (see methods for  
 213 details). Summary data for 2009 (Total 09) are restricted to GPS coordinates sampled in 2008 to  
 214 facilitate comparison (marked with an asterisk).

Census	Living taxa	Dead taxa	Living individuals	Dead individuals (corrected)	Dead individuals (minimum)	Dead individuals (maximum)
CS08	9	73	115	1219	1054	1299
CS09*	14	127	148	3823	3311	4070
Fe08	10	68	119	1172	992	1259
Fe09a*	21	97	168	1701	1469	1812
Fe09b	21	127	178	6631	5712	7089
Ge09	13	89	450	3206	2726	3439
PC08	9	36	104	305	256	324
PC09a*	25	73	407	1983	1730	2106
PC09b	17	88	408	4784	4147	5099
So08	5	27	30	237	199	254
So09*	14	79	313	2290	1909	2478
To09	22	115	210	7462	6285	8045
Total 08	13	103	368	2933	2501	3136
Total 09	30	157	1036	9797	8419	10466

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### **2.3 Interannual and short-term within-season variation**

Four sites (CS, Fe, PC, So) were sampled both in 2008 and 2009, making it possible to assess interannual variation. We compared these sites with respect to their taxa richness (i.e. total number of taxa), abundance (i.e. total number of individuals), and several measures of live-dead agreement using linear models in which site and year were included as predictors. Two sites were sampled twice in 2009 (PC, Fe) – only the first 2009 censuses for these sites are included in the interannual analysis. These secondary censuses, collected in time intervals of 11 (PC) and 17 (Fe) days, were used to quantify short-term temporal variation. Secondary samples were collected ca. 200 m from the original census site to avoid the resampling of shell-depleted sediments, and are thus not replicates in the strict sense. We computed differences in taxa richness, abundance and live-dead agreement between temporal collections, and compared these to the average difference between randomly chosen censuses carried out in 2009 using non-parametric Wilcoxon rank sum tests. Nonmetric multidimensional scaling (NMDS) using Bray-Curtis dissimilarities of abundance data was carried out using the function “metaMDS” in the R-package “vegan” (Faith et al., 1987, Minchin, 1987) to provide a visual summary of spatial and temporal patterns of biodiversity.

### **2.4 Live-dead agreement in taxa rank abundance**

Nonparametric Spearman rank-order tests (Spearman’s rho) were used to analyze rank-order agreement in taxa abundance. Correlation coefficients between living and dead abundances were obtained for both the full dataset and for a dataset restricted to taxa recovered in the living assemblage.

## 2.5 Live-dead agreement in taxa richness

Diversities (i.e. taxa richness) of dead censuses could be higher than those of living censuses simply because death assemblages typically consist of many more individuals. To control for this potential sampling bias, rarefied numbers of dead taxa were computed individually for all censuses by drawing  $N$ , the number of individuals in the living census, from the dead census for each site. Mean rarefied diversities are based on 1000 permutations. We then computed  $\Delta S$ , which is the logarithmic difference between rarefied dead and living diversity ( $\Delta S = \log(\text{sample-size standardized number of dead taxa}) - \log(\text{number of living taxa})$ ) (Olszewski & Kidwell, 2007).  $\Delta S$  is zero when dead and living diversity are equal,  $>0$  when dead diversity is higher, and  $<0$  when living diversity is higher.

## 2.6 Estimating sampling incompleteness

A taxa accumulation curve shows the increase in the number of recovered taxa for repeated censuses (Gotelli & Colwell, 2011). Each point on the curve indicates the mean number of taxa present in a given number of censuses following permutation. Taxa accumulation curves were calculated using the function “specaccum” in the R-package “BiodiversityR” (Kindt & Coe, 2005) with 1000 permutations. In addition, we estimated the asymptotic minimum taxa richness ( $S_{\text{est}}$ ) for each census based on the number of taxa represented with exactly one individual (“singletons”) and exactly two individuals (“doubletons”) in the sample (Chao et al., 2009). The ratio between the observed ( $S_{\text{obs}}$ ) and estimated ( $S_{\text{est}}$ ) minimum taxa richness provides a second measure of how completely a living or dead census reflects a community’s true taxonomic diversity.

## 2.7 Habitat information

To understand why species diversity is typically higher in dead than in living communities, it is important to know whether a species is indigenous to a sampling site. We evaluated the number of allochthonous (i.e. non-indigenous) taxa recovered in the dead record by extracting habitat information for individual taxa from the literature (references in Supplementary Table 5). For each taxon only habitat information from published ecological studies that found living specimens of the taxon was included – these data were supplemented with information from four systematic reviews (Goto & Poppe, 1991, Goto & Poppe, 1993, Kiliyas, 1997, Huber, 2010, Supplementary Table 5). Habitat information was lacking for a single species (*Copulabyssia corrugata*). An average of 3.4 species-specific and 5.4 genus-specific habitat references (total 8.8) were compiled for each of the remaining 195 taxa (Supplementary Table 6). Each taxon was then classified as either “indigenous” or “allochthonous” (Supplementary Table 6). A taxon was considered “indigenous” when it was more or equally common to soft-bottom habitats than to hard substrates or marine vegetation, and was reported from a depth of 5-10 m at least once. This classification is conservative in as much as euryoecious taxa will not spuriously increase the number of allochthonous taxa, but flexible enough to reflect habitat preferences of taxa with broad biotic and abiotic requirements. When classifications based on species- and genus-specific habitat information disagreed, priority was given to the classification based on species-specific information.

## 2.8 Likelihood of local extinction

Some taxa identified as indigenous based on literature data were common in death assemblages but absent from living communities, suggesting that they may be locally extinct. To assess the



280 probability of the local extinction of these taxa, we developed a set of predictors, including (1)  
281 the number of censuses in which a taxon was present; (2) the probability of failing to distinguish  
282 living from dead specimens, particularly if specimens are very small; and (3) the probability of  
283 taxonomic misidentification when using intact living specimens. We considered local extinction  
284 most plausible when a taxon was found dead in many or all censuses, when living specimens  
285 could easily and unequivocally be recognized as being alive, and when both living and dead  
286 specimens of all age classes had a low probability of misidentification. The mean abundance of a  
287 taxon in death assemblages was not used in the calculation of extinction probabilities.

288

## 3. Results

### 3.1 Summary statistics

A total of 37'463 individuals belonging to 196 taxa of molluscs were found across all censuses of living and death assemblages (Table 2). Most taxa were gastropods (107, 54.6%) or bivalves (84, 42.9%), with only a few scaphopods (4, 2.0%) and polyplacophorans (1, 0.5%). 195 taxa (99.5%) could be identified at least to the family level, 179 taxa (91.3%) at least to the genus level, and 145 taxa (74.0%) to the species level. A total of 2'650 individuals (7.1%) were found alive (Table 2), and these individuals could be assigned to a total of 43 taxa, 21.9% of the total taxa richness. The majority of taxa found alive could be identified to the species level (86.0%), with only two and four taxa identified to the family and genus level, respectively. Despite similar numbers of bivalve and gastropod taxa, bivalves constituted the vast majority of all individuals (80.9%) and made up most of the living community, both in terms of individuals and taxa (see Supplementary Results 1). All censuses except So08 are comprised of >100 living individuals (Table 2), and are thus considered datasets appropriate for rigorous live-dead comparison (Kidwell, 2002a).

Temporal variation in molluscan communities was evident, and while both taxa richnesses and abundances were higher in 2009 than in 2008 at all four sites sampled in consecutive years (PC, Fe, CS and So) (Table 2, Supplementary Results 2), live-dead agreement (preservation potential, rank abundance, and taxa richness) did not differ between the two sampling years (Table 3, Supplementary Results 2 and Supplementary Table 7). Significant short-term temporal variability was also reflected in the fact that replicate censuses conducted in 2009 at two sites (Fe, PC) were not more similar than expected by chance (Supplementary Results 3 and Supplementary Table 8).

310 A NMDS plot clearly discriminates between living and dead communities, and reveals  
311 compositional differences within each of these groups (Figure 2).

312 **Table 3**

313 Measures of live-dead agreement assessing the extent to which death assemblages diverge from local living communities, calculated  
 314 separately for all censuses. Dead individual numbers are corrected for disarticulated valves of single bivalve individuals following  
 315 Gilinsky & Bennington (1994). The ratio of dead to living taxa was calculated using both raw data and rarefied data standardized for the  
 316 number of living individuals present in a census.  $\Delta S = \log(\text{rarefied number of dead taxa}) - \log(\text{number of living taxa})$  (Olszewski &  
 317 Kidwell, 2007). Taxa were classified as indigenous or allochthonous based on habitat information in the literature. Spearman's rho  
 318 measures the rank-order agreement between a taxon's living and dead abundance. Significant rho values ( $P < 0.05$ ) are shown in bold.  
 319 Mean values for 2009 censuses (Mean 09) only include GPS coordinates previously sampled in 2008 (marked with an asterisk), while  
 320 mean values of all censuses (n=12) are shown for comparison.

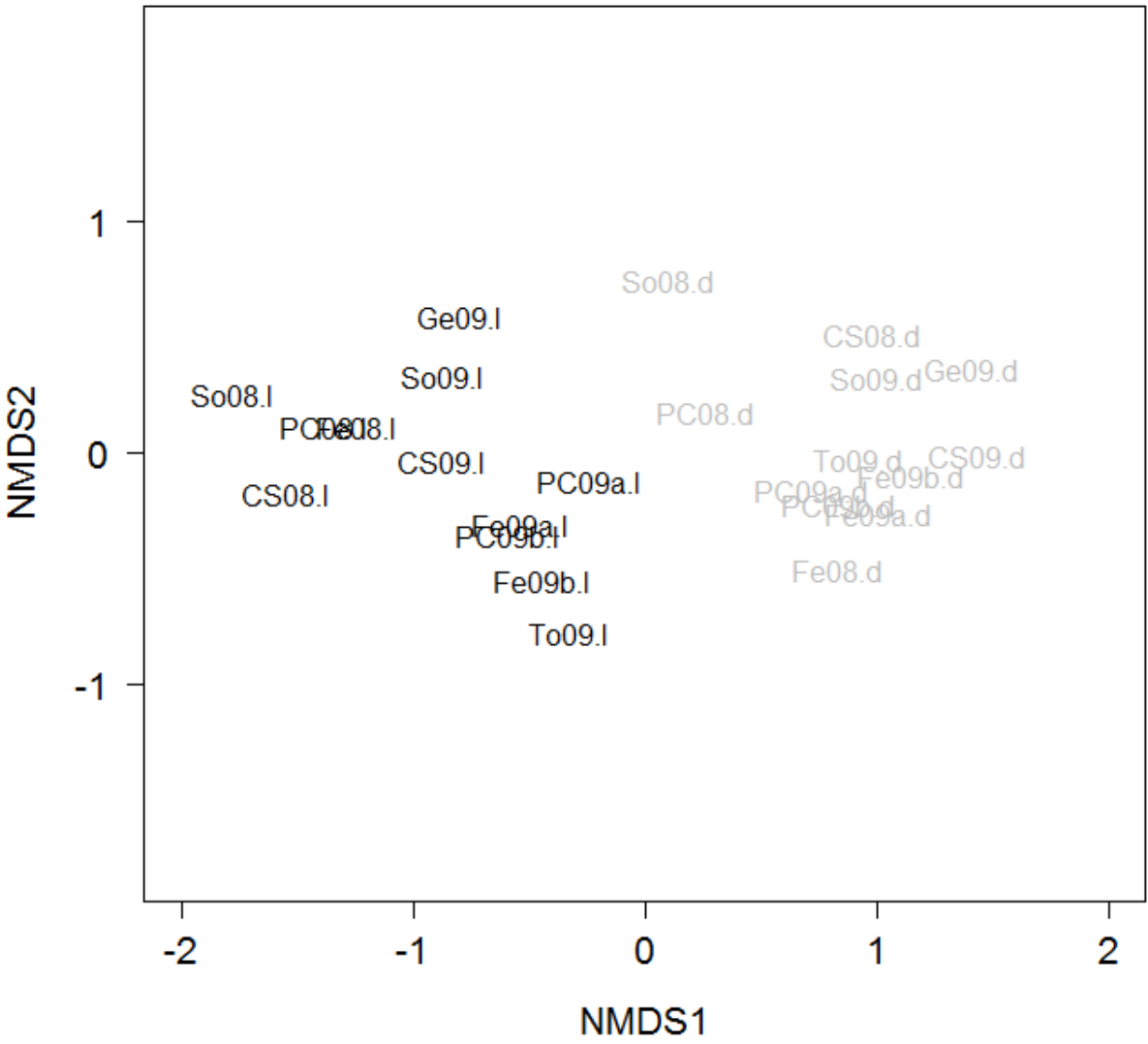
Census	Proportion of living taxa found dead	Ratio of dead to living taxa number		Difference in log of rarefied taxa number ( $\Delta S$ )	Proportion of dead taxa found alive		Proportion of dead individuals belonging to taxa found alive		Spearman's rho		
		Raw data	Rarefied data		All taxa	Only indigenous taxa	All taxa	Only indigenous taxa	All taxa	Only indigenous taxa	Only taxa found alive
CS08	77.8%	8.1	3.1	1.13	9.6%	17.1%	51.3%	57.2%	<b>0.28</b>	<b>0.36</b>	<b>0.74</b>
CS09*	100%	9.1	2.6	0.96	11.0%	19.2%	46.5%	51.2%	<b>0.35</b>	<b>0.44</b>	<b>0.74</b>

Fe08	90.0%	6.8	2.8	1.04	13.2%	18.4%	56.9%	59.3%	<b>0.36</b>	<b>0.40</b>	<b>0.89</b>
Fe09a*	95.2%	4.6	1.9	0.64	20.6%	31.3%	59.3%	64.7%	<b>0.47</b>	<b>0.53</b>	<b>0.74</b>
Fe09b	90.5%	6.0	1.7	0.53	15.0%	23.2%	62.0%	67.3%	<b>0.39</b>	<b>0.45</b>	<b>0.53</b>
Ge09	92.3%	6.8	3.5	1.26	13.5%	23.1%	76.5%	84.4%	<b>0.36</b>	<b>0.46</b>	<b>0.83</b>
PC08	77.8%	4.0	2.8	1.02	19.4%	25.9%	48.9%	51.7%	<b>0.36</b>	<b>0.39</b>	0.40
PC09a*	92.0%	2.9	1.7	0.55	31.5%	46.0%	52.5%	69.4%	<b>0.53</b>	<b>0.61</b>	<b>0.74</b>
PC09b	100%	5.2	2.4	0.89	19.3%	28.3%	46.8%	61.6%	<b>0.45</b>	<b>0.52</b>	<b>0.56</b>
So08	100%	5.4	2.2	0.79	18.5%	26.3%	63.7%	68.3%	<b>0.43</b>	<b>0.51</b>	<b>0.97</b>
So09*	92.9%	5.6	2.6	0.96	16.5%	26.5%	85.0%	89.5%	<b>0.45</b>	<b>0.56</b>	<b>0.61</b>
To09	95.5%	5.2	1.5	0.43	18.3%	28.4%	67.9%	70.1%	<b>0.48</b>	<b>0.56</b>	<b>0.70</b>
Mean 08	86.4%	6.1	2.7	1.00	15.2%	21.9%	55.2%	59.1%	0.36	0.42	0.75
Mean 09	95.0%	5.6	2.2	0.78	19.9%	30.7%	60.8%	68.7%	0.45	0.54	0.71
Mean all	92.0%	5.8	2.4	0.85	17.2%	26.1%	59.8%	66.2%	0.41	0.48	0.71

321

**Figure 2**

Nonmetric multidimensional scaling plot of Bray-Curtis dissimilarities of abundance data for living (in black) and dead censuses (in gray).



## 3.2 Preservational potential

If taxa sampled alive differ in their potential to persist in the local death assemblage, death assemblages will be systematically biased and a poor reflection of historical molluscan communities. The probability that a resident shelled taxon leaves a local sedimentary record can be expressed as the proportion of living taxa that are also found dead. In the present dataset,  $92.0 \pm 0.02\%$  (mean  $\pm$  SE) of living taxa were also recovered in the dead record (Table 3), indicating that few taxa were found only in a living state. In fact, when censuses of 2008 and 2009 are pooled, only two species occurred live-only: the comparatively large gastropod *Bolinus brandaris*, and *Pinna nobilis*, one of the largest bivalves in the world (Goto & Poppe, 1993). Only a single individual (*P. nobilis*) and three individuals (*B. brandaris*) of these species were recovered living, something that may explain the lack of these two taxa in the dead record. We are thus confident that the preservational potential of living taxa in the present dataset is sufficiently high to allow for analyses of live-dead agreement.

## 3.3 Live-dead agreement in taxa rank abundance

Abundance in the dead record should be correlated with a taxon's original abundance in the living community. To test the relationship between living and dead abundance, we examined rank-order agreement in taxa abundance (Spearman's rho) and found the correlation between living and dead rank abundances to be  $0.41 \pm 0.02$  (mean  $\pm$  SE), and significantly positive in all censuses (Table 3). When analyses were restricted to taxa present in the living community for each census, rank-order agreement increased significantly ( $0.71 \pm 0.05$ ; Wilcoxon signed rank test:  $V=0$ ,  $P<0.001$ ; Table 3).

### 3.4 Live-dead agreement in taxa richness

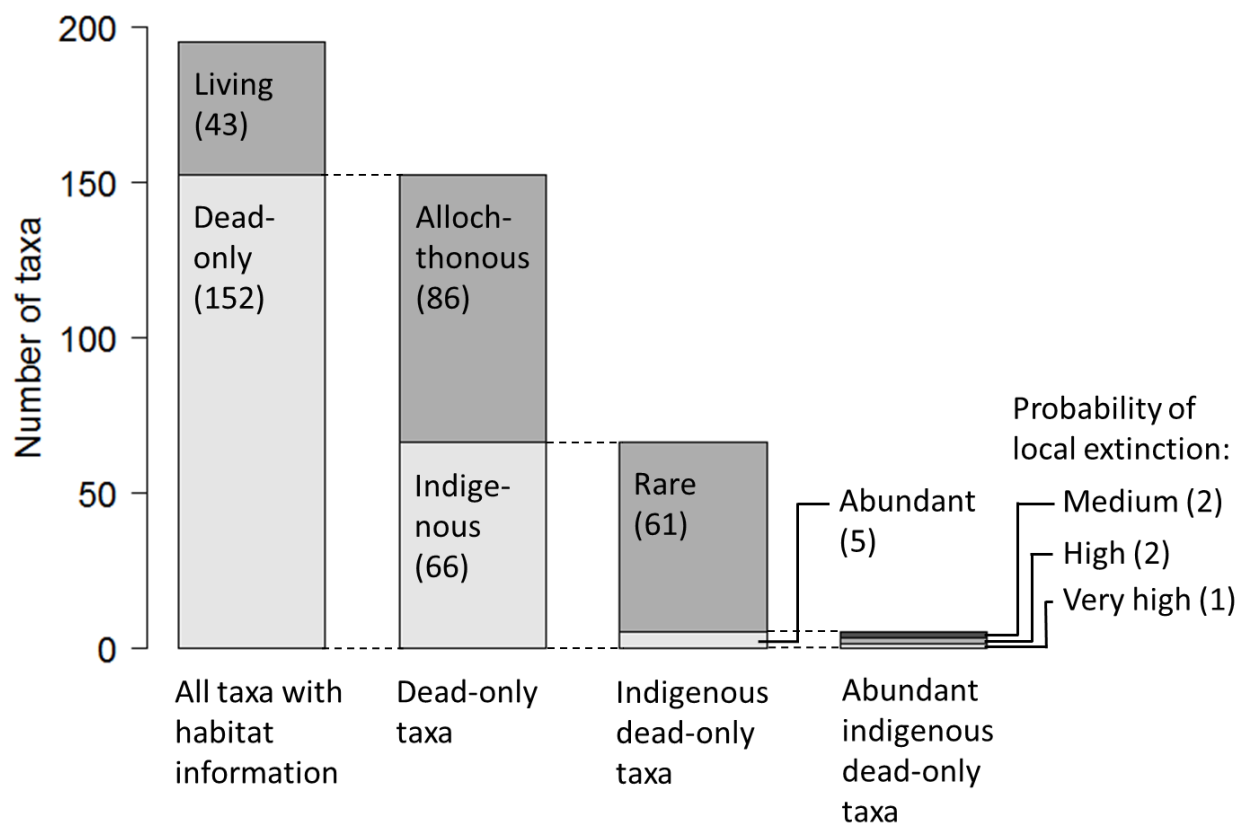
In all twelve censuses, dead diversities far exceeded living diversities. On average, the ratio of dead to living taxa was  $5.8 \pm 0.5$  (mean  $\pm$  SE), ranging from 2.9 (PC09a) to 9.1 (CS09) (Table 3). As surveys of death assemblages typically yield more individuals than censuses of living individuals, at least part of the high dead diversity could simply be a result of different sample sizes. We therefore standardized all dead diversities to the sample sizes of their corresponding living censuses. Even after rarefaction, sediment samples still contained on average  $2.4 \pm 0.2$  times more dead than living taxa (Table 3). Accordingly, the difference between the logarithmic rarefied dead and living diversity ( $\Delta S$ ) (Olszewski & Kidwell, 2007) was consistently positive ( $0.85 \pm 0.08$ , Table 3).

A total of 153 taxa (78.1%), 152 (77.6%) of which could be identified to the family level or better, were never recovered as part of the living community (Figure 3). This pattern was consistent at the individual census level, where only  $17.2 \pm 1.7\%$  (mean  $\pm$  SE) of the taxa recovered dead were found alive (Table 3). When considering abundance data, only  $59.8 \pm 3.5\%$  of the dead individuals within a census were members of taxa sampled as part of the corresponding living community (Table 3).



### **Figure 3**

High diversity in the dead record can be explained by the presence of allochthonous taxa (57%), the time-averaged accumulation of rare taxa (40%), and potential local extinctions (3%). The bar on the left includes all 195 taxa for which habitat information could be found in the literature. Taxa numbers are provided in brackets. Of the 43 taxa recovered alive, 41 were also present in the dead record. Based on literature data, taxa were classified as indigenous or allochthonous, and were considered rare if they had dead abundances of  $<1\%$  in all censuses. The probability of local extinction was judged based on the number of censuses in which dead individuals were recovered and on the ability to reliably discriminate taxa in both the dead and living community (Table 5).



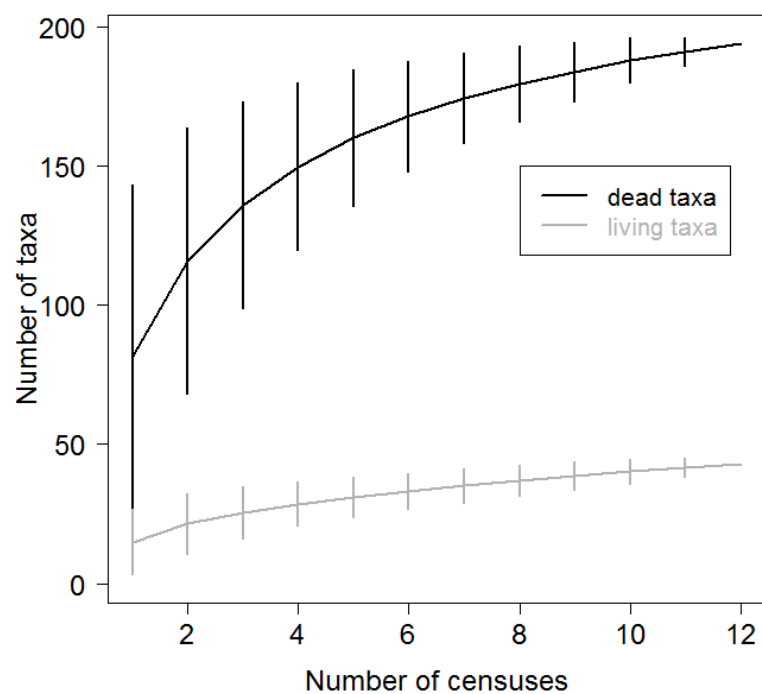
### **3.5 Explaining high community diversity in death assemblages**

#### **3.5.1 Hypothesis 1: Sampling incompleteness**

To judge the degree of completeness to which molluscan communities were sampled in the present study we computed taxa accumulation curves (Gotelli & Colwell, 2011), separately for dead and living molluscan biodiversities (Figure 4). While the fact that both curves have not yet reached an asymptote indicates that both living and dead diversities are not yet fully sampled, the slope of the death assemblage curve is steeper throughout than that of the living assemblages, indicating that the diversity of the living communities has been sampled more comprehensively than that of the death assemblages. The true difference in diversity between the living and death assemblages is thus likely even larger than that detected here. A similar conclusion is reached when comparing a census' observed number of taxa with its estimated asymptotic minimum taxa richness (Table 4), based on a census' number of very rare taxa (Chao et al., 2009). On average,  $81.4 \pm 4.7\%$  (mean  $\pm$  SE) of the estimated taxa richness of the living assemblage was revealed, compared to  $78.9 \pm 3.2\%$  of the taxa richness in the death assemblage (Table 4), demonstrating that sampling thoroughness does not differ significantly between death and living assemblages (Wilcoxon signed rank test:  $V=34$ ,  $P=0.72$ ). As living and dead communities seem to be equally sampled, the high dead-taxa diversity appears to be genuine.

390 **Figure 4**

391 Taxa accumulation curves for dead and living censuses, drawn with 95% confidence intervals.



392

393 **Table 4**

394 Estimated asymptotic minimum taxa richness ( $S_{\text{est}}$ ), estimated number of undetected taxa ( $f_0$ ), and  
 395 the ratio between observed ( $S_{\text{obs}}$ ) and estimated ( $S_{\text{est}}$ ) taxa richness, separately computed for all  
 396 living and dead censuses (Chao et al., 2009). Mean values of 2009 censuses (Mean 09) only  
 397 include GPS coordinates previously sampled in 2008 (marked with an asterisk), while mean  
 398 values of all censuses (n=12) are shown for comparison.

Census	Living community			Dead community		
	$S_{\text{est}}$	$f_0$	$S_{\text{obs}}/S_{\text{est}}$	$S_{\text{est}}$	$f_0$	$S_{\text{obs}}/S_{\text{est}}$
CS08	15.0	6.0	0.60	90.0	17.0	0.81
CS09*	16.3	2.3	0.86	140.7	13.7	0.90
Fe08	12.0	2.0	0.83	95.6	27.6	0.71
Fe09a*	33.3	12.3	0.63	109.0	12.0	0.89
Fe09b	45.5	24.5	0.46	162.6	35.6	0.78
Ge09	13.0	0.0	1.00	109.2	20.2	0.82
PC08	9.5	0.5	0.95	56.2	20.2	0.64
PC09a*	29.5	4.5	0.85	121.0	48.0	0.60
PC09b	17.7	0.7	0.96	96.0	8.0	0.92
So08	5.5	0.5	0.91	28.8	1.8	0.94
So09*	16.0	2.0	0.88	112.8	33.8	0.70
To09	26.1	4.1	0.84	151.0	36.0	0.76
Mean 08	10.5	2.3	0.82	67.6	16.6	0.78
Mean 09	23.8	5.3	0.80	120.9	26.9	0.77
Mean all	19.9	4.9	0.81	106.1	22.8	0.79

399

### 3.5.2 Hypothesis 2: Allochthonous taxa

Habitat information compiled for 195 of the 196 taxa found in this study (99.3% of dead-only taxa, and all 43 taxa from the living community) was used to classify each taxon as either indigenous or allochthonous. Based on these classifications, 90/195 taxa (46.2%) were classified as allochthonous. The preferred habitat types of these taxa were either rocky substrates (72.2%), seagrass meadows (12.2%), both rocky substrates and seagrass meadows (3.3%), other habitats such as the pelagic zone (5.6%), or habitats either shallower or deeper than those sampled here (6.7%, Supplementary Table 6). Four taxa classified as allochthonous based on literature data were recovered in the living community (4/43; 9.3%) – these four taxa were classified as indigenous in subsequent analyses.

Among the 152 dead-only taxa for which habitat information was available, 86 (56.6%) were classified as allochthonous (Figure 3). Accordingly, the proportion of dead taxa that were recovered alive in a census sample increased significantly after excluding these taxa ( $17.2 \pm 1.7\%$  to  $26.1 \pm 2.2\%$ ; Wilcoxon signed rank test:  $V=0$ ,  $P<0.001$ ; Table 3), as did the proportion of dead individuals belonging to taxa sampled alive ( $59.8 \pm 3.5\%$  to  $66.2 \pm 3.4\%$ ; Wilcoxon signed rank test:  $V=0$ ,  $P<0.001$ , Table 3). Also live-dead agreement in taxa rank abundance was significantly higher when restricted to indigenous taxa ( $0.41 \pm 0.02$  to  $0.48 \pm 0.02$ ; Wilcoxon signed rank test:  $V=0$ ,  $P<0.001$ , Table 3). While the presence of allochthonous taxa explains 57% of the high dead diversity, 66/152 taxa (43.4%) occurring in the dead record were not recovered alive in a single census sample despite being classified as indigenous (Figure 3).

### 3.5.3 Hypothesis 3: Time-averaged accumulation of rare taxa

140/152 (92.1%) dead-only taxa identified to the family level or lower, and 61/66 (92.4%) dead-only taxa classified as indigenous, were rare, making up <1% of all individuals recovered in the dead record (Figure 3). Overall, rare indigenous taxa explained 40.1% of the dead-only taxa for which habitat information was available (61/152). This suggests that the vast majority of putative dead-only taxa might nevertheless be part of the living community, and would have been recovered alive had sampling been sufficiently exhaustive. In line with this hypothesis, the 36 taxa recovered alive in at least one census sample despite being rare in the corresponding dead community were present with very few living individuals in these censuses, comprising on average ( $\pm$  SE) only  $1.8 \pm 0.2\%$  of the living community, and could have been easily overlooked in a less thorough sample.

### 3.5.4 Hypothesis 4: Local extinction

Although most dead-only taxa were rare, five out of 66 (7.6%) indigenous dead-only taxa were found at abundances of  $\geq 1\%$  in one or more census samples (Figure 3, 3.3% of dead-only taxa with habitat information). As the 21 living taxa with dead abundances of  $\geq 1\%$  in at least one census were generally found at high frequency in the corresponding living community (each comprising on average  $11.2 \pm 1.5\%$  of living individuals), these five taxa would be expected to be recovered in the living assemblage of taxa present at these sites. We developed a set of predictors to predict the likelihood that absence of these taxa from living assemblages is the result of local extinction (Table 5). This analysis suggests that the bivalve species *Spisula subtruncata* is a strong candidate for local extinction. Shells of this species were recovered in all twelve censuses, the species is distinctive in its living state, and it is not easily confounded with other taxa. Its

abundance in the dead record suggests that it was once common in local communities of living molluscs. Two additional species, *Abra segmentum* and *Ensis minor*, are also candidates for local extinction based on the intermediate number of censuses in which they were found, but are inferred to have been relatively rare in past living communities at these sites (Table 5). *Loripes lucinalis*, despite being recovered in high numbers in eleven of twelve censuses, cannot be identified as locally extinct with confidence, as juveniles of this species can easily be confused with *Lucinella divaricata* when living specimens are not destructively sampled. Analogously, potential difficulties in distinguishing living individuals of *Hydrobia* sp. / *Odostomia* sp. from dead individuals mean that the local extinction of these taxa cannot be concluded with confidence.



**Table 5**

Dead-only taxa inferred to be candidates for local extinction. The probability of local extinction is based on (1) the number of censuses in which dead individuals were recovered; (2) the ease of specimen identification; and (3) whether living specimens can be easily confused with dead specimens. Mean dead abundances are provided as an indicator of metrical abundance, but were not used in the calculation of extinction probabilities. Specimens of *Hydrobia* sp. / *Odostomia* sp. are very small, and live specimens of *Loripes lucinalis* can potentially be misidentified as *Lucinella divaricata*, particularly at the juvenile stage, when internal shell characters are unavailable for analysis.

Taxon name	Taxonomic class	Number of censuses with dead individuals	Mean abundance in these censuses $\pm$ SE	Identification unproblematic?	Living individuals easily recognizable?	Probability of local extinction
<i>Spisula subtruncata</i>	Bivalvia	12	161.9 $\pm$ 70.6	yes	yes	very high
<i>Abra segmentum</i>	Bivalvia	7	29.6 $\pm$ 11.6	yes	yes	high
<i>Ensis minor</i>	Bivalvia	8	10.6 $\pm$ 3.0	yes	yes	high
<i>Hydrobia</i> sp. / <i>Odostomia</i> sp.	Gastropoda	10	109.5 $\pm$ 61.4	yes	no	medium
<i>Loripes lucinalis</i>	Bivalvia	11	118.8 $\pm$ 56.8	no	yes	medium

## 4. Discussion

### 4.1 Live-dead agreement of species richness and rank abundance

Our data demonstrate how various causes of discordance between living and dead communities can be disentangled and their relative impact quantified by carefully analyzing and filtering raw census data. All twelve censuses, spanning two sampling years and six localities in south-east Sardinia, showed considerably higher dead than living diversities. Death assemblages contained on average 5.8x (median: 5.5x) more taxa than associated living communities, and 2.4x more even after rarefaction (Table 3). In meta-analyses of 85 and 109 global habitat-level datasets, death assemblages were found to be 2.6x (median; Kidwell, 2002b) and 3.9x (mean; Kidwell, 2009) more diverse than living assemblages before rarefaction, respectively, and 1.3x more diverse after rarefaction (median; Kidwell, 2002b), values considerably lower than those found here. The difference between the logarithmic rarefied dead and living diversity ( $\Delta S$ ) was also markedly lower in a meta-analysis including 132 global datasets (mean 0.16, range -0.61 to 0.74; Olszewski & Kidwell, 2007) than in the present study (mean 0.85, range 0.43 to 1.26, Table 3).

The exceptional diversity of the Sardinian death assemblage relative to the local living communities at each site may be attributed in part to the high density sampling design used here. Even after pooling all censuses, a process that should increase the probability of detecting living specimens, only 21% of taxa sampled dead and identified to the family level or better were recovered alive. Within individual censuses, on average only 17% of the taxa found dead were recovered alive (Table 3). This is a rather low proportion, given that in 80 global datasets ca. 46% of dead species were also present in the living community (Kidwell, 2001a). The same is true for the proportion of dead individuals that are from taxa also collected alive, which averages 60% in

the present study (Table 3) but 82% in 67 global datasets (Kidwell, 2001a). Importantly, the preservational potential of taxa found alive in the present study was high, with only two live-only taxa, yielding an average probability of 92% that living taxa were also found dead in the same census (Table 3), a value comparable to that of 80 previous surveys (89%, Kidwell, 2008).

While information on dead diversity is known to be strongly time-averaged, there is typically a closer match between live and dead abundances (Kidwell, 2002b). The preservation of proportional abundances of living molluscs tends to be especially reliable and manifests itself in stable rank-order agreement between a species' living and dead abundance in most studied communities (Kidwell, 2001b, Kidwell, 2007, Tomašových & Kidwell, 2009). Rank-order agreement in taxa abundance (Spearman's rho) tends to be lower in areas of known anthropogenic eutrophication (Kidwell, 2007, Kidwell, 2009) and in datasets processed with a fine mesh ( $\leq 1$  mm, Kidwell, 2001b, Kidwell, 2007). In the present study, conducted at sampling sites of limited human impact and using an intermediate mesh size (1.3 mm), rho ranged between 0.28 and 0.53 (mean 0.41), and was significantly positive in all censuses (Table 3). Mean rho was found to be 0.45 and 0.37 in 85 (Kidwell, 2001b) and 109 (Kidwell, 2009) global habitat-level datasets, respectively, indicating that the relationship between taxa abundance in living and dead assemblages is consistent with that found in other soft-bottom molluscan communities.

We found that live-dead agreement of rank abundance in the present study was strongly influenced by the high number of taxa in the dead record, as rank-order agreement of living against dead abundances was significantly higher after excluding dead-only taxa (Table 3). Given such consistently and substantially increased dead diversities across collections, a systematic

analysis of the potential drivers of increased taxonomic diversity in the dead record is appropriate.

## **4.2 Why is dead diversity so much higher than living diversity?**

Increased diversity in the dead record can arise artificially if living communities are undersampled (Kidwell, 2001a, Kidwell, 2002b, Kidwell, 2009). However, several lines of evidence indicate that living diversity is sampled as thoroughly as dead diversity in this study, and accurately reflects the conditions at each site. First of all, the live-dead comparisons here are based on 2-3 censuses for most sites and are thus less likely to underestimate diversity relative to studies based on single samples (Carthew & Bosence, 1986, Kidwell, 2001a, Kidwell, 2001b, Kidwell, 2002a, Kidwell, 2002b, Kidwell, 2007, Kidwell & Rothfus, 2010). Secondly, almost all censuses include >100 living individuals (Table 2), and are thus considered large datasets (Kidwell, 2002a). Thirdly, the taxa accumulation curve for death assemblages was clearly still ascending, while it was slowly approaching an asymptote for living assemblages (Figure 4). Finally, the ratio of detected to estimated asymptotic taxa richness (Chao et al., 2009) was almost identical in living and death assemblages (Table 4).

An obvious cause of increased dead diversities are empty shells of non-indigenous species transported to a sampling site post-mortem (Carthew & Bosence, 1986, Henderson & Frey, 1986, Kidwell & Bosence, 1991, Kidwell, 2001a, Kidwell, 2002b). In the present study, more than half (57%) of all dead-only taxa were classified as allochthonous based on habitat information extracted from the literature (Figure 3). The majority of these allochthonous taxa are typically found on rocky substrates (72%), being either rock-grazers or members of the byssate or cementing epifauna (Supplementary Table 6). A second, smaller fraction of these taxa (12%) are

typical of seagrass habitats. While sparse seagrass mounts may be present in the areas surveyed, the closest rocky shores were a minimum of several hundred meters from the census sites. Hence, shells of rocky intertidal and rocky subtidal taxa must have been transported over some distance, most likely by wave action during storms, but potentially also by associated organisms (see Zuschin et al., 2000, Zuschin & Stachowitsch, 2007). Out-of-habitat transport is thought to be common in steeply sloped or intermittently high-energy environments, but of reduced importance in flat sublittoral settings (Kidwell & Bosence, 1991). As the sites sampled here are extensive, flat, subtidal sandy bottoms at almost eight meters depth (Table 1), our study shows that frequent out-of-habitat transport may also be common in such environments.

Four species found alive were incorrectly classified as likely allochthonous based on our review of the literature (9.3% of living taxa). Tellingly, each of these four species has been reported from various habitat types including soft bottoms (references in Supplementary Tables 5 and 6), suggesting that these species could be considered euryoecious, despite a slight preference for hard substrates or marine vegetation. In line with this hypothesis, all four taxa were present at very low abundance in our survey (1 individual of *Jujubinus exasperatus* and *Mytilaster solidus*, 2 of *Musculus costulatus* and 3 of *Ctena decussata*).

Sixty-six taxa were not found alive despite being classified as indigenous (Figure 3). The vast majority of these taxa were relatively rare (92%, Figure 3). The recovery of large numbers of rare species in surveys of molluscan diversity is common (Kidwell & Bosence, 1991, Zuschin et al., 2000, Kidwell, 2001a, Bouchet et al., 2002, Kidwell, 2002b, Zuschin & Oliver, 2005, Kidwell & Tomasovych, 2013), and the presence of rare, indigenous species in molluscan death assemblages

is generally attributed to the process of within-habitat time-averaging (Kidwell, 2002b, Kidwell, 2009).

While >90% of dead-only taxa were rare, four bivalve taxa and one gastropod taxon, all classified as indigenous, were common in dead records but entirely absent from living communities (Figure 3, Table 5). Given the high abundance of these taxa in the dead record, they would be expected to also occur in a living state at these sites. Their absence from the living community suggests that they may be relicts of past local communities (i.e. are locally extinct) or have experienced significant declines from historical levels (Kidwell, 2002b, Kidwell, 2009). Local extinctions of molluscan species have been documented or strongly suspected in earlier studies (e.g., Bourcier, 1980, Callender & Powell, 2000, Brown et al., 2005). Here, the bivalve *Spisula subtruncata* was identified as the most likely to have experienced local extinction in the study area (Table 5). This species was documented in high numbers in the western Mediterranean in 2007, and was also dominant in 2004 and 2005 at sites both with and without eelgrass (Rueda & Salas, 2008, Rueda et al., 2009). Before that time, it was found at low abundances in most regions of the Mediterranean Sea (Cinar et al., 1998, Rueda et al., 2001, De Biasi et al., 2003, Terlizzi et al., 2003, Arroyo et al., 2006, Albayrak et al., 2007, Mastrototaro et al., 2008, but see also Cosentino & Giacobbe, 2008). We did not find any evidence suggesting that this species could be particularly sensitive to environmental conditions. The potential extirpation of *Spisula subtruncata* in coastal south-east Sardinia must therefore currently be considered a local phenomenon and will need to be verified in future studies – as will the fate of other taxa identified as potential candidates for local extinction.

### **4.3 Temporal variability**

All study sites sampled in consecutive years showed considerable temporal changes in both taxa richness and abundance, and high degrees of within-season variability in living and dead communities were also evident at two sites sampled repeatedly at time intervals of only 11 and 17 days, respectively (Supplementary Results 2 and 3, Supplementary Tables 7 and 8). Substantial compositional volatility in molluscan benthic assemblages does not appear to be unusual, as similar magnitudes of temporal variability of both living and dead molluscan communities have been found in previous research (Staff et al., 1986, Nicolaidou et al., 2006, Ferguson & Miller, 2007, Rueda et al., 2009). Interestingly, measures of live-dead agreement in our study were consistent across the two sampling years despite the marked differences in taxa richness and abundance (Supplementary Table 7). This is a reassuring finding, as it emphasizes the robustness of results obtained from live-dead comparisons.

### **4.4 Conclusions and Implications**

We showed here that molluscan benthic assemblages in south-east Sardinia had strikingly higher dead than living diversities. This surplus of dead taxa could not be attributed to a lower degree of sampling completeness of the living community, but instead was explained by three phenomena of decreasing importance: the post-mortem transport of allochthonous taxa from nearby rocky and seagrass habitats (57% of dead-only taxa), the time-averaged accumulation of rare indigenous taxa in death assemblages (40% of dead-only taxa), and the presence of indigenous taxa in death assemblages that are candidates for local extinction (3% of dead-only taxa).

These findings have several important implications. First of all, the high taxonomic diversity of death assemblages points out how much longer taxa lists can be once dead shells are included,

593 underpinning the value of death assemblages in assessing local biodiversity (Bouchet et al., 2002,  
594 Warwick & Light, 2002, Warwick & Turk, 2002, Zuschin & Oliver, 2005, Albano & Sabelli,  
595 2011, Kidwell & Tomasovych, 2013).

596 Secondly, our findings also demonstrate how the effective application of habitat information from  
597 the literature can help to identify the frequency of post-mortem transport from outside the survey  
598 area. Combining raw census data with ecological knowledge and filtering it accordingly appears  
599 to be a feasible method of correcting for the influence of allochthonous taxa in contemporary  
600 molluscan communities, an approach which has been previously suggested for fossil assemblages  
601 (Kidwell & Bosence, 1991). A classification of taxa as either indigenous or allochthonous also  
602 makes it possible to test for an association between autochthony and abundance.

603 Finally, inventories of rare indigenous species, whether found alive or dead-only, are also of great  
604 value for conservation efforts (Kidwell & Tomasovych, 2013). Knowledge about likely candidate  
605 taxa for local extinction may prove particularly valuable, especially when paired with  
606 geographical data on potential extinction events. Dating select shells from putative extinctions  
607 could be used to provide an estimate of the timing of the extinction event (for reviews see  
608 Kowalewski & Bambach, 2003, Kosnik et al., 2009, Kidwell, 2013). Our approach demonstrates  
609 the exceptional value of dead records in assessing biodiversity loss and in evaluating how local  
610 nearshore communities have changed over recent time.



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This study is dedicated to the memory of Georg Ribi, in honor of his long-term commitment to research on Mediterranean ecology and biodiversity.

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