# Young death assemblages with limited time-averaging in rocky and *Posidonia oceanica* habitats in the Mediterranean Sea

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**Abstract:** Death assemblages (DAs) are increasingly recognized as a valuable source to reconstruct past ecological baselines, due to the accumulation of skeletal material of non-contemporaneous cohorts. We here quantify the age and time-averaging of DAs on shallow subtidal (5–25 m) rocky substrates and in meadows of *Posidonia oceanica* in the eastern Mediterranean. We show that such DAs are very young – median ages 9–56 years – with limited time-averaging, one to two orders of magnitude less than on even nearby soft substrates. On rocky substrates, out-of-habitat transport is likely the main cause of loss of older shells. In *Posidonia oceanica* meadows, the root and rhizome system creates a dense structure – the *matte* – that quickly entangles and buries shells and limits the potential for bioturbation. The *matte* is, however, a peculiar feature of *Posidonia oceanica*, and age and time-averaging in meadows of other seagrass species may be different. The young age of DAs in these habitats requires a careful consideration of their appropriateness as baselines. The large difference in DA age between soft substrates, subject to numerous studies, and hard and seagrass substrates, rarely inspected with geochronological techniques, implies that DA dating is important for studies aiming at using DAs as baselines.

**Supplementary material:** Details on methods and shell radiocarbon ages are available at https://doi.org/10.6084/m9.figshare.c.6315678

Death assemblages (DAs) are the taxonomically identifiable, dead or discarded organic remains encountered in a landscape (e.g. bones and the skeletal remains of other continental organisms) or seabed (e.g. teleost fish otoliths and hard parts of marine invertebrates) (Kidwell 2013). Due to their slow degradation and the generally low sedimentation rates, surficial DAs accumulate information on taxonomic and functional composition of ecosystems over decades to millennia (Kidwell and Tomašových 2013). This archiving capacity makes DAs precious sources of information on the ecosystem past that can be used as baselines to assess change due to natural or human activities (Dietl *et al.* 2015; Kidwell 2015).

In this perspective, two critical properties of DAs are their age and the degree of time-averaging, that is, the extent of temporal mixing caused by the fact that skeletal remains are typically accumulated from multiple non-contemporaneous generations into a single assemblage. This is due to the combined effects of their high durability and the low burial rates in most settings. Age and time-averaging should be commensurate with the time frame of the studied processes to provide meaningful results. For example, if DAs are younger than the environmental changes of interest, they would represent an already shifted baseline and would thus lead to an underestimation of impacts.

Notwithstanding the importance of quantifying these properties when comparing death to living assemblages in order to infer ecosystem change, the cost of dating skeletal material and constraints on the minimum sample size for successful analysis hindered its broad application in the past. However, recent technical developments in amino acid

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racemization (Miller *et al.* 2013) and radiocarbon dating (Bush *et al.* 2013; Gottschalk *et al.* 2018; Bright *et al.* 2021) have rendered dating individual shells affordable and applicable to ever-decreasing carbonate masses. Even so, the quantification of age and time-averaging of DAs has been mostly limited to soft substrates so far (e.g. Flessa and Kowalewski 1994; Carroll *et al.* 2003; Kidwell *et al.* 2005; Krause *et al.* 2010; Albano *et al.* 2016*a*; Harnik *et al.* 2017; Tomašových and Kidwell 2017), with a single study quantifying them in tropical seagrass substrates (Hyman *et al.* 2019). However, rocky substrates and seagrass meadows constitute important habitats for conservation as they host a higher biodiversity than soft substrates at similar depths (Guidetti 2000) and are under major human pressures such as coastal development, fisheries, sedimentation and global warming (Waycott *et al.* 2009; Bevilacqua *et al.* 2018; Rossi *et al.* 2022). The establishment of research protocols that include DA dating is an important step towards the application of live–dead comparisons to the assessment of their status.

Here, we quantify the median age and time-averaging of DAs on shallow subtidal hard substrates and in meadows of the seagrass *Posidonia oceanica* in the eastern Mediterranean Sea. We then discuss the causes of the patterns we found and their consequences for the use of DAs in these habitats for conservation purposes.

## Materials and methods

We sampled the rocky substrate in 2018 between 11 and 20 m depth off Ashqelon (31.69° N, 34.55° E) and west of Rosh HaNikra islands (33.07° N, 35.09° E), in the south and the north, respectively, of the Mediterranean Israeli shelf (Fig. 1). In Ashqelon, we collected on rocky reefs emerging from the siliciclastic soft substrates, whose DA were also sampled and dated by Albano *et al.* (2021). In Rosh HaNikra, we sampled large calcareous rock substrates. Due to the absence of *Posidonia oceanica* meadows in Israel (Boudouresque *et al.* 2006), we compare these results with those of a pristine meadow in Plakias, southwestern Crete, Greece, along a 5–20 m depth transect sampled in 2017 (35.18° N, 24.40° E) (Holzknecht and Albano 2022) (Fig. 1). In the meadow we deployed a suction sampler on the rhizomes after defoliation to enhance sampling efficacy (Bonfitto *et al.* 1998). This procedure collects material from the well-oxygenated sediment layer without penetrating the underlying mat, where the environment is characterized by sulfide production through high organic matter input and by oxygen supply through radial oxygen release from the roots (van der Heide *et al.* 2012). Details on the sampled locations can be found in Supplementary material S1.

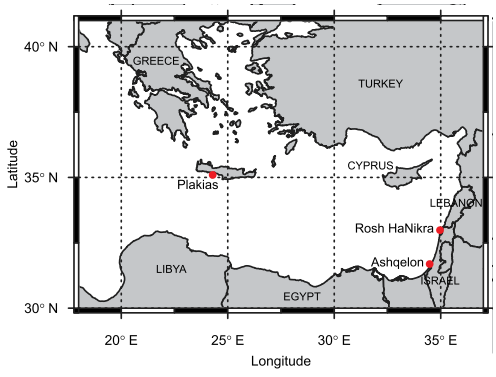


**Fig. 1.** Locations where the death assemblages from the rocky (Ashqelon and Rosh HaNikra in Israel) and seagrass (Plakias, Crete, Greece) substrates were collected.

At both locations, we sampled 1 $m^2$ quadrats with an air-lift suction sampler with a 0.5 mm mesh bag (Templado *et al.* 2010). This device collects organisms and the associated surface sediment enabling the contemporaneous collection of both the living and the death assemblages. Samples were then sieved, and shells for dating picked from the fractions coarser than 1 mm to ensure a minimum carbonate mass of 1 mg.

To quantify DA age and time-averaging, we radiocarbon dated ten valves per site of the bivalves *Striarca lactea* (Linnaeus, 1758) and *Glans trapezia* (Linnaeus, 1767) in Israel and Crete, respectively. These are common bivalves living byssally attached to hard substrates in the shallow subtidal. Bivalves are particularly suitable targets for dating because of their abundance and because of their shape that limits the retention of sediments and contaminants. Gastropods, equally abundant, have spires that are often filled with carbonate particles that either require a more time-consuming preparation or may bias the dating results. We selected both species based also on the presence of living individuals in our samples to avoid the truncation of the young end of the age frequency distribution.

Dating was conducted by accelerator mass spectrometry (AMS) using powdered carbonate targets (Bush *et al.* 2013; Bright *et al.* 2021) at the University of California Irvine, with a typical analytical precision of better than 0.6% ($1\sigma$). Radiocarbon ages were converted to calendar years using OxCal v. 4.4.2 (Bronk Ramsey 2009), Marine20 data (Heaton *et al.* 2020), and a constant regional marine reservoir correction ($\Delta R$) of $-142 \pm 66$ years, which is the weighted mean of eight published pre-bomb $\Delta R$ values from Israel and Lebanon (Reimer and

McCormac 2002; Boaretto *et al.* 2010). For samples younger than AD 1950, the fraction of modern carbon ($F^{14}C$) was converted to calendar ages using a regional marine calibration curve and the calibration software OxCal v4.2. The post-1950 regional marine curve was constructed using 10 live-collected *Corbula gibba* shells collected along the coast of Israel. For details on the radiocarbon analysis and age calibration, please refer to section 1.3 of Supplementary material S1 and Albano *et al.* (2022). All ages are here reported in years before the year of collection. Dating results are reported in Supplementary material S2.

DA age was quantified by the median age of the dated shells, whereas time-averaging was quantified by the total age range, the 95% age range and the inter-quartile range (IQR). Computations and plotting were run in the R statistical environment (R Development Core Team 2019).

## Results

All dated DAs showed a very young median age ranging between 18 and 56 years on rocky substrates and between 9 and 15 years in the *Posidonia oceanica* meadow (Table 1). Among the 80 dated shells, only two remarkable outliers were present: one shell of age 2810 years on the rocky reef at 25 m water depth, and one of age 1997 years in 20 m in the *Posidonia oceanica* meadow (Fig. 2, Supplementary material S2). Two and three shells of a few centuries old were also present in 5 and 20 m depth, respectively, in the meadow.

Consequently, at most sites, total and 95% age ranges are limited to a few decades (Table 1). The IQR ranges between 0 (rocky substrate, −12 m) and 251 (seagrass, −20 m) years (Table 1).

## Discussion

The large majority of the shells from the rocky and seagrass DAs are only up to a few decades old. The young age of these assemblages strongly contrasts with older ages usually reported from shallow subtidal non-vegetated soft substrates, where median ages and inter-quartile ranges can be several hundreds to thousands of years (Flessa and Kowalewski 1994; Carroll *et al.* 2003; Kidwell *et al.* 2005; Krause *et al.* 2010; Harnik *et al.* 2017; Tomašových and Kidwell 2017). This result is even more evident when comparing the age distributions on the hard substrates with those of nearby (few hundred metres away) soft substrates sampled off Ashqelon in southern Israel (Fig. 3) reported by Albano *et al.* (2020). Shells collected from the soft substrate station at 10 m depth had a median age of 656 years and an IQR of 1062 years, in striking contrast with the

**Table 1.** *Median age and metrics of time-averaging of marine death assemblages on rocky substrates and in a* Posidonia oceanica *meadow*

| Locality | Rocky substrate | | | | *Posidonia oceanica* meadow | | | |
|---|---|---|---|---|---|---|---|---|
| | Ashqelon (Israel) | Ashqelon (Israel) | Rosh HaNikra (Israel) | Rosh HaNikra (Israel) | Plakias (Crete, Greece) | Plakias (Crete, Greece) | Plakias (Crete, Greece) | Plakias (Crete, Greece) |
| Water depth (m) | 12 | 25 | 11 | 20 | 5 | 10 | 15 | 20 |
| Number of dated specimens | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Median age (years) | 56 | 18 | 33 | 37 | 14 | 9 | 11 | 15 |
| Total age range (years) | 36 (20–56) | 2803 (7–2810) | 51 (6–57) | 117 (4–121) | 259 (4–263) | 51 (4–55) | 50 (5–55) | 1994 (3–1997) |
| 95% age range (years) | 20 (36–56) | 1565 (7–1572) | 46 (11–57) | 87 (5–92) | 227 (5–232) | 51 (4–55) | 50 (5–55) | 1242 (4–1246) |
| Inter-quartile range (IQR) (years) | 0 (56–56) | 51 (7–58) | 35 (21–56) | 44 (12–56) | 40 (7–47) | 49 (6–55) | 18 (7–25) | 251 (5–256) |

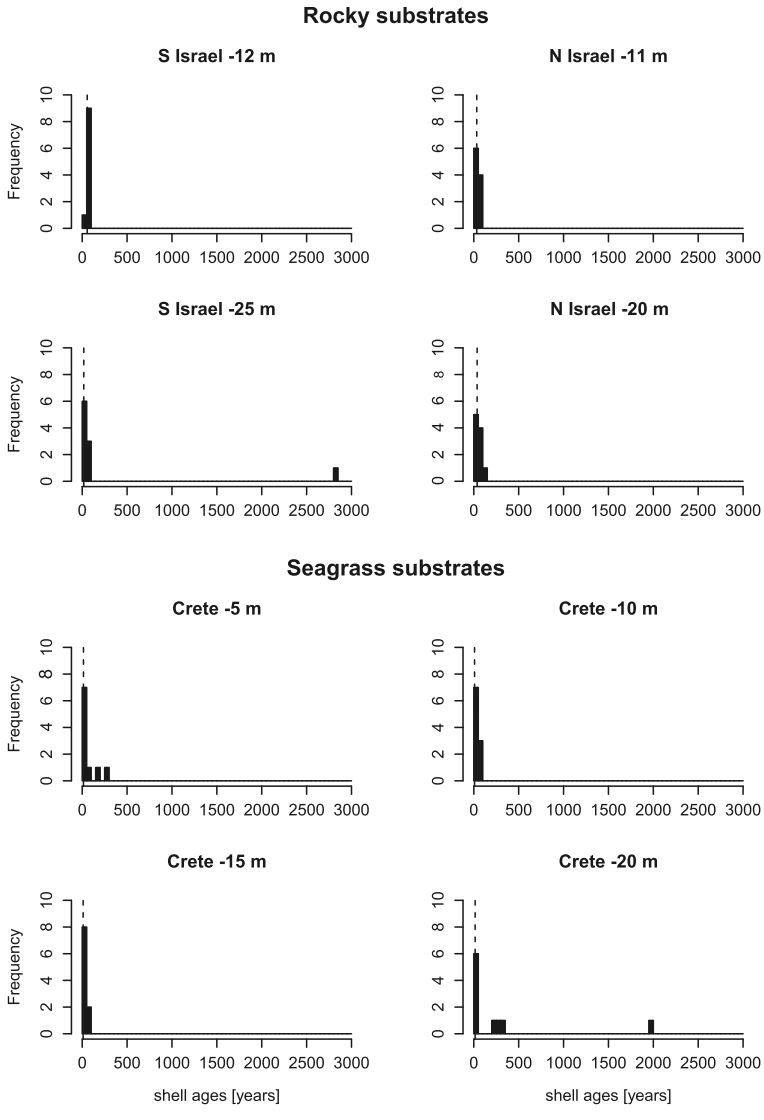


**Fig. 2.** Age frequency distributions (median probability ages in 50 year bins) based on calibrated radiocarbon ages for bivalve shells in rocky (upper panel) and seagrass (*Posidonia oceanica*) (lower panel) substrates. Dashed lines indicate median ages.

median age of 56 years and the null IQR on nearby hard substrates. At 30 m depth, the soft substrate shells had a median age of 1465 years and an IQR of 1312 years, contrasting the median age of 18 years and the IQR of 51 years of the nearby rocky reef.

Due to aboveground nuclear detonations mostly in the late 1950s and early 1960s, radiocarbon levels in the atmosphere, oceans and biosphere increased beginning in 1955 (Hua *et al.* 2022). As a result of fast transport of excess $^{14}C$ from the atmosphere to the surface ocean and then to deeper oceans, the surface ocean $^{14}C$ level of a given site typically reached its peak in the 1970s and 1980s (Grottoli and Eakin 2007), depending on its local/regional ocean circulation, and then declined. This shape of a local/regional oceanic bomb $^{14}C$ curve implies that for each measured $F^{14}C$ value of modern samples, two calendar ages are possible, one in the rising and the other in the falling arm of the curve, implying large confidence intervals. This uncertainty is limited to a few decades around the mid-1960s and therefore

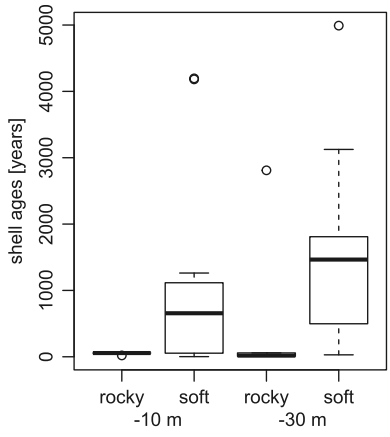


**Fig. 3.** Age distributions on nearby rocky and soft substrates off Ashqelon, southern Israel. The median age and the range of shell ages on hard substrates are one to two orders of magnitude smaller than on soft substrates.

does not undermine the main conclusions of the study.

The young median ages and short time-averaging may be due to different processes on hard substrates v. in seagrass habitats. On hard substrates, especially in shallow water, death assemblages are subject to intense hydrodynamic processes that enhance the transport of shells outside the habitat of production and hinders sedimentation and thus burial (Airoldi *et al.* 1996). This is even more marked when hard substrates have complex topographies with slopes and drop-offs, where gravity contributes to transporting shells away from the habitat of the living assemblage (Airoldi 2003). In seagrass habitats like those formed by *Posidonia oceanica*, the root and rhizome system creates a dense structure – the *matte* – that grows between 0.06 and 0.41 cm $a^{-1}$ (Mateo *et al.* 1997) with reported values up to 4 cm $a^{-1}$ (Marbà and Duarte 1998). This implies that shells are quickly entangled and buried in the thick and complex root network. Therefore, those that are sampled in the rhizome layer are the ones most recently produced. In contrast to rocky substrates, hydrodynamism is very low within the meadow, owing to the protective role of the leaf layer, that can be up to 40 cm long (Gobert *et al.* 2006), facilitating the deposition of fine sediments and avoiding out-of-habitat transport by storms and currents. However, the root network may make it more difficult for burrowing organisms to rework older shells upward from deeper sediment layers. It must be highlighted, however, that among seagrasses only *Posidonia oceanica* forms such an intricate and thick *matte*. The other *Posidonia* species, which are distributed around Australia, are horizontal spreaders with little vertical shoot production (Gobert *et al.* 2006). Other seagrass genera – including those in tropical seas – also do not produce the *matte* structure. Therefore, DAs in these seagrass meadows may show older median ages as well as larger time-averaging, as reported for seagrass habitats in the eastern Gulf of Mexico where bivalves showed median ages an order of magnitude older than in our study (Hyman *et al.* 2019).

Mismatch in structure and composition between living and death assemblages can be reliable evidence for major human impacts (Kidwell 2007, 2008, 2013; Kidwell and Tomašových 2013). Consequently, this approach is increasingly used to detect impact even in the absence of suitable baseline data (Albano and Sabelli 2011; Weber and Zuschin 2013; Korpanty and Kelley 2014; Negri *et al.* 2015; Zuschin and Ebner 2015; Albano *et al.* 2016*a*, *b*, 2021; Bizjack *et al.* 2017; Dietl and Smith 2017; Powell *et al.* 2017; Michelson *et al.* 2018; Tweitmann and Dietl 2018; Meadows *et al.* 2019; Haselmair *et al.* 2021). Live–dead comparisons for environmental assessment rely, however, on the archiving capacity of the DA. Its memory should be long enough to precede the onset of the pressures under study, otherwise the impact may be underestimated.

The significant amount of data available on DA ages in soft substrates is not matched by a proportionate effort on hard substrates and seagrass meadows, notwithstanding the latter are a significant target for marine conservation and DAs may be the only source of information on their ecological baselines. The large differences among habitats reported here and the very young DAs in these latter habitats show that the archival capacity of surficial DAs can also be low. Given the results of the above comparison, and the more affordable costs of dating techniques, we recommend the dating of DAs to become a common practice when using them for environmental assessment in conservation palaeobiology studies.

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**Author contributions** **PGA**: conceptualization (lead), data curation (lead), formal analysis (lead), funding acquisition (lead), investigation (lead), validation (lead), writing – original draft (lead), writing – review & editing (lead); **QH**: formal analysis (supporting), investigation (supporting), validation (supporting), writing – review & editing (supporting); **DSK**: formal analysis (supporting), investigation (supporting), validation (supporting), writing – review & editing (supporting); **MZ**: funding acquisition (supporting), validation (supporting), writing – review & editing (supporting).

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**Data availability** All data generated or analysed during this study are included in its supplementary information files.

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