

Multiple phyla, one time resolution? Similar time averaging in benthic foraminifera, mollusk, echinoid, crustacean, and otolith fossil assemblages

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ABSTRACT

Time averaging of fossil assemblages determines temporal precision of paleoecological and geochronological inferences. Taxonomic differences in intrinsic skeletal durability are expected to produce temporal mismatch between co-occurring species, but the importance of this effect is difficult to assess due to lack of direct estimates of time averaging for many higher taxa. Moreover, burial below the taphonomic active zone and early diagenetic processes may alleviate taxonomic differences in disintegration rates in subsurface sediments. We compared time averaging across five phyla of major carbonate producers co-occurring in a sediment core from the northern Adriatic Sea shelf. We dated individual bivalve shells, foraminiferal tests, tests and isolated plates of irregular and regular echinoids, crab claws, and fish otoliths. In spite of different skeletal architecture, mineralogy, and life habit, all taxa showed very similar time averaging varying from ~1800 to ~3600 yr (interquartile age ranges). Thus, remains of echinoids and crustaceans—two groups with multi-elemental skeletons assumed to have low preservation potential—can still undergo extensive age mixing comparable to that of the co-occurring mollusk shells. The median ages of taxa differed by as much as ~3700 yr, reflecting species-specific timing of seafloor colonization during the Holocene transgression. Our results are congruent with sequestration models invoking taphonomic processes that minimize durability differences among taxa. These processes together with temporal variability in skeletal production can overrule the effects of durability in determining temporal resolution of multi-taxic fossil assemblages.

INTRODUCTION

Time averaging—mixing of remains of organisms that lived at different times in a single sedimentary layer—dictates the temporal resolution of the fossil record (Kowalewski and Bambach, 2008; Kidwell, 2013). Stratigraphic co-occurrence of organisms separated by centuries or millennia affects not only paleoecological inferences but also the resolution of geochemical and geochronological records based on their biomineralized remains. The extent of time averaging is expected to correlate with intrinsic skeletal durability (e.g., Kowalewski, 1997): remains of taxa with robust skeletons should survive longer in the taphonomic active zone (TAZ) and thus be, on average, older and more time averaged than co-occurring remains of fragile taxa (Broecker and Clark, 2011; Mekik, 2014), as observed in molluscan and foraminiferal assemblages

(e.g., Barker et al., 2007; Kosnik et al., 2009). The variation in durability across higher taxa may be even the main factor controlling the temporal resolution of fossil assemblages, as suggested by the millennial time averaging of robust bivalve shells contrasting with the yearly resolution of more fragile echinoid tests (Kowalewski et al., 2018).

The evaluation of this hypothesis, however, is hindered by narrow taxonomic coverage of the previous dating efforts, which, with a few exceptions (e.g., Krause et al., 2010; Kowalewski et al., 2018; Lin et al., 2019; Albano et al., 2020), focused mostly on aragonitic bivalves (Kidwell, 2013). Moreover, the effects of durability on time averaging can be overwhelmed by variation in timing of skeletal production (Tomašových et al., 2019a, 2019b) and by spatial variation in sedimentation rates and depth of mixing (Krause et al.,

2010; Albano et al., 2020). Finally, differences in time averaging documented in the TAZ do not necessarily translate into the subsurface stratigraphic record (Olszewski, 2004). Sequestration processes that lead to burial and early diagenetic stabilization allow fragile skeletal elements to escape rapid disintegration near the sediment-water interface (Olszewski, 2004; Tomašových et al., 2014) and may generate highly time-averaged assemblages formed by fragile remains.

We used individually dated specimens sampled from the subsurface stratigraphic record of the northern Adriatic Sea shelf to quantify variation in time averaging among five major phyla: Foraminifera (foraminiferal tests), Mollusca (bivalve shells), Echinodermata (echinoid tests and plates), Arthropoda (crab claws), and Chordata (fish otoliths), which play an important role in marine ecosystems. To contrast the effects of taxonomic variation in durability with the role of sequestration and sedimentation rates, we compared the observed extent of time averaging to (1) the ranking of species according to their mineralogical stability and size, and (2) the scale of time averaging expected from the long-term sedimentation rate and the bioturbation depth.

MATERIAL AND METHODS

Study Area and Sampling

The Gulf of Trieste (Fig. 1) is located in the northeastern Adriatic Sea. Its offshore parts, with a maximum depth of 25 m, have limited terrigenous input, low net sedimentation rates (<0.5 mm/yr), and reduced thickness of marine Holocene deposits (<5 m) compared to more onshore locations (Trobec et al., 2018). The sites currently at ~20 m water depth were flooded at ca. 9500–10,000 yr B.P. during the Holocene marine transgression (Fig. 1).

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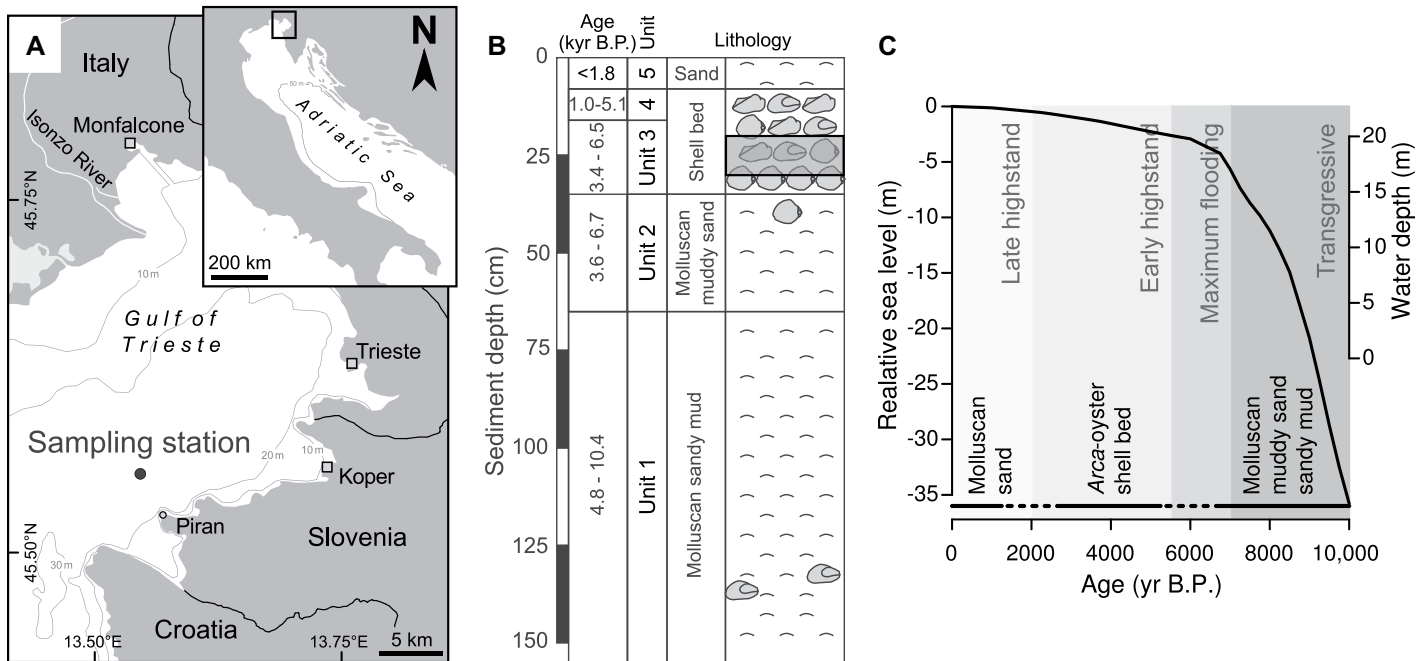


Figure 1. (A) Location of sampling station in the Gulf of Trieste, Adriatic Sea. Bathymetric contours are in m, contour interval is 10 m. **(B)** Stratigraphy of core Piran 2 M53 with position of the sampled interval (gray rectangle) (modified from Tomašových et al., 2019a). Age of the stratigraphic units is based on the 25th and 75th percentiles of bivalve shell ages. **(C)** Relative sea level in the Gulf of Trieste over the past 10 k.y. (Lambeck et al., 2011) and corresponding water depth at the coring station currently located at 22.7 m below sea level, with major sea-level phases in northern Adriatic Sea (Gallmetzer et al., 2019). Age ranges of the stratigraphic units (Mautner et al., 2018) are marked with horizontal lines with dashed intervals indicating uncertainty around their boundaries.

In 2013 CE, three 150-cm-long piston cores were collected 4 km off Piran (Slovenia; 45.563200°N, 13.537033°E) in the southern Gulf of Trieste at a depth of 22.7 m (Fig. 1A; Mautner et al., 2018). The cores were subdivided into five stratigraphic units, which correspond chronologically to the major sea-level phases in the northern Adriatic (Figs. 1B and 1C; Gallmetzer et al., 2019). One 16-cm-diameter core was sliced into 2- to 5-cm-thick increments and wet sieved. Mollusk shells, foraminiferal tests, elements of echinoderms and crustaceans, and fish otoliths were picked from the 1 mm sieve fraction. The core age model, stratigraphic framework, and changes in mollusk assemblages were reported by Mautner et al. (2018), Gallmetzer et al. (2019), and Tomašových et al. (2019a). Surface sediments at this coring station consist of skeletal muddy sands, underlain by a densely packed, poorly sorted molluscan shell bed located at 8–35 cm below the sediment surface (Fig. 1B). The base of the shell bed, interpreted as the maximum flooding zone, was dated to ca. 6500 yr B.P. (Tomašových et al., 2019a). The material analyzed here comes from two increments at 20–25 cm and 25–30 cm depth that were combined to obtain adequate sample sizes.

Target Taxa

Species were selected based on their abundance and to cover a wide range of skeletal properties and life habits (Table S1 in the Sup-

plemental Material¹). The aragonitic shells of bivalves *Corbula gibba* and *Gouldia minima* were previously dated using ¹⁴C-calibrated amino acid racemization (AAR) methods (Tomašových et al., 2019a). Here, we present the radiocarbon ages of two benthic foraminifera (the high-Mg calcitic miliolid *Adelosina intricata* and the low-Mg calcitic rotaliid *Elphidium crispum*), the minute irregular clypeasteroid echinoid *Echinocyamus pusillus*, the regular camarodont echinoids *Paracentrotus lividus* and *Psammechinus microtuberculatus* (all echinoids with high-Mg calcitic stereom), the brachyuran crustacean *Pilumnus* sp. (with low-Mg calcitic chelae), and the teleost fish *Gobius niger* (with aragonitic otoliths). We selected only complete bivalve valves or fragments with umbo, foraminifera with >60% of the test preserved, complete or partly preserved (>40%) tests of *E. pusillus*, isolated madreporite plates of the two regular echinoid species (which were analyzed together to increase sample size), isolated elements of chelae (dactyli and propodi) of *Pilumnus* sp., and sagittal otoliths of *G. niger*. All unique specimens were dated, except foraminifera and

¹Supplemental Material. Details on methods, Tables S1 and S2, Figures S1–S4, Appendix S1 (radiocarbon and AAR ages), and Appendix S2 (R script for analyzing the age data). Please visit <https://doi.org/10.1130/GEOL.S.19593418> to access the supplemental material, and contact editing@geosociety.org with any questions.

bivalves, for which 20–30 specimens were randomly selected per sample.

Radiocarbon Dating

Six taxa not dated by AAR were analyzed with the direct carbonate accelerator mass spectrometry radiocarbon technique (Bush et al., 2013). Application of powdered carbonate targets allows dating of submilligram samples and produces ages that are consistent with the results of the standard graphite ¹⁴C method (Bright et al., 2021). Radiocarbon ages were calibrated to calendar ages (see the Supplemental Material) and are reported in years before present (yr B.P., i.e., relative to the year 1950 CE).

Data Analysis

We used the interquartile age range (IQR) to quantify the extent of time averaging of each taxon. Although IQR is less sensitive to sample size than other measures of dispersion, these values should be treated as minimum estimates due to relatively small sample sizes (Table 1; Olszewski, 1999). Higher age errors associated with AAR dating of bivalve shells can inflate estimates of time averaging, but accounting for this effect does not affect our conclusions (Fig. S1 in the Supplemental Material). We estimated bias-corrected percentile confidence intervals around the IQRs and median ages using a bootstrap procedure with 10,000 iterations, and applied the non-parametric Kruskal-Wallis test followed by the pairwise Wilcoxon test with Holm-Bonferroni

TABLE 1. SUMMARY STATISTICS FOR THE AGE-FREQUENCY DISTRIBUTIONS OF THE EIGHT TAXA

Taxon	Taxonomic affiliation	N*	Median age (yr B.P.)†	Interquartile age range (yr)	Minimum age (yr B.P.)	Maximum age (yr B.P.)	Age range (yr)	Skewness
<i>Corbula gibba</i>	Bivalvia	25	5695	2229	3318	8917	5599	0.14
<i>Gouldia minima</i>	Bivalvia	30	3786	1802	2240	7016	4776	0.38
<i>Adelosina intricata</i>	Foraminifera	40	6881	3230	2382	8974	6592	-0.55
<i>Elphidium crispum</i>	Foraminifera	40	3194	2968	1126	6785	5659	0.37
<i>Echinocyamus pusillus</i>	Echinoidea	25	5472	1980	677	7440	6763	-0.88
<i>Psammechinus microtuberculatus</i> – <i>Paracentrotus lividus</i>	Echinoidea	14	4498	3640	1462	7450	5988	0.09
<i>Pilumnus</i> sp.	Brachyura	17	5709	3011	578	7856	7278	-0.61
<i>Gobius niger</i>	Teleostei	16	5198	2847	1396	7637	6241	-0.51
			(3608–6396)	(1586–5122)				

Note: 95% bootstrap confidence intervals for median age and interquartile age range are given in parentheses.

*N—number of dated specimens.

†Ages are in years before present (before 1950 CE).

correction to compare median ages of the taxa. Age offset between taxa was calculated as the difference between their median ages.

To evaluate whether taxonomic variation in time averaging is determined by durability, first we tested for correlation between per-taxon IQR and median age. If durability controls time averaging, while the shell input is constant through time and mixing by burrowers is limited to the TAZ, per-taxon IQR and median age should be positively correlated in subsurface increments.

However, sequestration of shells by burrowers or physical mixing below the TAZ and temporal variability in skeletal production can decouple median age and IQR (Tomašových et al., 2014). Second, we assessed whether time averaging is related to mineralogical stability and size of skeletal elements. Finally, we compared the scale of time averaging observed in the shell bed to its extent expected from the net sedimentation rate and the depth of mixing, estimated based on downcore changes in median age of

the increments (see the Supplemental Material). All analyses were performed in R version 4.1.2 (R Core Team, 2021).

RESULTS

The median ages of age-frequency distributions (AFDs) differ strongly between the taxa (Kruskal-Wallis test $\chi^2 = 46.37$, $df = 7$, $p < 0.001$; Table S2) but do not covary with their mineralogy, size, or life habit (Figs. 2 and 3; Table 1; Table S1). Median ages

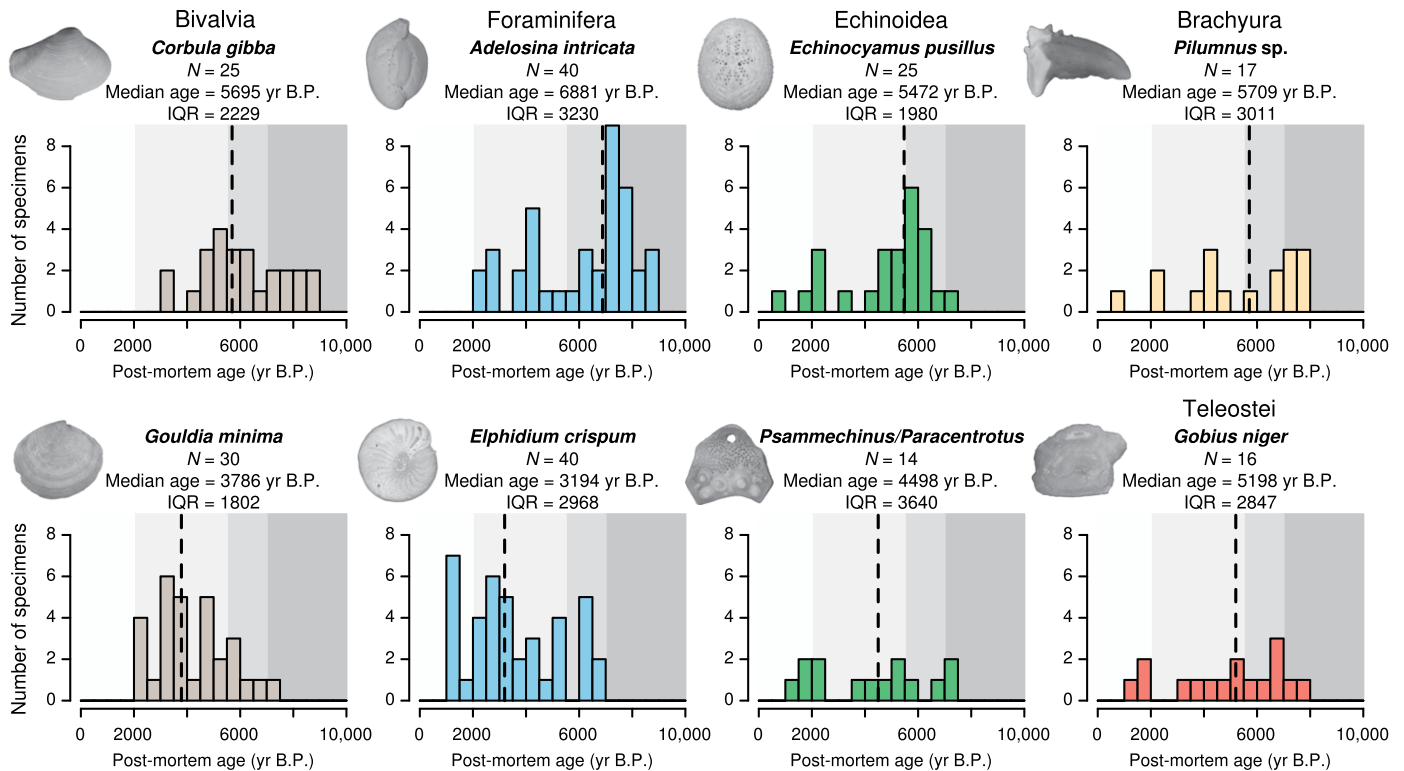


Figure 2. Age-frequency distributions (AFDs) for bivalve shells, foraminiferal tests, tests of irregular echinoids, isolated madreporites of regular echinoids, crab chelae, and fish otoliths in a 10-cm-thick shell bed interval from core Piran 2 M53 (4 km off Piran, Slovenia). AFDs are based on ^{14}C -calibrated amino acid racemization ages for bivalves and calibrated ^{14}C ages (median probability ages in 500 yr bins) for all other taxa. Dashed lines represent median ages, and shading marks sea-level phases (see Fig. 1C). IQR—interquartile age range. Photographs are not to scale.

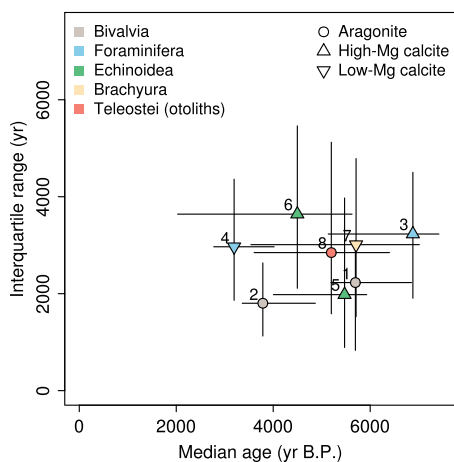


Figure 3. Median ages and interquartile age ranges of eight taxa (interval from core Piran 2 M53, 4 km off Piran, Slovenia) with 95% bootstrap confidence intervals. 1—*Corbula gibba*; 2—*Gouldia minima*; 3—*Adelosina intricata*; 4—*Elphidium crispum*; 5—*Echinocyamus pusillus*; 6—*Psammechinus microtuberculatus-Paracentrotus lividus*; 7—*Pilumnus sp.*; 8—*Gobius niger*.

differ by ~ 3700 yr between the two foraminifera, by ~ 1900 yr between the two bivalves, and by ~ 1000 yr between the irregular and regular echinoids. The smallest between-species age offset (14 yr) was observed between taxa with fundamentally different skeletal architecture and life habit: the bivalve *C. gibba* and the crab *Pilumnus sp.* However, the scale of time averaging is similar across all taxa (Fig. 3; Table 1): IQRs vary from ~ 1800 yr in *G. minima* to ~ 3600 yr in regular echinoids. Median ages and IQRs are not correlated (Pearson $r = 0.13$, $p = 0.75$). Neither per-taxon median age nor IQR is related to the average size of the dated elements (Fig. S2), and remains with different mineralogical stability have similar IQRs (~ 3000 , $2000\text{--}3600$, and $1800\text{--}2800$ yr for low-Mg calcitic, high-Mg calcitic, and aragonitic taxa, respectively). The extent of time averaging across the taxa is thus independent of their durability. On the other hand, the observed IQRs are very similar to values expected from the net sedimentation rate of 0.006 cm/yr and mixing depth of $10\text{--}20$ cm estimated for the shell bed interval (expected IQR: $1800\text{--}3700$ yr; Fig. S3).

DISCUSSION

Absence of Durability Effects

Our findings demonstrate that remains of taxa with fundamentally different skeletal characteristics, including multi-elemental skeletons of echinoids and crustaceans, can undergo similarly extensive, millennial-scale time averaging. Thus, intrinsic durability, at least among biomineralized taxa, is less important in controlling the duration of time averaging than other factors such as sedimentation rate, sequestration, or temporal variability in production. Similar

scales of time averaging of bivalve, otolith, and foraminiferal assemblages, observed here and in previous studies (Martin et al., 1996; Albano et al., 2020), underscore the lack of significant differences between taxa of different size and skeletal mineralogy. Time averaging of the two foraminifera is nearly identical, even though low-Mg hyaline tests dissolve at lower rates than high-Mg porcelaneous tests in laboratory experiments (Peebles and Lewis, 1991). Thus, just like macrofossils, microfossil records can be time averaged over 10^3 yr in shallow-water sediment-starved environments.

The extensive time averaging of isolated decapod claws and echinoid plates points to their high fossilization potential. These remains can be commonly identified to low taxonomic levels, yet they are commonly overlooked components of death assemblages (Plotnick et al., 1990; Mancosu and Nebelsick, 2020). Decapod cuticles usually undergo rapid decay and fragmentation near the sediment-water interface due to high organic content (Plotnick, 1990). However, claws are the most heavily calcified parts of decapod skeletons (Mutel et al., 2008) and are overrepresented in death assemblages (Stempien, 2005). Similarly, tests of regular echinoids disarticulate rapidly (Kidwell and Baumiller, 1990; Greenstein, 1991), but the large IQR (~ 3600 yr) of isolated madreporites indicates that individual echinoderm plates can withstand extensive temporal mixing.

The robustness of echinoid plates does not explain, however, the millennial averaging of articulated tests of *E. pusillus* (IQR = ~ 2000 yr). This value contrasts with yearly time averaging of tests of another clypeasteroid, *Leodia sexiesperforata*, from the Bahamas (IQR = 2 yr; Kowalewski et al., 2018). The two species differ strongly in size, but both have internal support structures and interlocking plates that increase test strength (Grun and Nebelsick, 2018).

Sequestration and Variability in Skeletal Production

The lack of differences in time averaging between taxa cannot be explained by unusually favorable conditions within the TAZ at Piran: (1) surface sediments in the southern Gulf of Trieste are reworked by storms, well mixed by burrowers (e.g., thalassinidean shrimps; Pervesler and Dworschak, 1985), and undersaturated with respect to aragonite (Ogrinc and Faganeli, 2003); (2) many dated specimens show high taphonomic alteration (Fig. S4); and (3) the shape of the AFD of *C. gibba* within the fully mixed layer at Piran indicates decadal-scale disintegration rate (Tomašových et al., 2019a). Under slow sedimentation estimated for the shell bed interval, such fast disintegration would lead to time averaging an order of magnitude lower than observed. Our data thus support a sequestration model (Tomašových et al., 2014, 2019b),

in which burial or early diagenetic stabilization in the subsurface buffers against rapid destruction in the TAZ while deep burrowing below the TAZ leads to mixing of skeletal elements of vastly different ages. As skeletal remains are temporally sequestered in the subsurface sediments and occasionally exhumed, this mechanism decouples time averaging from the effect of intrinsic durability. However, initial differences in disintegration rate, prior to sequestration, still lead to over-representation of more robust remains in fossil assemblages.

In spite of similar time averaging, median ages of the eight taxa differ by as much as $10^2\text{--}10^3$ yr. These large age offsets most likely resulted from diachronous shifts in local abundance (and thus skeletal production rates) in response to changes in water depth and substrate during the Holocene sea-level rise (Fig. 1C). Upcore replacement of *C. gibba* by *G. minima*, preferring muddy and sandy substrates, respectively, produces age offsets between these species persisting throughout the core (Tomašových et al., 2019a). Such age differences between co-occurring taxa are commonly reported from Holocene death assemblages on continental shelves (Kosnik et al., 2009; Krause et al., 2010; Tomašových et al., 2019b).

CONCLUSIONS

Our results suggest that sequestration of skeletal remains below the TAZ coupled with slow sedimentation and deep mixing has both positive and negative consequences for paleoecological inferences: taxa differing in durability can have comparable temporal resolution, but significant age offsets between co-occurring species can complicate interspecific analyses of multi-taxic fossil assemblages and make core age models sensitive to taxon choice.

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