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Quantitative Fidelity of Brachiopod-Mollusk Assemblages from Modern Subtidal Environments of San Juan Islands, USA

Michał Kowalewski*
Department of Geological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Monica Carroll
Department of Geology, University of Georgia, Athens, GA 30602, USA

Lorraine Casazza
Department of Integrative Biology, Museum of Paleontology, University of California, Berkeley CA 94720, USA

Neal S. Gupta
Department of Earth Sciences and School of Chemistry, University of Bristol, Bristol, BS8 1RJ, UK

Bjarte Hannisdal
Department of Geophysical Sciences, University of Chicago, Chicago, IL 60637, USA

Austin Hendy
Department of Geology, University of Cincinnati, Cincinnati, OH 45221, USA

Richard A. Krause Jr.
Department of Geological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Michael LaBarbera
Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA

Dario G. Lazo
Departamento de Ciencias Geológicas, Universidad de Buenos Aires, Buenos Aires 1428, Argentina

Carlo Messina
Department of Geological Sciences, University of Catania, 95124 Catania, Italy

Stephaney Puchalski
Department of Geological Sciences, Indiana University, Bloomington, IN 47405, USA

Thomas A. Rothfus
Department of Geophysical Sciences, University of Chicago, Chicago, IL 60637, USA

Jenny Sälgeback
Department of Earth Sciences, Uppsala University, Norbyvagen 22, SE-752 36 Uppsala, Sweden

Jennifer Stempien
Department of Geological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Rebecca C. Terry
Department of Geophysical Sciences, University of Chicago, Chicago, IL 60637, USA

Adam Tomašových
Institut für Paläontologie, Würzburg Universität, Pleicherwall 1, 97070 Würzburg, Germany

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* E-mail: michalk@vt.edu

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Whereas a majority of previous fidelity studies have dealt exclusively with mollusks, this study evaluates the compositional fidelity of mixed brachiopod-mollusk benthic assemblages sampled from the San Juan Islands area (Washington State, USA). A total of ca. 2500 live specimens and over 7500 shells and shell fragments were recovered from nine samples dredged along a subtidal transect. The shell material was dominated by fragments; less than 500 dead specimens were represented by complete valves or shells. The compositional fidelity was high: over 60% of live species and over 70% of live genera were also found in the death assemblage and over 60% of dead species and genera were represented in the life assemblage. These high numbers were consistent for all analyzed size fractions (2.3, 4, and 12mm). The life and death assemblages displayed a significant Spearman rank correlation (r = 0.41, p = 0.0001) suggesting that, despite the biasing action of taphonomic processes and time-averaging, the relative abundance of species in the original communities is at least partly preserved in the resulting death assemblages. The results also indicate that a restrictive analytical approach, with fragments excluded from the datasets, appears to provide more credible estimates of diversity and fidelity than an exhaustive approach, which included all fragments. Differences between the two analytical strategies most likely reflect the presence of several genera (e.g., *Chlamys*), which were readily identifiable from fragments (the five most abundant species in the exhaustive death assemblage were all identifiable from even small and heavily altered fragments). The "*Chlamys* effect" illustrates a general principle, because species often vary in their morphological distinctness, the inclusion of fragments is likely to notably distort the taxonomic composition of the studied death (or fossil) assemblages and may depress estimates of diversity and evenness. This study suggests that mixed brachiopod-mollusk associations are reasonably well preserved in the death assemblage in terms of taxonomic composition and rank abundance of dominant taxa. Moreover, despite considerable microstructural and compositional differences between brachiopod and mollusk shells, the class-level fidelity is excellent when fragments are excluded from the analysis. The results are highly congruent with patterns observed previously in fidelity studies focused exclusively on mollusks.

Keywords: TAPHONOMY, FIDELITY, BRACHIOPODS, MOLLUSKS, SAN JUAN ISLANDS, RECENT

Introduction

The fidelity of paleontological data – the extent to which fossils reflect their source biota – is the key measure of the quality of the fossil record with broad relevance to all who use fossils in their research (Behrensmeyer *et al.*, 2000; Kidwell, 2001*a*; and references therein). Indeed, determining the degree of fidelity has been one of the central themes of taphonomy over the past several decades. The concept of fidelity encompasses a wide array of topics, including biochemical signatures, anatomical completeness, spatiotemporal resolution, ecological/ compositional fidelity, large-scale biases, and temporal/stratigraphic completeness (Kidwell, 2001*a*).

This study focuses on the compositional fidelity of marine benthic assemblages, which can be defined as "…the quantitative faithfulness of the record of morphs, age classes, species richness, species abundance, trophic structure, etc. to the original biological signals..." (Behrensmeyer *et al.*, 2000: 120). A thorough understanding of compositional fidelity is a fundamental prerequisite for virtually any numerical analysis based on bulk samples of marine invertebrate fossils, one of the foremost sources of data available in the fossil record. The estimates of compositional fidelity are primarily obtained in live-dead comparisons from present-day depositional surfaces: samples of live biota are either compared to samples of dead remains found in the same area or evaluated hypothetically in terms of the expected fossilization potential. In the case of benthic invertebrates, these studies may either include all collected macro-organisms (e.g., Schopf, 1978) or may be restricted to the "preservable" portion of

living communities, as represented by those organisms that secrete bio-mineralized structures such as shells, tests, or tubes (e.g., Cadée, 1968; Carthew & Bosence, 1986; Pandolfi & Minchin, 1995; Greenstein & Pandolfi, 1997; Zuschin *et al.*, 2000; Kidwell, 2001*b*, 2003; and references therein).

Numerous case studies of the compositional fidelity of marine benthic assemblages have been conducted in a wide variety of settings, primarily focusing on shelly mollusks (e.g., Cadée, 1968; Carthew & Bosence, 1986; Cummins *et al.*, 1986; Staff *et al.*, 1986; Palmquist, 1993; Zuschin *et al.*, 2000; for more references and details see Kidwell & Bosence, 1991; Kidwell, 2003). Recent compilations of these studies not only suggest that death assemblages provide a good taxonomic representation of the original shelly biota (Kidwell & Bosence, 1991; Kidwell & Flessa, 1995) but also indicate that the rank order of dominant species in death assemblages reflects the source mollusk communities (Kidwell, 2001*b*, 2003). This is a highly significant taphonomic vindication of quantitative paleobiology: many death assemblages offer credible abundance data, and such data are critical for many questions of modern macroecology and paleobiology (Kidwell, 2001*b*).

Despite these significant advancements, our understanding of fidelity is still limited because the studies conducted to date have been primarily restricted to mollusks. Other paleontologically-important groups such as corals or echinoids have received much less attention, and that only recently (Nebelsick, 1992; Greenstein & Pandolfi, 1997; Pandolfi & Greenstein, 1997; Greenstein *et al.*, 1998). The fidelity of many other heavily skeletonized groups such as brachiopods and bryozoans has remained virtually unstudied (see also Behrensmeyer *et al.*, 2000; Kidwell, 2003; but see Smith & Nelson, 1992). Also, prior fidelity studies of skeletonized biotas almost invariably have focused on a single major taxon, even though fossil assemblages mixing various higher taxa are the norm rather than the exception in the fossil record. Thus, our current knowledge is not only "molluskocentric" (or even "bivalvocentric"), but also lacking in its understanding of assemblage fidelity when multiple higher taxa are present.

This study evaluates the compositional fidelity of mixed, brachiopod-mollusk benthic assemblages from present-day subtidal environments of the San Juan Islands, Washington State, USA. The analyses presented here encompass multiple higher taxa of the marine benthos and, to our knowledge, represent the first fidelity study of assemblages in which brachiopods are locally common. This study includes two distinct analytical levels. The "transect level" fidelity analysis focuses on data pooled across many sub-environments. This approach provides averaged estimates of regional (basin-scale) fidelity, most closely analogous to (1) deposits produced by extensive spatial mixing (e. g., a major storm deposit or perhaps even a transgressive ravinement) or (2) datasets created by analytical pooling of data from many fossil sites across depositional gradients. In contrast, the "sample level" fidelity analysis represents a series of finer-scale tests of fidelity focused on individual sampling sites.

It is important to emphasize that individual samples collected from a life assemblage at any given site may not be entirely representative of local communities, while samples collected from death assemblages may be both spatially and temporally mixed. Thus, the estimates presented here should not be viewed as realistic estimates of the faunal composition, diversity, and other quantitative aspects of biological communities, but rather relative (sampled) estimates that are meaningful only in comparative analyses of samples obtained from similar environmental settings using compatible sampling methods.

Study Area, Material, and Methods

The study was conducted in the San Juan Islands in the center of Puget Sound off the coast of the northwestern USA (Figure 1a). The samples were collected along an onshore-offshore transect across the San Juan Channel between Lopez Island and San Juan Island (Figure 1b). This location was selected because the area is known to contain

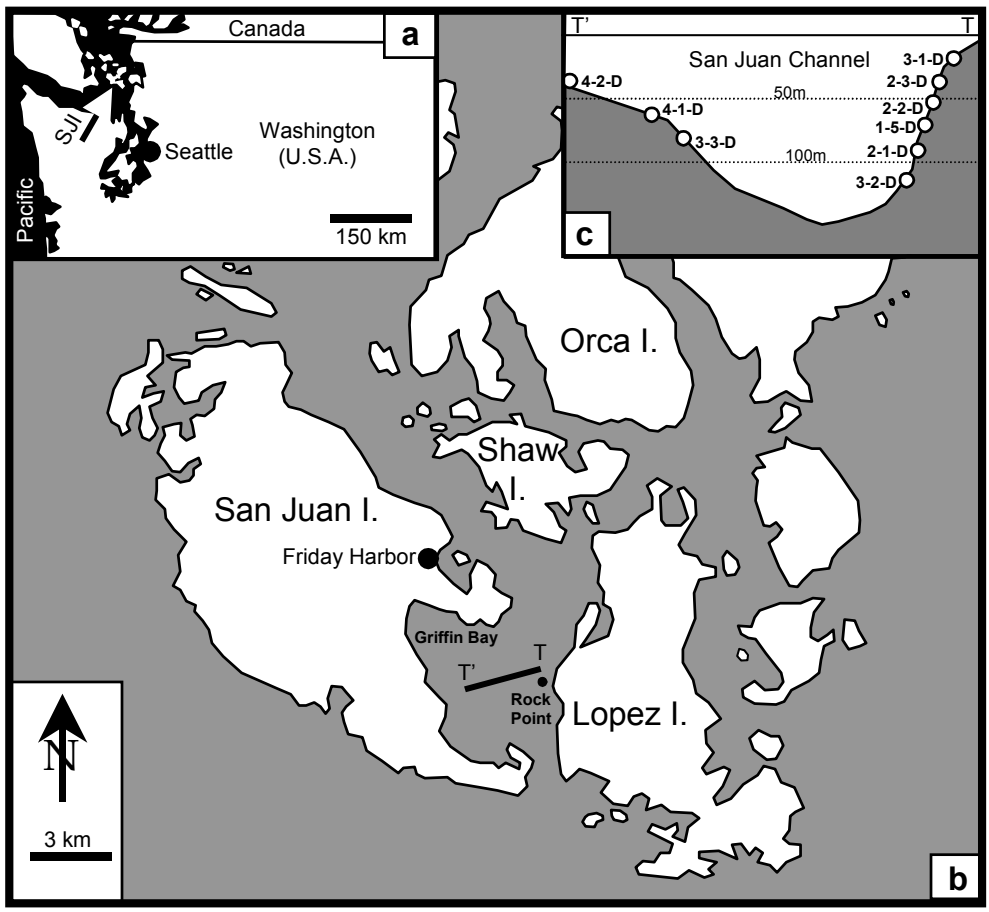

Figure 1. The study area. A. Map of the region; San Juan Islands indicated with an arrow. B. A close-up map of San Juan Islands with the sampled transect marked by the T' – T line. C. Cross-section across the San Juan Channel looking north. Approximate position of the samples included in this study is indicated on the transect. Modified after an unpublished figure designed by Richard A. Krause, Jr. (Virginia Tech).

brachiopod populations (e.g., Thayer, 1975; Schumann, 1991) and provides an opportunity to sample mixed mollusk-brachiopod assemblages from a wide range of bathymetric settings and substrate types. The transect includes a steep slope between Lopez Island and the deepest part of the channel and a much gentler slope westward toward San Juan Island (Figure 1c). The samples encompass a wide range of water depths from ~18m (10 fathoms) to ~119m (65 fathoms) (Figure 1b-c) (1 fathom = 1.83m). Due to the high energy of bottom currents between the islands, the channel floor consists mostly of bare rocky substrate, with samples dominated by cobbles and boulders. Fine sediments were nearly absent in samples collected at the deeper, distal sites along the transect, but were present, occasionally in substantial quantities, at shallower, proximal sites.

A series of dredge samples (n = 9) along an onshore-offshore depth transect (Figure 1c) were collected with a rock dredge in July 2002 aboard the R/V *Nugget*, a University of Washington research vessel (Figure 2). Each dredge haul was made over a relatively short distance (50 to 75 m)

Table 1. A summary of sampling information for samples dredged along the studied transect (see Figure 1).

Sample ID	Number of Specimens (live+dead)	Number of Species [genera] (live+dead)	Collection Date	Geographic Location		Depth
				Starting point	Ending point	
1-5-D	1235	37 [36]	July 17, 2002	N 48° 29.926' W 122° 56.846'	N 48° 29.774' W 122° 56.886'	40 fathoms (~73m)
2-1-D	901	35 [37]	July 17, 2002	N 48° 29.689' W 122° 57.109'	N 48° 29.907' W 122° 57.291'	50 fathoms (~91m)
2-2-D	818	24 [25]	July 17, 2002	N 48° 29.650' W 122° 56.857'	N 48° 29.800' W 122° 56.777'	30-31 fathoms (~55 to ~57m)
2-3-D	952	38 [34]	July 17, 2002	N 48° 29.826' W 122° 56.689'	N 48° 29.945' W 122° 56.616'	20-22 fathoms (~37 to ~40m)
3-1-D	1082	44 [43]	July 18, 2002	N 48° 29.745' W 122° 56.656'	N 48° 29.824' W 122° 56.615'	10-11 fathoms (~18 to ~20m)
3-2-D	89	17 [19]	July 18, 2002	N 48° 29.687' W 122° 57.381'	N 48° 29.450' W 122° 57.328'	60-65 fathoms (~110 to ~119m)
3-3-D	1201	32 [35]	July 18, 2002	N 48° 29.317' W 122° 59.272'	N 48° 28.959' W 122° 59.000'	46 fathoms (~84m)
4-1-D	1004	40 [38]	July 23, 2002	N 48° 29.629' W 122° 59.702'	N 48° 29.249' W 122° 59.500'	36 fathoms (~66m)
4-2-D	1469	49 [49]	July 23, 2002	N 48° 28.421' W 122° 59.122'	N 48° 28.305' W 122° 58.882'	20-21 fathoms (~37 to ~38m)

*In some cases, number of genera exceeds number of species in a sample. This is because some genera lack species assignment. For example, sample 2-1-D contains 35 taxa identified to species level and 37 taxa identified to genus level.

parallel to isobaths (usually roughly parallel to the shoreline and thus approximately perpendicular to the run of the transect). Several Van Veen grab samples collected in addition to dredging yielded variable, but generally limited amounts of shelly material and were thus found an ineffective sampling strategy incompatible with the research goals of this study. Whereas the dredge provides a poorer spatial resolution than point samples (e.g., box cores, Van Veen grabs, etc.), the live samples used in this study are unlikely to have been seriously affected by mixing of fauna from different habitats. First, given the short length of each dredge (50 – 75 m; see also Table 1), samples are unlikely to significantly mix different faunal associations, although some averaging of small-scale patchiness, inherent to many benthic communities, may affect our data. Second, dredges were acquired along isobaths, and thus, mixed fauna from areas with a nearly constant bathymetry and reasonably uniform substrate, again minimizing habitat mixing. Finally, three Van Veen grab samples collected along one of the dredging sites all yielded samples that were consistent in composition with the much larger sample provided by the dredge (detailed data not shown here). In contrast to life assemblage samples, death assemblage samples may be prone

Figure 2. Dredge sampling and sample processing. A. A rock dredge containing a sample obtained in a single haul. B. An example of a dredge sample placed on a sorting table prior to splitting. C. A close-up of a material sampled from the rocky substrate including live and dead invertebrates. White arrows point to specimens of live-collected brachiopods (*Terebratalia transversa*). All photographs by Adam Tomašových.

to substantial mixing of specimens from different environments because the study area is characterized by high-energy bottom currents and steep topographic gradients. This taphonomic setting makes thus fidelity tests particularly conservative. It should be noted finally that dredging may induce fragmentation of specimens, both dead and alive. However, fragments of dead specimens are explicitly considered in this study and all live specimens damaged during dredging can readily be recognized by presence of soft tissue.

A potentially more serious problem is the fact that the dredged area is known for its brachiopod fauna and had been frequently sampled by researchers prior to our study (C. Staude, pers. comm., 2002). Repeated dredging may (1) change relative abundance of species, (2) alter the ratio of epifaunal to infaunal taxa, (3) induce an increase in dominance, and (4) cause a decrease in diversity (for reviews, case examples, and references see Dayton et al., 1995; Jennings & Kaiser, 1998; Veale et al., 2000). Because previous dredging activities may have altered living communities, our estimates of fidelity may be biased. However, previous sampling concentrated only in an intermediate-depth part of the transect – for various practical and research-related reasons, very few dredges had been previously conducted in areas corresponding to the shallowest and deepest sites sampled here (C. Staude, pers. comm., 2002). We have found no systematic bias in fidelity estimates when comparing the intermediate-depth samples (where the bias should be most severe) with the shallowest and deepest sites (where the bias should be minimal). Thus, previous dredging either did not significantly distort benthic communities or the dredged sites had not been disturbed notably in the past.

For each dredge sample, a 5 gallon (~20 liter) bucket was filled with a subset of the material acquired in the dredge. Each 5-gallon sample was obtained by spreading all dredge material on a sorting table (Fig. 2b), splitting the table into equal-area sectors, and collecting all material from one or more arbitrarily selected sectors. The samples included both live and dead skeletal material as well as the sediment composing the substrate (Figure 2c). The remaining material from each dredge was sorted for a variety of other projects.

The material from the bucket was wet sieved through 12mm, 4mm, 2.3mm, 1mm, and 0.063mm mesh screens. Multiple sieve size fractions were used to facilitate the sorting process and make results more easily comparable with other projects. Studies in invertebrate taphonomy employ a wide range of sieves, and the choice of mesh size can have a significant effect on results in paleoecological and taphonomic studies (Kidwell, 2001*b*, 2003; Kidwell *et al.*, 2001; Hoffmeister & Kowalewski, 2002).

Following sieving, all live mollusks and brachiopods, including those killed during dredging, were picked and preserved in 70% ethanol. Specimens were stored separately for each size fraction. The remaining material (the skeletal death assemblage, whether whole or fragmentary, and sediment) from the 12, 4, and 2.3mm size fractions was sorted into three categories: mollusks, brachiopods, and "other material". Skeletal material from the two finest fractions (0.063 and 1mm mesh sizes) was extremely numerous and composed almost exclusively of unidentifiable fragments. Analyses were thus restricted to the three coarsest fractions: 2.3mm, 4mm, and 12mm.

Live-collected specimens and shells or shell fragments representing dead specimens were identified to species level, whenever possible. Identifications were made using the extensive zoological literature dedicated to the invertebrate fauna of the San Juan Islands and the northwestern USA (Kozloff, 1996; and references therein). Unidentified species were typically represented by few or single specimens. Each unidentified specimen was assigned a unique label (e.g., "*Fusinus* sp." or "Bivalvia gen. sp."). Specimens from the same genus were assigned to the same unique label (i.e., more than one specimen and more than one species can be included under the label "*Fusinus sp.*"). The approach is conservative in that all undetermined specimens within a given genus are counted as a single species (e.g., all 16

Table 2. A list of brachiopod and mollusk species pooled across all samples and sieve fractions included in this study. Species are ranked and listed according to abundance of specimens. This list was generated via the exhaustive analytical approach (see text) with raw counts (N) representing total uncorrected numbers of specimens (each fragment and disarticulated element was counted as 1 specimen). Data listed and ranked (R) separately for the life and death assemblages. The "life rank" (LR) is indicated for each species from death assemblages.

Life Assemblage					Death Assemblage					
Group	Genus	Species	N	R	Group	Genus	Species	#	R	LR
Gastropoda	*Calyptraea*	*fastigiata*	454	**1**	Bivalvia	*Chlamys*	*rubida*	1581	**1**	**19**
Bivalvia	*Acila*	*castrensis*	384	**2**	Bivalvia	*gen.*	*sp.*	1091	**2**	**36**
Bivalvia	*Modiolus*	*modiolus*	288	**3**	Bivalvia	*Chlamys*	*hastata*	946	**3**	**20**
Bivalvia	*Cyclocardia*	*ventricosa*	135	**4**	Bivalvia	*Modiolus*	*modiolus*	649	**4**	**3**
Bivalvia	*Pododesmus*	*cepio*	133	**5**	Bivalvia	*Pododesmus*	*cepio*	603	**5**	**5**
Brachiopoda	*Terebratalia*	*transversa*	128	**6**	Brachiopoda	*Terebratalia*	*transversa*	541	**6**	**6**
Gastropoda	*Homalopoma*	*luridum*	100	**7**	Bivalvia	*Clinocardium*	*blandum*	248	**7**	**21**
Bivalvia	*Nutricola*	*lordi*	83	**8**	Bivalvia	*Humilaria*	*kennerleyi*	226	**8**	**23**
Gastropoda	*Amphissa*	*columbiana*	62	**9**	Bivalvia	*Macoma*	*balthica*	177	**9**	**29**
Bivalvia	*Miodontiscus*	*prolongatus*	46	**10**	Brachiopoda	*Hemithiris*	*psittacea*	156	**10**	**.**
Gastropoda	*Lottia*	*instabil*	45	**11**	Bivalvia	*Mya*	*truncata*	143	**11**	**35**
Bivalvia	*Nuculana*	*minuta*	45	**11**	Gastropoda	*Calyptraea*	*fastigiata*	136	**12**	**1**
Gastropoda	*Crepidula*	*dorsata*	40	**13**	Bivalvia	*Saxidomus*	*gigantea*	133	**13**	**23**
Gastropoda	*Puncturella*	*cucullata*	38	**14**	Bivalvia	*Cyclocardia*	*ventricosa*	129	**14**	**4**
Gastropoda	*Margarites*	*pupillus*	37	**15**	Gastropoda	*Amphissa*	*columbiana*	128	**15**	**9**
Gastropoda	*Calliostoma*	*ligatum*	32	**16**	Bivalvia	*Protothaca*	*staminea*	97	**16**	**31**
Polyplacop.	*Lepidozona*	*retiporosa*	31	**17**	Gastropoda	*Trichotropis*	*cancella*	68	**17**	**25**
Polyplacop.	*Ischnochiton*	*interstinctus*	30	**18***	Bivalvia	*Gari*	*californica*	66	**18**	**.**
Bivalvia	*Chlamys*	*rubida*	26	**19**	Bivalvia	*Glycymeris*	*subobsoleta*	63	**19**	**.**
Bivalvia	*Chlamys*	*hastata*	25	**20**	Bivalvia	*Acila*	*castrensis*	56	**20**	**2**
Gastropoda	*Amphissa*	*versicolor*	22	**21**	Gastropoda	*Amphissa*	*versicolor*	49	**21**	**21**
Bivalvia	*Clinocardium*	*blandum*	22	**21**	Gastropoda	*gen.*	*sp.*	40	**22**	**53**
Bivalvia	*Humilaria*	*kennerleyi*	18	**23**	Gastropoda	*Lottia*	*instabilis*	36	**23**	**11**
Bivalvia	*Saxidomus*	*gigantea*	18	**23**	Gastropoda	*Crepidula*	*dorsata*	30	**24**	**13**
Gastropoda	*Trichotropis*	*cancellata*	17	**25**	Gastropoda	*Puncturella*	*cucullata*	30	**24**	**14**
Gastropoda	*Astysis*	*sp.*	16	**26**	Bivalvia	*Nuculana*	*minuta*	30	**24**	**11**
Bivalvia	*Lyonsia*	*californica*	15	**27**	Gastropoda	*Nucella*	*lamellos*	24	**27**	**32**
Bivalvia	*Lucinida*	*sp.*	13	**28***	Bivalvia	*Nutricola*	*lordi*	24	**27**	**8**
Bivalvia	*Macoma*	*balthica*	12	**29**	Bivalvia	*Astarte*	*esquimalti*	22	**29**	**38**
Gastropoda	*Alvania*	*compacta*	11	**30***	Gastropoda	*Homalopoma*	*luridum*	19	**30**	**7**
Bivalvia	*Protothaca*	*staminea*	10	**31**	Gastropoda	*Calliostoma*	*ligatum*	15	**31**	**16**
Gastropoda	*Nucella*	*lamellosa*	9	**32**	Bivalvia	*Semele*	*rubropicta*	13	**32**	**53**
Bivalvia	*Cardiomya*	*pectinata*	8	**33**	Bivalvia	*Miodontiscus*	*prolongatus*	9	**33**	**10**
Bivalvia	*Glycymeris*	*septentrionalis*	8	**33**	Bivalvia	*Panomya*	*ampla*	8	**34**	**.**
Bivalvia	*Mya*	*truncata*	6	**35**	Gastropoda	*Margarites*	*pupillus*	7	**35**	**15**
Polyplacop.	*Ischnochiton*	*trifidus*	5	**36**	Gastropoda	*Crepidula*	*perforans*	5	**36**	**.**
Bivalvia	*gen.*	*sp.*	5	**36**	Gastropoda	*Naticidae*	*sp.*	5	**36**	**.**
Bivalvia	*Astarte*	*esquimalti*	4	**38**	Gastropoda	*Solariella*	*sp.*	5	**36**	**44**
Polyplacop.	*Lepidozona*	*mertensi*	3	**39**	Gastropoda	*Nucella*	*conicula*	4	**39**	**53**
Polyplacop.	*Lepidozona*	*trifida*	3	**39**	Bivalvia	*Diplodonta*	*impolita*	4	**39**	**.**

(Table 2, continued)

Polyplacop.	*Mopalia*	*spectabilis*	3	**39**	Bivalvia	*Lucinoma*	*amulatum*	4	**39**	.
Gastropoda	*Ocenebra*	*interfossa*	3	**39**	Bivalvia	*Solen*	*sicarius*	4	**39**	.
Brachiopoda	*Terebratulina*	*unguicula*	3	**39**	Gastropoda	*Cerastostma*	*foliatum*	3	**43**	**53**
Bivalvia	*Astarte*	*elliptica*	2	**44**	Gastropoda	*Crepidula*	*numaria*	3	**43**	.
Gastropoda	*Diodora*	*aspera*	2	**44**	Gastropoda	*Natica*	*sp.*	3	**43**	**53**
Polyplacop.	*Lepidozona*	*rugatus*	2	**44**	Bivalvia	*Macoma*	*calcarea*	3	**43**	.
Polyplacop.	*Lepidozona*	*sp.*	2	**44**	Bivalvia	*Macoma*	*nasuta*	3	**43**	.
Bivalvia	*Macoma*	*sp.*	2	**44**	Gastropoda	*Astysis*	*sp.*	2	**48**	**26**
Gastropoda	*Neptunea*	*phoenici*	2	**44**	Gastropoda	*Diodora*	*aspera*	2	**48**	**44**
Bivalvia	*Ophiodermella*	*cancellata*	2	**44**	Gastropoda	*Fusitriton*	*oregonen*	2	**48**	**53**
Polyplacop.	*gen.*	*sp.*	2	**44**	Gastropoda	*Margarites*	*lirulata*	2	**48**	.
Gastropoda	*Solariella*	*sp.*	2	**44**	Polyplacop.	*Lepidozona*	*retiporoza*	2	**48**	**17**
Gastropoda	*Calliostoma*	*annulatum*	1	**53**	Bivalvia	*Astarte*	*elliptica*	2	**48**	.
Gastropoda	*Cerastostoma*	*foliatum*	1	**53**	Gastropoda	*Acmaea*	*mitra*	1	**54**	.
Bivalvia	*Compsomyax*	*subdiaphana*	1	**53**	Gastropoda	*Acmaea*	*sp.*	1	**54**	.
Bivalvia	*Entodesma*	*navicula*	1	**53**	Gastropoda	*Boreatrophon*	*orpheus*	1	**54**	.
Gastropoda	*Fusinus*	*sp.*	1	**53**	Gastropoda	*Boreatrophon*	*stuarli*	1	**54**	.
Gastropoda	*Fusitriton*	*oregonen*	1	**53**	Gastropoda	*Cylichne*	*cultertella*	1	**54**	.
Gastropoda	*Lacuna*	*sp.*	1	**53**	Gastropoda	*Margarites*	*succinctus*	1	**54**	.
Gastropoda	*Lacuna*	*variegata*	1	**53**	Gastropoda	*Neptunea*	*phoenici*	1	**54**	**44**
Bivalvia	*Laternula*	*mariliana*	1	**53**	Gastropoda	*Neptunea*	*sp.*	1	**54**	**53**
Gastropoda	*Lirularia*	*lirulata*	1	**53**	Gastropoda	*Neptunea*	*tabulata*	1	**54**	.
Gastropoda	*Lirularia*	*succincta*	1	**53**	Gastropoda	*Ocenebra*	*sp.*	1	**54**	.
Bivalvia	*Lyonsia*	*sp.*	1	**53**	Gastropoda	*Odostomina*	*vancouverensis*	1	**54**	.
Polyplacop.	*Mopalia*	*cirrata*	1	**53**	Gastropoda	***Pteropoda***	*sp.*	1	**54**	.
Polyplacop.	*Mopalia*	*sp.*	1	**53**	Polyplacop.	*Cryptochiton*	*stelleri*	1	**54**	.
Polyplacop.	*Mopalia*	*swani*	1	**53**	Polyplacop.	*Ischnochiton*	*trifidus*	1	**54**	**36**
Bivalvia	*Mya*	*arenaria*	1	**53**	Polyplacop.	*Mopalia*	*swani*	1	**54**	**53**
Bivalvia	*Nassarius*	*mendicus*	1	**53**	Polyplacop.	*gen.*	*sp.*	1	**54**	**44**
Gastropoda	*Natica*	*sp.*	1	**53**	Bivalvia	*Compsomyax*	*subdiaphana*	1	**54**	**53**
Gastropoda	*Neptunea*	*lyrata*	1	**53**	Bivalvia	*Lyonsia*	*californica*	1	**54**	**27**
Gastropoda	*Neptunea*	*sp.*	1	**53**	Bivalvia	*Lyonsia*	*sp.*	1	**54**	**53**
Gastropoda	*Pandora*	*filosa*	1	**53**	Bivalvia	*Macoma*	*sp.*	1	**54**	**44**
Gastropoda	*Pandora*	*wardiana*	1	**53**	Bivalvia	*Musculus*	*sp.*	1	**54**	.
Bivalvia	*Semele*	*rubropicta*	1	**53**	Bivalvia	*Mytilus*	*sp.*	1	**54**	.
Gastropoda	*Velutina*	*velutina*	1	**53**	Bivalvia	*Nucula*	*exigua*	1	**54**	.
Gastropoda	gen.	*sp.*	1	**53**	Bivalvia	***Ostreiida***	*sp.*	1	**54**	.
.	.	.	.	**.**	Bivalvia	*Tonicella*	*sp.*	1	**54**	.
.	.	.	.	**.**	Bivalvia	***Venerida***	*sp.*	1	**54**	.

* Species represented by 10 or more specimens in the life assemblage that were not found in the death assemblage.

specimens of *Astysis* sp. found in the samples are assumed to represent the same species). Also, this tallying strategy provides more realistic diversity estimates than would be obtained by a total exclusion of all undetermined specimens and allows us to include into the rarefaction analyses (see below) all specimens that belong to genera unidentified to species level. Note that, even though proper species names are unknown for some genera, the specimens that belong to them must represent at least one species per genus. Consequently, this approach is more reasonable than literal counts of identifiable taxa (as reported in Tables 1 and 3), which falsely imply that there are more genera than species in some samples.

For many fragments, only higher-level taxonomic identification was possible. Data collection focused on mollusks and brachiopods; skeletal remains from other groups were excluded from all analyses (e.g., echinoid spines and plates, barnacle plates, crustacean claws, etc.). Except for locally abundant fragments of barnacle plates, these other groups constituted only a small fraction of the death assemblages and represented higher taxa with relatively low fossilization potential. Fidelity analyses were performed at the class/phylum (gastropods, bivalves, and brachiopods), genus and species levels.

Because all live specimens of brachiopods and bivalves were represented by articulated shells (even specimens damaged by dredging were invariably articulated), raw counts of specimens provided direct estimates of the actual number of individuals. In the case of the death assemblages, however, many specimens were disarticulated valves of bivalved invertebrates or valve/shell fragments. Although all valves (including fragments) may represent unique individuals when the *sampling domain* is large (see Gilinsky & Bennington, 1994), some correction for disarticulated elements still needs to be applied when bivalved or multivalved organisms (e.g., bivalves, brachiopods, chitons) are analyzed together with univalved organisms (e.g., gastropods, scaphopods). This is because univalved specimens are half as likely to be sampled as bivalved organisms (see Bambach & Kowalewski, 2000; Kowalewski, 2002; for more detailed discussion). Consequently, the number of bivalve/brachiopod valves should be corrected by factor of 0.5 and the number of chiton plates should be corrected by factor of 0.125.

Because the sampled dead material was dominated by fragments that in many cases could be only identified as "mollusks", the correction for element frequency could not be applied to all material in the samples (i.e., the unknown proportion of unidentified fragments came from univalved gastropods, and not bivalves). Consequently, two separate analyses were conducted to determine the influence of this correction on our conclusions: (1) exhaustive analyses where all fragments and valves were included and counted, but without any correction for expected element frequency; and (2) restrictive analyses where only complete valves and shells were included and the correction was applied to bivalves and brachiopods (# specimens = # valves * 0.5) and chitons (# specimens = # * 0.125). Note that the restrictive approach was not applied to individual samples because it would limit samples to too few observations to provide meaningful statistical estimates. All statistical analyses were performed in SAS and SAS/IML version 8.12 (SAS Institute, 1989*a*, 1989*b*).

Results

A summary of raw counts of specimens is provided in Table 2. A total of ca. 2500 live specimens and over 7500 shells and shell fragments were recovered from the nine samples dredged along the transect. The shell material was dominated by fragments: less than 500 dead specimens were represented by complete valves or shells. Individual samples averaged over 1000 specimens (a sum of live specimens + shells/valves + fragments). Except for sample 3-2-D (89 specimens total), collected from the deepest part of the channel, each individual sample included at least 800 specimens. The fidelity analyses were conducted at two levels: (1) the transect level, with individual samples pooled; and (2) the sample

Table 3. Compositional fidelity of benthic assemblages based on species-level and genus-level comparisons of the death and life assemblages. To maximize sample sizes, all sample-level analyses are based on exhaustive approach and include all size fractions.

Sample	Number of specimens		Number of species [genera]*		Percent live taxa also found dead		Percent dead taxa also found live	
	live	dead	live	dead	species	genera	species	genera
All samples	2439	7677	63 [57]	61 [63]	61.9	77.2	63.9	69.8
All samples (restrictive)**	2439	480.5	63 [57]	50 [49]	55.5	66.7	70.0	77.6
All samples >4 mm	2003	5205	57 [49]	57 [55]	66.7	77.6	66.7	69.1
All samples >12 mm	1233	2646	41 [35]	36 [38]	61.0	74.3	69.4	68.4
All samples 2.3 – 12 mm	1206	5024	48 [47]	55 [56]	64.6	76.6	71.4	64.3
All samples 2.3 – 4 mm	436	2472	35 [38]	37 [42]	68.6	71.0	64.9	64.3
All samples 4 – 12 mm	770	2552	42 [38]	50 [47]	71.4	78.9	60.0	63.8
Sample 1-5-D	370	865	28 [26]	31 [31]	78.6	80.3	71.0	67.7
Sample 2-1-D	194	707	21 [22]	30 [32]	76.2	77.3	53.3	53.1
Sample 2-2-D	81	737	14 [13]	22 [23]	85.7	84.6	54.5	47.8
Sample 2-3-D	198	754	22 [19]	32 [29]	72.7	73.7	50.0	48.3
Sample 3-1-D	261	821	34 [30]	32 [36]	64.7	76.7	68.6	63.9
Sample 3-2-D	32	57	10 [11]	11 [12]	40.0	36.4	36.4	33.3
Sample 3-3-D	291	910	22 [22]	26 [29]	72.7	72.7	61.5	55.2
Sample 4-1-D	181	823	23 [22]	34 [34]	73.9	81.8	50.0	52.9
Sample 4-2-D	648	821	38 [38]	33 [35]	57.9	63.2	66.7	68.6
Per-sample mean***	278	805	25 [24]	30 [31]	72.8	76.3	59.4	57.2

*In some cases, number of genera exceed number of species in a sample. This is because some genera lack species assignment, and were included in literal counts of identifiable genera but excluded from counts of identifiable specimens (see also text).

** Restrictive analyses excluded fragments and included a correction for counts of disarticulated elements (see text).

***Per-sample means computed as unweighted arithmetic means (sample 3-2-D was excluded owing to its too small

level, where each of the nine samples was analyzed separately. Although the "transect level" fidelity analysis averages samples from many different sub-environments across San Juan Channel, it provides a useful estimate of an overall fidelity of a single depositional system and gives us a fidelity estimate that is relevant for studying fossil assemblages contained within spatial mixed deposits or for evaluating fidelity of paleontological datasets that represent pooled data across many fossil sites from a single depositional system.

Transect level analysis

To evaluate the overall fidelity of the death

assemblage in the San Juan Channel, all specimens were pooled across the samples and the resulting transect-level death and life assemblages were compared.

The compositional fidelity was high when all samples and all size fractions were pooled: 61.9 % of live species and 77.2% of live genera were also found in the death assemblage and, conversely, 63.9% of dead species and 69.8% dead genera were represented in the life assemblage. In the restrictive analysis, with fragments excluded and counts corrected for disarticulation, the live-dead fidelity dropped slightly: 55.5% of live species and 66.7% of live genera were also found among dead whole shells or valves. Conversely, the dead-live fidelity increased: 70.0% of the species and 77.6% of the genera of complete dead shells/valves also occurred in the life assemblage. Both these patterns are primarily an artifact of the exclusion of fragments. Due to this exclusion, samples acquired from the death assemblage decrease notably in size. Consequently, the diversity estimates, which are directly dependent on sample size, must decline as well (Table 3).

The high estimates of fidelity were obtained consistently for various combinations of the size fractions included in the analysis. As summarized in Table 3, the data analyzed for five different sieve ranges show limited variation and are remarkably consistent with the analysis of data pooled across all size fractions. Thus, the percentage of live taxa also found dead varies among different size fractions from 61.0 to 71.4% for species and from 71.0 to 78.9% for genera, respectively. The percentage of dead taxa also found live varies in a comparably narrow range from 60.0 to 71.4% for species and from 63.8 to 69.1% for genera, respectively.

The life assemblage along the transect was dominated by the gastropod (1) *Calyptraea fastigiata,* the bivalves (2) *Acila castrensis,* (3) *Modiolus modiolus,* (4) *Cyclocardia ventricosa,* and (5) *Pododesmus cepio;* and the brachiopod (6) *Terebratalia transversa* (Figure 3a). When fragments were included (the exhaustive analysis), the death assemblage pooled across the transect was dominated by the bivalve mollusks (1) *Chlamys rubida,* (2) unidentified bivalve fragments, (3) *Chlamys hastata,* (4) *Modiolus modiolus,* and (5) *Pododesmus cepio;* and the brachiopod (6) *Terebratalia transversa* (Figure 3b). Although the rank abundance of species in the life assemblage differed notably from the exhaustive death assemblage, the six most common species found in the death and life assemblages, respectively, shared three species (Figure 3a-b). Of the top 20 live species only one was not found dead and only three out of the top 20 dead species were not found in the life assemblage (Table 2). The two assemblages displayed a significant, positive Spearman rank correlation ($r = 0.41$, $p = 0.0001$, $n = 84$ species). The transect-level fidelity improved somewhat when fragments were excluded and counts of individuals were corrected for disarticulation (Figure 3c-d). The most common live species was ranked second in the restrictive death assemblage (it ranked 12th in the exhaustive death assemblage). Also, the restrictive death assemblage shared a larger proportion of the 20 most common species with the life assemblage than did the exhaustive death assemblage (13 [65%] vs. 9 [45%] species, respectively). Nevertheless, the Spearman rank correlation was only slightly higher than in the case of the exhaustive analysis ($r = 0.44$, $p < 0.0001$).

When fragments were excluded and bivalved specimens corrected for disarticulation, the coarsest (class level) compositional fidelity was very high (Figure 4a vs. Figure 4c); the restrictive death assemblage and the life assemblage were indistinguishable statistically and the value of the log-likelihood statistic was very low ($G=0.26$, $p=0.88$). Moreover, at the phylum level (all mollusk groups combined), the relative abundance of brachiopods and mollusks in the life assemblage (94.6% vs. 5.4%) was nearly identical to that estimated by the restrictive death assemblage (94.8% vs. 5.2%). In contrast, the exhaustive analysis (with fragments included) failed to support the high class-level fidelity. Gastropods and chitons were severely underrepresented and bivalves were grossly overrepresented in the death assemblage; the proportion of brachiopods was nearly twice as high as in the life assemblage

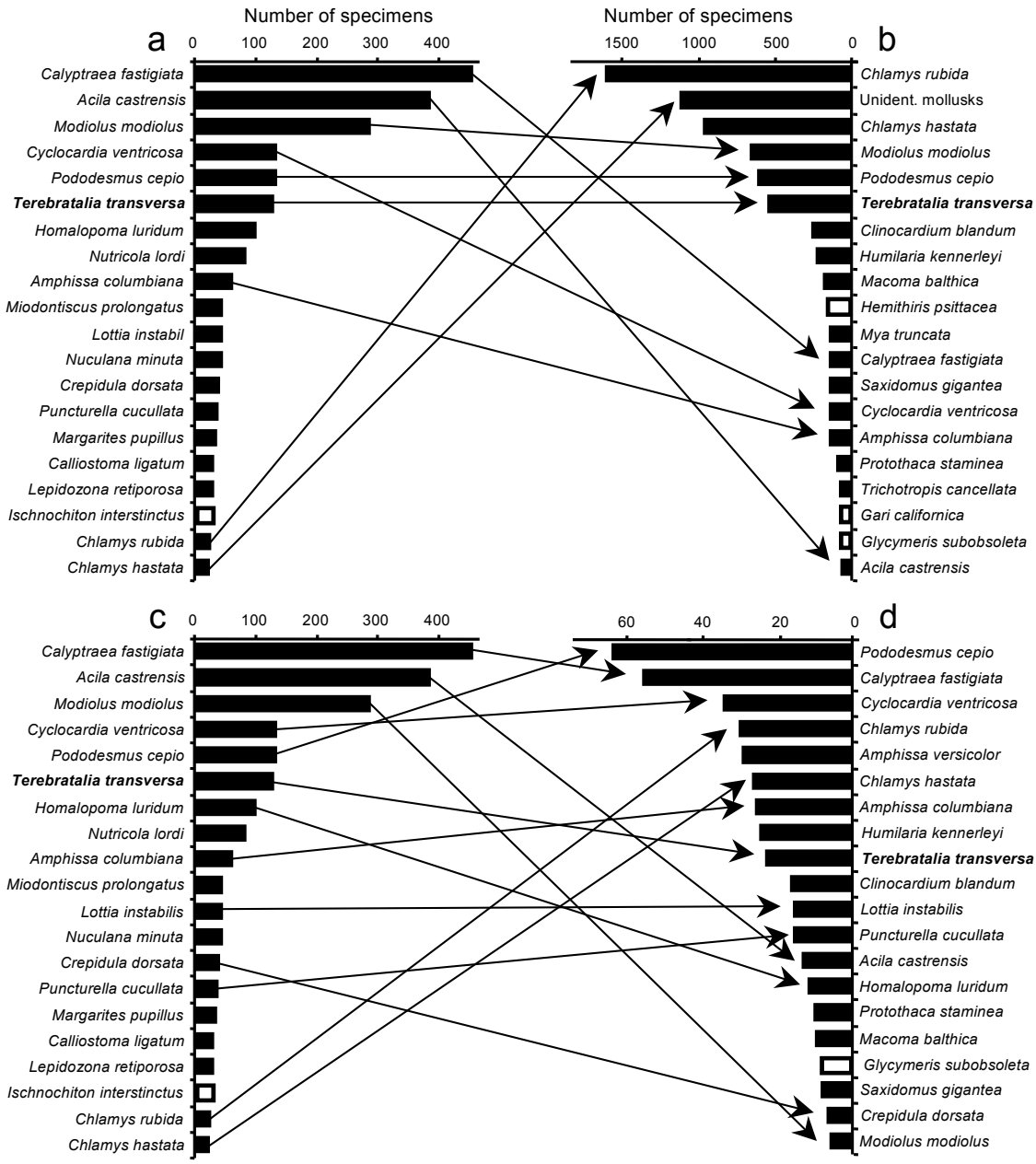

Figure 3. Species-level taxonomic composition of the life and death assemblages for data pooled across all samples along the transect. All charts restricted to the 20 most abundant species. Solid bars indicate live (or dead) species also found dead (or live). Open bars indicate live (or dead) species that were not found dead (or live). A. The life assemblage. B. Exhaustive death assemblage with fragments included. C. The life assemblage (the same as Figure 3A). D. Restrictive death assemblage with fragments excluded and counts corrected for disarticulation. Arrows connect the relative rankings of selected species in the life and death assemblages.

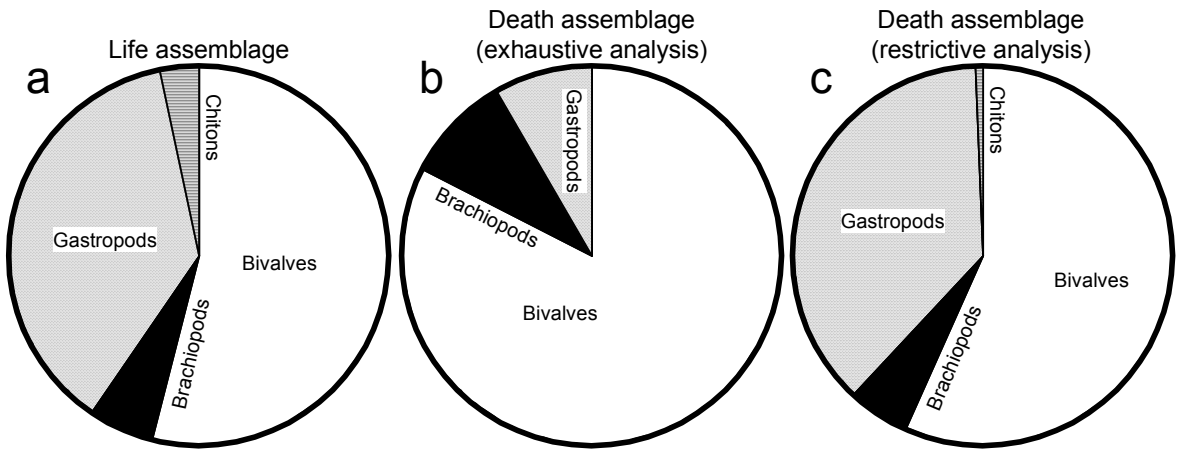

Figure 4. Class-level taxonomic fidelity for data pooled across all samples along the transect. A. The life assemblage. B. Exhaustive death assemblage with fragments included. C. Restrictive death assemblage with fragments excluded and counts corrected for disarticulation.

(9.1% vs. 5.4%, respectively). The difference in the class-level composition between the exhaustive death assemblage and the life assemblage were highly significant ($G=1095.7$, $p < 0.0001$).

The transect–level diversity of the life assemblage (for all samples combined) totaled 77 species, when all unidentified genera and species were counted (for a complete list see Table 2), and 63 species when only identified species were included. The exhaustive death assemblage totaled 79 species, including all unidentified genera and species (see Table 2 for a complete list), and 61 species when only identified species were included. The restrictive death assemblage contained 60 species including unidentified species and 50 species excluding unidentified species. The decrease in diversity in the restrictive death assemblage represents a loss of species that are represented by fragments only.

Because the estimated diversity is a function of sampling intensity (i.e., number of specimens sampled) and because the datasets included in these analyses vary greatly in sample size, some sample standardization method (e.g., rarefaction) needs to be applied. Rarefaction and related techniques -- commonly used in paleontology (e.g., Raup, 1975; Foote, 1992; McKinney, 1995; Alroy, 1996; Miller & Foote, 1996) -- aim to standardize samples to a common size by random subsampling of observations (without replacement) from those samples (for more details on the procedure applied here, see Kowalewski *et al.*, 2002). The sample-standardized data produced by rarefaction can then be used to directly compare the diversity of datasets that originally differed in sample size.

The rarefaction analyses conducted in this study include unidentified species, with all undetermined specimens within a given genus counted as a single species – an approach bound to yield conservative estimates of the sampled species-level diversity, but still more realistic than an estimate obtained by a total exclusion of undetermined specimens (see above). Note, however, that such exclusion was appropriate in the species-level fidelity analysis – for example, the inclusion of *Astysis* sp. could overestimate fidelity if different species of this genus were present in the life and death assemblages. This is why the estimates of species diversity are lower in the fidelity analyses (Table 3) than in the

rarefaction analysis (Figure 5).

The rarefaction curve based on the exhaustive death assemblage indicates that the diversity of the death assemblage increases with sample size at a much slower rate than is the case for the life assemblage and the restrictive death assemblages. Also, for a given sample size, the exhaustive death assemblage yields significantly lower diversity estimates than is the case for the life assemblage or the restrictive death assemblage (Figure 5). However, the exhaustive death assemblage is overwhelmed by fragments and, as discussed below, may yield biased diversity estimates. The restrictive death assemblage, which is much more directly comparable to the life assemblage than the exhaustive assemblage is (i.e., the individual elements sampled are comparable), provides diversity estimates that are significantly higher than those estimated for the life assemblage: there appears to be more diversity recorded in that death assemblage than was present at the moment of our sampling in the life assemblage.

Sample-level analyses

The sample-level analyses are primarily based on the exhaustive approach; the exclusion of fragments precludes almost any sample-level analysis because of extremely small sample size. The transect-level results (above) suggest that the exhaustive analysis is either consistent with or more conservative than the restrictive approach. Thus, the exhaustive approach is likely to underestimate the sample-level fidelity.

Except for the numerically limited sample 3-2-D, individual samples of dead material provided a good taxonomic representation of the life assemblage and vice versa (Table 3). On average, over 70% of live species and genera were also found dead and nearly 60% of dead species and genera were also found live. Although these

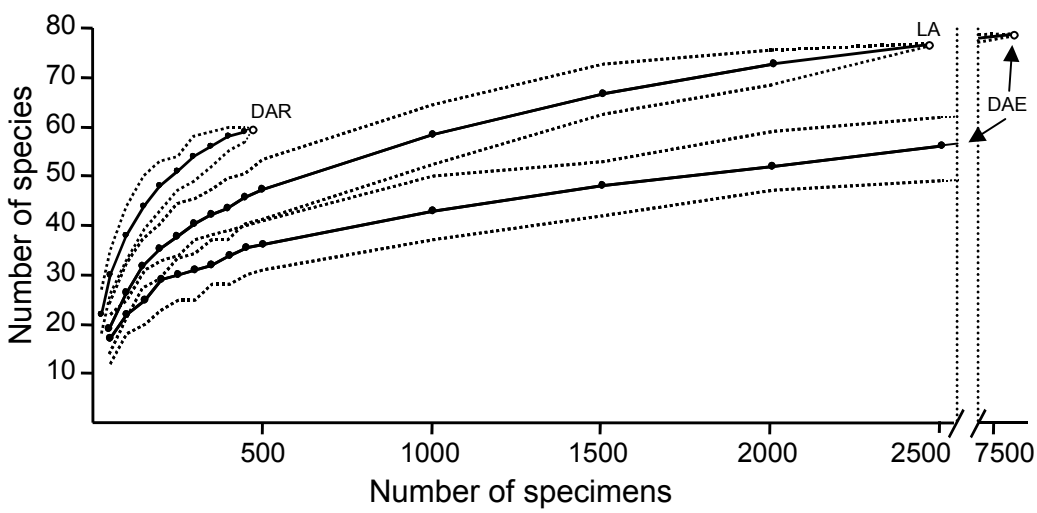

Figure 5. Rarefaction of species diversity for data pooled across all samples along the transect. The open circles indicate the total species richness for a given type of assemblage. Solid points indicates the median diversity obtained from 100 random samples of *n* specimens drawn without replacement from the original data. Dashed lines represent 95% confidence intervals based on 2.5th and 97.5th percentile estimated from the 100 random samples. Abbreviations as follows: LA – the life assemblage; DAE – the exhaustive death assemblage (fragments included in the analysis); DAR – the restrictive death assemblage (fragments excluded).

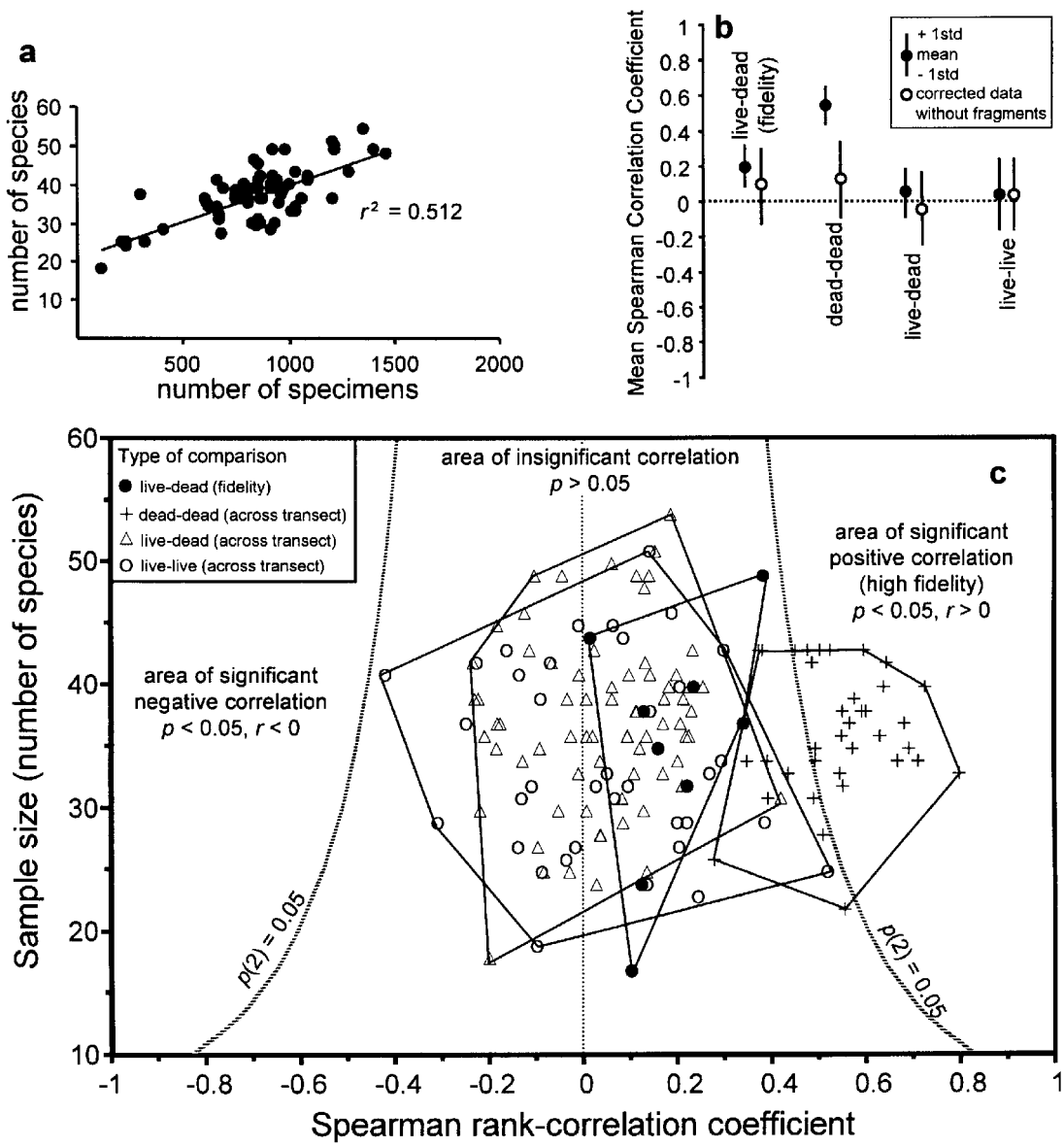

Figure 6. Sample-level fidelity analyses. A. Scatter graph of the number of specimens in a given pairwise comparison of two samples plotted against the total number of unique species represented by these two samples. Symbols: *r* – Pearson correlation coefficient. B. Mean Spearman correlation coefficients computed as arithmetic means of all pairwise correlation analyses for a given comparison type (e.g., dead sample vs. dead sample). C. Scatter graph of Spearman rank correlation coefficients for individual pairwise comparisons plotted against the sample size (i.e., the total number of unique species in the comparison; note that the number of taxa determines the number of degrees of freedom and thus directly relates to the power of the Spearman test). Dashed lines indicate the critical values of the Spearman *r* at a given sample size.

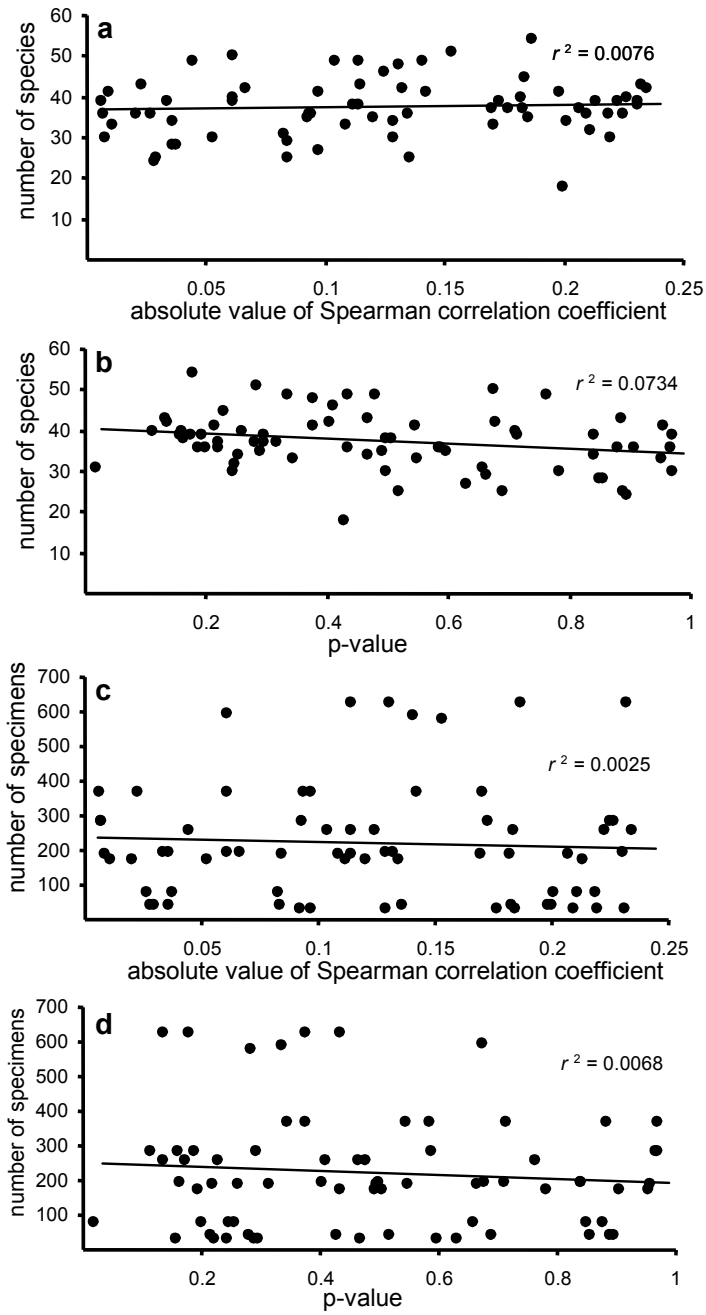

Figure 7. Scatterplots of number of species or number of specimens plotted against the values of the Spearman *r* and their associated *p* values. Each point represents one pairwise comparison. Symbols: *r* – Pearson correlation coefficient.

estimates fluctuated noticeably among samples, they rarely dropped below 50% (Table 3).

The compositional similarity between dead and live material was estimated for each site separately using the Spearman rank correlation (see Kidwell, 2001*b*). The results (Figure 6) are presented here at the species level only (genus level analyses yielded similar results). For all within-sample fidelity comparisons (i.e., the within-site pairwise comparisons labeled "live-dead (fidelity)") the Spearman correlations were positive. Although these correlation coefficients were not statistically significant (Figure 6b, c), they were always above 0 (Figure 6c). In contrast, the dead-live comparisons across sites (i.e., pairwise comparisons of death-assemblage vs. life-assemblage samples from two different sites) and live-live comparisons (i.e., pairwise comparisons of life-assemblage samples across the transect) show frequently correlation values $r < 0$ (Figure 6c), and their average compositional fidelity is very poor, with average *r* values approximating zero in both cases (Figure 6b). Finally, dead-dead fidelity comparisons (i.e., pairwise comparisons of death-assemblage samples across the transect) yielded much higher (often significant) correlation coefficients (Figure 6c). Note that when the restrictive approach was employed, the mean correlation coefficients did not change markedly, except for a substantial decrease in mean *r* for the dead-dead fidelity (Figure 6b).

It is noteworthy that the high dead-dead fidelity (Figure 6b-c) is unlikely to be a spurious consequence of the larger number of specimens in death-assemblage samples. Whereas the number of specimens correlates with number of species (Figure 6a) – and thus, affects the power of the Spearman test – there is no obvious correlation between Spearman *r* values and associated *p* values on one hand and the number of specimens and species on the other (Figure 7).

Discussion

Compositional fidelity patterns

Previous studies focused on mollusks suggest that, although the compositional taxonomic fidelity can vary greatly from one case study to another, the average live-dead fidelity levels are quite high (Kidwell & Bosence, 1991; Kidwell & Flessa, 1995; Kidwell, 2001*b*, 2003). On average, in marine bights and continental shelves, 78% of species living in the area are also found in the death assemblage; the percentage is even higher in the intertidal and coastal subtidal habitats (Kidwell & Bosence, 1991; Kidwell & Flessa, 1995). The results presented above for mollusk-brachiopod assemblages (Table 3; Figure 3) suggest somewhat lower fidelity levels. However, given the high variability among published case studies and the difference in sampling acquisition methods (dredging in this study and various methods in previous projects), these estimates are certainly consistent with, and well within the range of, values previously reported for mollusks.

The low dead-live fidelity of death assemblages (note that the "live-dead" fidelity discussed in the preceding paragraph deals with % live species also found dead, whereas the "dead-live" fidelity discussed in this paragraph deals with % dead species found also alive) observed in mollusk-focused studies (Kidwell & Bosence, 1991) is only weakly manifested in our data. The low dead-live fidelity has been previously interpreted as an artifact of inadequate sampling of living communities: when assemblages are based on more exhaustive and/or repeated sampling, the dead-live fidelity improves (Plotnick *et al.*, 1990; Kidwell & Bosence, 1991). The above-average dead-live fidelity observed in this study may reflect a reasonably adequate sampling: 278 live-collected specimens per sample, on average (see Table 3). Other factors that may have influenced these estimates may include the repeated dredging of the study area by previous researchers (although this does not seem very likely; see comments in the method section above) and extensive spatial and temporal mixing of death assemblages, which would increase number of taxa in the death assemblage in all, or majority of, the sampled sites.

The restrictive diversity analysis suggests that the rarefied species richness of the death

assemblage is significantly higher than that of the life assemblage (Figure 5). This interpretation agrees with the pattern observed in many previous studies and is intuitively expected. Typically, shelly death assemblages are time-averaged, with specimens varying in age by hundreds to thousands of years (see Powell and Davis, 1990; Flessa *et al.*, 1993; Flessa & Kowalewski, 1994; Martin *et al.*, 1996; Meldahl *et al.*, 1997; Kowalewski *et al.*, 1998; Carroll *et al.*, 2003). In contrast, life assemblages (even when sampled over multiple years) represent a short-term snapshot of the ecosystem. This dramatic difference in the temporal coverage of samples was invoked repeatedly as the most likely explanation for higher diversity levels observed in mollusk death assemblages (e.g., Cadée, 1984; Carthew & Bosence, 1986; Kidwell & Bosence, 1991). It should be noted that the exhaustive diversity analysis suggests the opposite pattern (Figure 5): lower rarefied diversity levels in the death assemblage. However, this contradictory outcome is very likely a direct consequence of the inclusion of a large number of fragments of easily identifiable taxa (especially *Chlamys rubida* and *Chlamys hastata*). This inclusion severely alters the diversity structure (evenness) of the dataset and suppresses diversity estimates obtained via rarefaction (see also below).

At the level of individual samples, the compositional fidelity of rank abundance of taxa estimated in this study appears to be much poorer than that reported in meta-analyses presented by Kidwell (2001*b*, 2003). None of the nine sampled sites display a significant rank correlation between the life and death assemblages (Figure 6) and the Spearman coefficients tend to be low. However, it should be noted that individual samples are relatively small in terms of number of species and therefore the Spearman test has a limited power. In addition, the sample-level comparisons are based on the exhaustive approach, which clearly underestimates fidelity (see also below). Thus, taken at their face value, the low correlation values are inconclusive: it is impossible to detect if taphonomic processes contributed to the observed low fidelity because correlation coefficients were depressed anyway by small sample sizes and the inclusion of fragments. However, it is noteworthy that even though the correlation coefficients are all insignificant, they are all positive (Figure 6). This contrasts with patterns obtained for live-dead comparisons across the sampled sites: rank correlation coefficients include both negative and positive values and the average coefficient closely approximates $r = 0$ (Figure 6). In other words, the death assemblage from a given site is, on average, more similar to the life assemblage from that site than to life assemblages from other sites from the same sampling area. This pattern indicates that the local small-scale spatial variability in the composition of the sampled life assemblages is recorded, to some extent, in the corresponding death assemblages despite the mixing which might occur due to the spatial extent of the dredge sample. (Note that the significant spatial fidelity across death assemblage, "dead-dead fidelity" in Figure 6c, is most likely due to the effect of several species readily identifiable from fragments; see below.)

The rank correlation becomes high and significant when data are pooled across the samples; that is, at the transect level, the compositional fidelity of the brachiopod-mollusk assemblage becomes comparable to the typical values reported previously for mollusks (Kidwell, 2001*b*, 2003). In addition, the class-level fidelity (Figure 4) is noteworthy – especially, the excellent agreement between the mollusk-brachiopod ratios in the restrictive death assemblage vs. life assemblage– given that brachiopod and mollusk shells differ from one another in terms of microstructure and chemistry. This observation is consistent with the general tendency of death assemblages to be dominated by remains of organisms that died recently (see also Olszewski, 1999; Kidwell, 2002). In other words, differential preservation may seriously alter compositional fidelity of skeletal remains with long post-mortem histories, but it is unlikely to affect remains of organisms that died only recently, even if these remains vary substantially in their taphonomic properties (see also Flessa *et al.*, 1993; Carroll *et al.*, 2003).

Analytical effects: the inclusion of fragments

The effects of an analytical approach on taphonomic patterns have been discussed extensively by numerous authors (e.g., Davies *et al.*, 1989, 1990; Kidwell *et al.*, 2001; Kidwell, 2003). These and other studies have clearly shown that analytical choices made in taphonomic analyses may notably affect the outcome of the analysis. For these reasons, the analyses presented above included examples of outcomes obtained for various size fractions and various tallying approaches (exhaustive vs. restrictive).

In this study, fidelity does not seem to be greatly affected by the exclusion of particular size fractions (Table 3). This observation may appear inconsistent with the recent work of Kidwell (2001*b*, 2003) who showed that mesh size can severely affect the outcome of fidelity analyses (for further discussion of biological and taphonomic effects of mesh size see also Okamoto & Leite, 1998; Peeters *et al.*, 1999; Kidwell *et al.*, 2001; Hoffmeister & Kowalewski, 2002; Gage *et al.*, 2002). However, a substantial decrease in fidelity was observed by Kidwell only when very fine mesh sizes were employed (1mm and smaller), whereas the size fractions included here are 2.3mm or higher.

The importance of analytical choices made in taphonomic analyses is much more strongly manifested by differences between the outcomes of the exhaustive and restrictive analyses. Although the exhaustive and restrictive approaches are consistent in some cases, they differ noticeably in others (see especially Figures 3 – 6). These differences appear to be mostly due to the inclusion of fragments of the easily identifiable species: unique features, discernible even from minute and degraded shell fragments, are diagnostic for the five most common species in the exhaustive death assemblage. The two “most common” species, the bivalves *Chlamys hastate* and *Chlamys rubida* are readily identifiable due to their distinct sculpture. The third and fourth most common species *Modiolus modiolus* and *Pododesmus cepio* are identifiable, even when fragments are heavily degraded, from their unique shell color and/or distinct shell layering. The fifth most common species *Terebratalia transversa* is identifiable due to the distinct color and the presence of punctae. In addition, most of these species are unusually prone to fragmentation (their shells are either very thin or porous and fragile) and their ranking in the death assemblage roughly corresponds to their adult shell size. This correlation between body size and ranking is to be expected. For example, the number of fragments produced from one shell is many times higher for *Chlamys* spp., which often exceed 10cm in its maximum dimension, than for *Terebratalia transversa,* which rarely exceed 4cm in maximum dimension. The large size, thin shell, and distinct sculpture are thus the most likely reason why *Chlamys* includes the two most abundant species in the exhaustive analysis (Figure 3b). Note the four out of the top five species markedly drop in ranking when fragments are excluded and counts are corrected for disarticulation (Figure 3d).

This differential identifiability may also have contributed to the poor fidelity of the exhaustive death assemblage at the class-level (Figure 4): the inclusion of identifiable fragments of bivalves (*Chlamys* spp., *Modiolus modiolus,* and *Pododesmus cepio*) and the exclusion of less easily identifiable fragments of gastropods (which likely end up in the "unidentified mollusks" category) may easily account for a higher proportion of bivalves observed in the exhaustive death assemblage. Similarly, the inclusion of identifiable fragments in samples offers a possible explanation for the high spatial fidelity of dead-dead comparisons (Figure 6): the overrepresentation of *Chlamys* and other top contributors of identifiable bioclasts results in the inflation of their ranking in all samples – identifiable fragments homogenize the dead samples in terms of their relative abundance structure.

Finally, the inclusion of identifiable fragments may lower the evenness by inflating the dominance of readily identifiable species of the death assemblage; consequently, estimates of sampled diversity may be underestimated: at a given sample size (collected or rarefied) fewer rare species will

be sampled when dominant species are overrepresented. This is the most likely explanation for a disagreement between the outcomes of the rarefaction analyses for the restrictive versus exhaustive death assemblages. The "*Chlamys* effect" illustrates an intuitively obvious, principle: because species often vary in their morphological distinctness, the inclusion of fragments in the quantitative analyses (or even in qualitative outcrop surveys) is likely to notably distort the taxonomic composition of the studied death and fossil assemblages. This potential problem could only be countered by a correction for number of fragments per individual (approximately proportional to adult size), and such correction is difficult to develop reliably in practice.

Summary

The fidelity analysis of the mixed brachiopod-mollusk assemblages along a single depth transect offers the first rigorous insight into fidelity of shell-rich assemblages where brachiopods are present in detectable quantities. The most important observations can be summarized as follows:

1. This study suggests that mixed brachiopod-mollusk assemblages are reasonably well represented in the death assemblage in terms of taxonomic composition and some aspects of rank abundance patterns in dominant taxa.

2. Despite the fact that brachiopod and mollusk shells differ from one another in terms of microstructure and chemistry, the class-level fidelity is excellent when fragments are excluded and counts of specimens are corrected for disarticulation.

3. The majority of the studied fidelity parameters display quantitative and qualitative characteristics that are highly congruent with patterns observed previously in fidelity studies that focused on mollusk assemblages.

4. A restrictive approach with fragments excluded appears to provide more credible estimates of sampled diversity and fidelity than the exhaustive approach, which includes fragments.

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