Holocene fish assemblages provide baseline data for the rapidly changing eastern Mediterranean

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Abstract
The eastern Mediterranean marine ecosystem is undergoing massive modification due to biological invasions, overfishing, habitat deterioration, and climate warming. Our ability to quantify these changes is severely hindered by the lack of an appropriate baseline; most ecological datasets date back a few decades only and show already strong signatures of impact. Surficial death assemblages (DAs) offer an alternative data source that provides baseline information on community structure and composition. In this study, we reconstruct the marine fish fauna of the southern shallow Israeli shelf before the opening of the Suez Canal based on fish otoliths. We quantify the age of the otolith DAs by radiocarbon dating, and describe its taxonomic composition, geographic affinity, and trophic structure. Additionally, we test by radiocarbon dating the hypothesis that *Bregmaceros*, a presumed Lessepsian invader with continuous presence in the Mediterranean throughout the late Cenozoic, is a relict species. The otolith DA dates back to the mid-Holocene because 75% of the dated otoliths of the native species are older than the opening of the Suez Canal in 1869, suggesting that the DA is a proper baseline for quantifying modern impacts. Consistently, 97% of the otoliths and 88% of the species we collected belong to native Mediterranean species. The native anchovy *Engraulis encrasicolus* dominates the DAs, although gobiids are the most diverse group (14 species, 28%). The DAs show similar trophic structure to present-day pristine Mediterranean coastal fish assemblages. Two non-indigenous species are recorded here for the first time in the Mediterranean Sea, *Amblygobius albimaculatus* and *Callogobius* sp., highlighting the importance of DAs for detecting non-indigenous species. Finally, *Bregmaceros* otoliths are modern, not supporting the previous hypothesis that the taxon is a Pleistocene relict.

Introduction

Collective human activities today substantially alter Earth's surface, atmosphere, and oceans. A case-in-point is the eastern Mediterranean marine ecosystem, which is undergoing severe changes due to rapid climate warming, overfishing, habitat deterioration, and the Lessepsian invasion, the entrance of Red Sea species into the Mediterranean after the opening of the Suez Canal in 1869 (CIESM, 2002; European Environmental Agency, 2019; Galil, 2000). Moreover, the post-industrial climate is changing faster and more abruptly than during the Holocene (Burke et al., 2018; Marcott et al., 2013), and human activities are affecting the environment on a larger scale and to a much higher degree. Nonetheless, the most common approach to assessing and predicting the impact of these phenomena on the eastern Mediterranean marine ecosystem is through comparison with time series reaching back the late 20th century at best (Arndt et al., 2018; Belmaker et al., 2013; Corrales et al., 2017a, 2017b; Givan et al., 2017; Goren et al., 2016). However, such short time series capture conditions already strongly modified by human activity.

In the eastern Mediterranean, the archeological record offers a potential source of information to reconstruct baselines. Archeological remains suggest that the eastern Mediterranean coasts contained a rich marine fish fauna, which was exploited for thousands of years (Zohar and Artzy, 2019). In fact, the agro-pastoral-marine subsistence system called the 'Mediterranean fishing

village' first appeared on the Levantine coasts around 9000 years BP (Van Neer et al., 2004; Zohar et al., 2001). The earliest such village was Atlit-Yam (a now submerged Neolithic establishment off the northern coast of Israel), with reported remains of Serranidae (sea basses), Sparidae (porgies), Sciaenidae (drums), Mugillidae (mullets), and other fishes (Galili et al., 2017a, 2017b). Despite their value as evidence of human consumption and exploitation of fishes, these archeological records are strongly biased in favor of commercial species and large specimens, and therefore they cannot be used to study entire fish assemblages (Van Neer et al., 2005). Historical records, such as catch records, also provide some data on the presence of certain species in particular areas or on the environmental conditions during specific periods (Lotze et al., 2006), as in the case of the Atlantic cod

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Gadus morhua (Rose, 2004; Rosenberg et al., 2005). However, similarly to archaeological remains, historical data are again usually limited to commercial species and cannot be used to evaluate the entire ecosystem.

In contrast, the young fossil record (especially that of the Holocene) is a precious source for defining baselines, quantifying the natural variability of the studied system, differentiating between anthropogenic and non-anthropogenic change, and recognizing ecological legacies that can be explained only by events or conditions that are not present in the system today (Dietl and Flessa, 2011; Dietl et al., 2015). In marine settings, surficial death assemblages (DAs), the taxonomically identifiable, dead or discarded organic remains (Kidwell, 2013), contain the most accessible Holocene record. In pristine conditions, DAs show a high degree of ecological fidelity to their corresponding living assemblages when appropriately sampled (e.g. Albano, 2014; Albano and Sabelli, 2011; Kidwell, 2001; Martinelli et al., 2016; Michelson et al., 2018; Zuschin and Ebner, 2015) with differences mostly due to the effects of time averaging (Kidwell and Tomašových, 2013; Tomašových and Kidwell, 2009). Consequently, such DAs are reliable recorders of past environmental conditions (Kidwell, 2015; Kowalewski, 2009) and increasingly used as benchmarks to detect human-induced ecosystem shifts (e.g. Dietl and Smith, 2017; Kidwell, 2007; Kowalewski et al., 2000, 2015; Tomašových and Kidwell, 2017) and other environmental impacts (e.g. Albano et al., 2016; Bizjack et al., 2017; Gilad et al., 2018; Korpanty and Kelley, 2014; Tweitmann and Dietl, 2018).

Fishes are particularly important because they form the majority of organisms in the higher trophic levels of marine ecosystems, exercising control on the biomass of all other groups (Coll et al., 2010). Fish otoliths are one of the best tools for reconstructing past fish faunas; they are useful paleobathymetric and paleoclimatic indicators (Agiadi et al., 2017, 2018) and increasingly used in conservation studies (Jones and Checkley, 2019; Lin et al., 2019; Rowell et al., 2008; Schwarzhans, 2013a). Otoliths are aragonitic incremental stone-like structures in the inner ear of Teleost fish that facilitate sound and balance perception (Schulz-Mirbach et al., 2018). They have species-specific morphology that enables species-level identification (Gierl et al., 2018; Nolf, 2013).

In this study, we use surficial otolith assemblages to describe, taxonomically and in terms of trophic structure, the baseline fish assemblage of the Mediterranean Israeli shallow shelf, which is among the most impacted areas in the eastern Mediterranean. We radiocarbon dated 77 otoliths of known native species to test the hypothesis that the assemblages belong to the Holocene, predate major anthropogenic drivers of change in the basin, including the opening of the Suez Canal, and can thus serve as baseline. In addition, we test the hypothesis that *Bregmaceros nectabanus*, a species considered non-indigenous in the modern Mediterranean (Goren and Galil, 2008) but with co-generic representatives in the late Cenozoic, is a Pleistocene relict by dating the only two *Bregmaceros* otoliths we found.

Material and methods

Study area and sampling methods

The study area is the Mediterranean coast of Israel (Figure 1). Surficial sediment samples were collected with a Van Veen grab (36.5 × 31.8 cm) onboard the RV 'Mediterranean Explorer' from 10 to 40 m depth at 10 m intervals in autumn 2016. The samples were taken along a transect off Ashqelon (stations coded as SG10, SG20, SG30, and SG40, with the number indicating the depth; details are available in the Supplemental Table S1, available online). The grab samples captured the first 5–20 cm of sediment, depending on grain size, which is considered a mixed layer without significant stratification at these depths, the so-called 'taphonomically active zone' (Olszewski, 2004; Tomašových et al.,
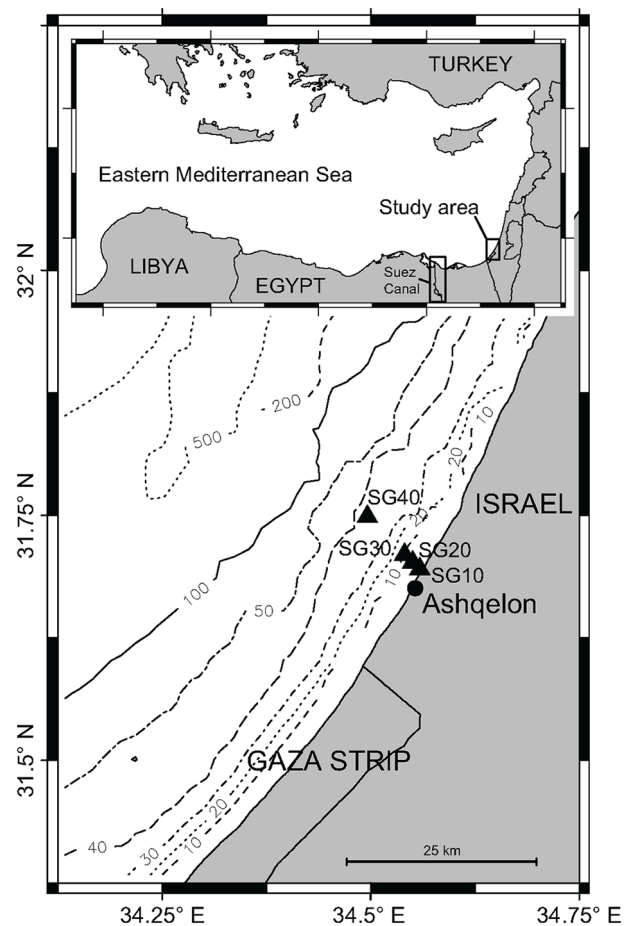

Figure 1. The study area and the position of the sampling stations.

2014). Five replicate samples were collected at each depth, sieved on a 0.5-mm mesh, and picked entirely to obtain an adequate quantity of otoliths. The identification of the otoliths was based on their morphological characteristics (Nolf, 1985) through direct comparison with fossil and recent specimens (Agiadi et al., 2018; Girone et al., 2006) and using the literature (Gierl et al., 2018; Lin et al., 2018; Lombarte et al., 2006, 2018; Nolf, 2013; Rivaton and Bourret, 1999; Smale et al., 1995; Tuset et al., 2008, 2011). Unidentifiable otoliths were excluded from the analysis. Taxonomic placement followed the widely accepted scheme of Nelson et al. (2016). Specimens from each species were photographed using a FEI INSPECT S50 scanning electron microscope with low-vacuum function without coating.

Otolith dating

To quantify the time range represented by the DAs, we dated 77 otoliths belonging to both demersal (*Ariosoma balearicum* (*n* = 20), *Gobius auratus* (*n* = 1), *Gobius cobitis* (*n* = 1), *Gobius niger* (*n* = 1), *Gobius paganellus* (*n* = 21), *Lesueurigobius friesii* (*n* = 5), and *Lesueurigobius suerii* (*n* = 1)) and pelagic (*Engraulis encrasicolus* (*n* = 25)) native species from the 10-m (20 otoliths), 30-m (47 otoliths), and 40-m (10 otoliths) stations. These specimens were randomly selected, and the age frequency distribution is thus representative of the whole assemblage (details on the analyzed otoliths are available in the Supplemental Table S2, available online). Radiocarbon dating of fish otoliths in DAs has been validated for pre- and post-bomb dating (Kalish, 1993) and successfully correlated to radiocarbon ages of planktonic foraminifera (Elder et al., 1996).

We used accelerator mass spectrometry (AMS) radiocarbon analysis using powdered carbonate targets (Bush et al., 2013).

The samples were prepared at the Northern Arizona University and dated at the University of California at Irvine. This method enables using very small sample size (we achieved successful measurements down to 0.5 mg otolith mass) and is thus particularly suitable for otoliths, which in our samples ranged between 0.1 and 10.1 mg, with a median of only 1.15 mg (based on 88 weighed otoliths of the dated species). More details on sample preparation are available in subsection S1.2 of the Supplemental material, available online. Radiocarbon ages were converted to calendar years with a constant regional marine reservoir correction (ΔR) of 3 ± 66 years, which is the weighted mean of eight published pre-bomb ΔR values from Israel and Lebanon (Boaretto et al., 2010; Reimer and McCormac, 2002). For samples younger than 1950 AD, 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 (for details see Albano et al., 2020). All ages were reported in calendar years before 2016, the year of sample collection. In addition, we dated the only two otoliths of *Bregmaceros nectabanus* that we found. These otoliths were treated as described by Gottschalk et al. (2018). In brief, the samples were loaded into septum-sealed glass vials and the air was replaced with helium. The samples were weakly leached using 0.01 M hydrochloric acid for 3 min at room temperature and the CO_2 that was produced was again replaced with helium. The carbonate material was then dissolved in 85% orthophosphoric acid so that CO_2 was formed, which was measured directly in the AMS MICADAS using the gas ion source at the University of Bern (Szidat et al., 2014).

Analysis of the fish community

We determined the assemblage abundance and species richness. The latter was compared across samples after coverage standardization (Chao and Jost, 2012). This approach enables a meaningful comparison between samples with different completeness. We visualized differences among stations with non-metric multidimensional scaling and tested for differences with a global and pairwise PERMANOVA, using the sequential Bonferroni correction to assess significance. All statistical analyses and plots were done in the R statistical environment (R Development Core Team, 2019).

We investigated the contribution of tropical, subtropical, and temperate-affinity taxa to the species richness and abundance of the DAs. Ecological data such as distribution, lifestyle, and biogeographic affinity were obtained from the Fishbase database (Froese and Pauly, 2019; the ecological data used appear in Supplemental Table S3 and S4, available online). The native versus non-indigenous status was assessed using specific literature on the first record of each species (Table 1), and review studies on the Red Sea fish fauna (Golani and Fricke, 2018) and the non-indigenous species in the Mediterranean Sea (Zenetos et al., 2010).

We determined the trophic structure of the DAs using the trophic levels obtained from Karachle and Stergiou (2017; Supplemental Table S3, available online). Assignment to different trophic groups followed the scheme proposed by Stergiou and Karpouzi (2002): (1) Herbivores (H; $2.0 <$ trophic level < 2.1); (2) Omnivores preferring plants (OV; $2.1 <$ trophic level < 2.9); (3) Omnivores preferring animal material (OA; $2.9 <$ trophic level < 3.7); (4) Carnivores preferring decapods and fish (CD; $3.7 <$ trophic level < 4.0); and (5) Carnivores preferring fish and cephalopods, also including the few top carnivores (CC; trophic level > 4.0). Although these trophic levels refer to modern estimates, and considering that fish exhibit feeding plasticity (Dabrowski and Portella, 2005), as well as temporal and spatial variability in feeding (Stergiou and Karpouzi, 2002), which cannot be detected with our approach, the young age of our DAs suggests that they are still indicative of the DAs community structure. Moreover, we reviewed the past and present distribution of the non-indigenous species we found in an attempt to detect any specific patterns and links to environmental factors that have controlled their distribution. Finally, we used the ratio of the pelagic versus demersal (benthic and benthopelagic) species' relative abundance as an index of nutrient inflow in oligotrophic environments (Pennino and Bellido, 2012).

Results

Geochronology

The obtained ages for the otoliths of the native species range from 4 to 7961 years before AD 2016, with a median age of 559 years, time-averaging (inter-quartile range) of 1097 years, and show the typical right-skewed distribution of surficial DAs still affected by skeletal input (Figure 2; Dexter et al., 2014; Tomašových et al., 2014, 2016). The 25%-quantile is 150 years, that is, 75% of the dated otoliths are older than the opening of the Suez Canal in 1869. The 20%-quantile is 37 years, that is, 80% of the dated otoliths are older than the seawater temperature increase reported for the last 30 years (Ozer et al., 2017). The occurrence of very old otoliths is consistent with low sedimentation rates, which were 0.4 mm/yr (Goodman-Tchernov et al., 2009) and 0.2 mm/yr (our own data based on sediment cores) at the 10 and 30 m stations, respectively. The 40 m station had a one-order-of-magnitude higher sedimentation rate estimated at 2.4 mm/yr from our sediment cores. Both otoliths of *Bregmaceros nectabanus* are younger than AD 1950 (i.e. post-bomb samples; Supplemental Table S2, available online).

Taxonomic composition

We identified 600 otoliths belonging to 57 species from 24 families and 10 orders (Figures 4 and 5, Table 1, and Supplemental Tables S5 and S6, available online and comments on otolith morphology in subsection S2.4 of the Supplemental material, available online). The sample completeness at each station was never lower than 0.8, and it was 0.97 for the whole transect (Table 2). Observed and coverage standardized species richness peaked at 30 m, possibly because of the greatest time-range of the assemblage (29–5012 yr; Albano et al., 2020). Especially the assemblages between 10 and 30 m depth are clearly clustered in multivariate space, and differ from each other (global test: $F = 4.695$, $p = 0.001$; pairwise tests significant at $\alpha = 0.05$; Figure 3).

The DAs are dominated by the native Mediterranean taxa, which account for 93–100% of their abundance and 86–100% of their richness. The most abundant families are Gobiidae, Engraulidae, Sparidae, Congridae, and Clupeidae (Figures 4 and 5; Supplemental Table S6, available online). The DAs are dominated by the only representative of Engraulidae, the anchovy *Engraulis encrasicolus*, at all stations apart from the 10-m station, where the most abundant species is the conger *Ariosoma balearicum*. Indeed, the anchovy is especially abundant at the 20-m station, where it increases the pelagic-demersal ratio to 2.57 (Table 2). However, Gobiidae are collectively more abundant at the 30- and 40-m stations of the south transect. Gobiidae are a highly diverse group that contains many cryptic species with many representatives in the modern Mediterranean (Kovačić et al., 2012). Specifically, we were able to recognize 15 gobiid species in the DAs (Figure 5). Overall, the identified species belong to two groups: (1) 51 native Mediterranean species, and (2) seven non-indigenous species, which have recently entered the Mediterranean basin from the Red Sea through the Suez Canal: *Bregmaceros nectabanus*, *Saurida undosquamis*, *Upeneus pori*, *Callionymus filamentosus*, *Amblygobius albimaculatus*, *Callogobius* sp., and *Oxyurichthys petersii* (Froese and Pauly, 2019; Table 1; Supplemental Table S5, available online).

Table 1. List of species recorded in the death assemblage, their abundance and the native/non-indigenous status.

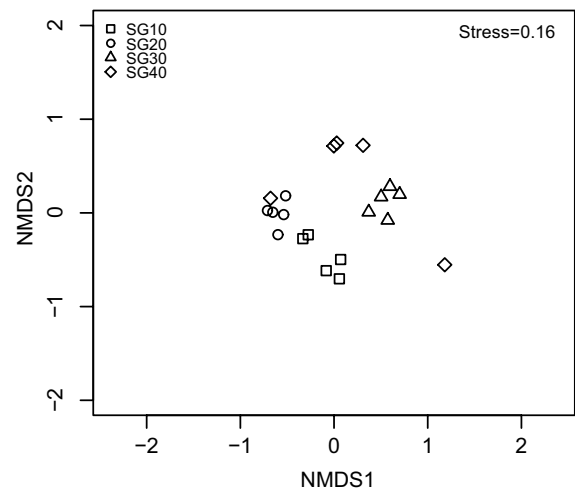| Family	Taxon	Abundances				Status in the Mediterranean
		SG10	SG20	SG30	SG40	
Heterenchelyidae	*Panturichthys* sp.	0	0	2	0	Native
Congridae	*Ariosoma balearicum* (Delaroche, 1809)	19	0	15	1	Native
Congridae	*Conger conger* (Linnaeus, 1758)	0	0	4	0	Native
Engraulidae	*Engraulis encrasicolus* (Linnaeus, 1758)	19	17	136	13	Native
Clupeidae	Clupeidae indet.	0	0	1	0	Native
Clupeidae	*Sardina pilchardus* (Walbaum, 1792)	0	0	2	0	Native
Clupeidae	*Sardinella aurita* (Valenciennes, 1847)	1	0	3	0	Native
Clupeidae	*Sardinella maderensis* (Lowe, 1838)	1	0	4	0	Native
Gonostomatidae	*Cyclothone braueri* (Jespersen and Tåning, 1926)	0	0	1	0	Native
Phosichthyidae	*Vinciguerria poweriae* (Cocco, 1838)	0	0	1	0	Native
Synodontidae	*Saurida undosquamis* (Richardson, 1848)	0	0	1	0	Non-indigenous (first recorded in 1962 from Cyprus by Ben-Tuvia, 1962)
Bregmacerotidae	*Bregmaceros nectabanus* (Whitley, 1941)	0	0	0	2	Non-indigenous (first recorded in 1965, erroneously identified as *Bregmaceros atlanticus*, from the Sicily straits by D'Ancona and Cavinato, 1965)
Ophidiidae	*Ophidion rochei* (Müller, 1845)	0	0	4	0	Native
Apogonidae	*Apogon imberbis* (Linnaeus, 1758)	0	0	3	0	Native
Apogonidae	*Apogon* sp.	0	0	1	0	Native
Gobiidae	*Aphia minuta* (Risso, 1810)	1	0	3	0	Native
Gobiidae	*Callogobius* sp.	0	0	3	0	Non-indigenous (first recorded in this study, only known so far from the Red Sea, including the Gulf of Suez, according to Golani and Fricke, 2018)
Gobiidae	*Chromogobius zebratus* (Kolombatović, 1891)	0	0	3	0	Native
Gobiidae	*Deltentosteus quadrimaculatus* (Valenciennes, 1837)	0	0	2	2	Native
Gobiidae	*Amblygobius albimaculatus* (Rüppell, 1830)	0	0	1	2	Non-indigenous (first recorded in this study, only known so far from the Red Sea, including the Gulf of Suez, according to Golani and Fricke, 2018)
Gobiidae	Gobiidae indet.	0	0	7	1	Native
Gobiidae	*Gobius auratus* (Risso, 1810)	0	0	4	1	Native
Gobiidae	*Gobius cobitis* (Pallas, 1814)	0	0	0	1	Native
Gobiidae	*Gobius niger* (Linnaeus, 1758)	0	0	0	1	Native
Gobiidae	*Gobius paganellus* (Linnaeus, 1758)	1	0	25	1	Native
Gobiidae	*Gobius* sp.	0	0	86	0	Native
Gobiidae	*Lesueurigobius friesii* (Malm, 1874)	0	0	27	13	Native
Gobiidae	*Lesueurigobius* sp.	0	0	8	0	Native
Gobiidae	*Lesueurigobius suerii* (Risso, 1810)	0	0	10	12	Native
Gobiidae	*Oxyurichthys petersii* (Klunzinger, 1871)	0	0	4	0	Non-indigenous (first recorded in 1983 from Israel by Ben-Tuvia, 1983)
Gobiidae	*Pomatoschistus marmoratus* (Risso, 1810)	2	3	17	0	Native
Gobiidae	*Thorogobius macrolepis* (Kolombatović, 1891)	0	0	9	2	Native
Gobiidae	*Zebrus zebrus* (Risso, 1827)	0	0	1	0	Native
Pomacentridae	*Chromis chromis* (Linnaeus, 1758)	0	0	2	0	Native
Belonidae	*Tylosurus* sp.	1	0	0	0	Native
Carangidae	*Trachurus mediterraneus* (Steindachner, 1868)	1	1	1	0	Native
Carangidae	*Trachurus* sp.	0	0	1	0	Native
Citharidae	*Citharus linguatula* (Linnaeus, 1758)	0	0	3	1	Native
Scophthalmidae	*Scophthalmus rhombus* (Linnaeus, 1758)	1	0	5	0	Native
Bothidae	*Arnoglossus laterna* (Walbaum, 1792)	2	1	7	1	Native
Bothidae	*Arnoglossus rueppelii* (Cocco, 1844)	0	0	2	0	Native
Bothidae	*Arnoglossus* sp.	0	1	1	0	Native
Soleidae	*Microchirus ocellatus* (Linnaeus, 1758)	0	0	2	0	Native
Soleidae	*Solea solea* (Linnaeus, 1758)	1	0	0	0	Native
Cynoglossidae	*Symphurus nigrescens* (Rafinesque, 1810)	0	0	10	0	Native
Callionymidae	*Callionymus filamentosus* (Valenciennes, 1837)	0	1	2	0	Non-indigenous (first recorded in 1953 from Israel by Ben-Tuvia, 1953)
Trachinidae	*Trachinus draco* (Linnaeus, 1758)	1	0	2	0	Native
Mullidae	*Upeneus pori* (Ben-Tuvia and Golani, 1989)	0	0	1	0	Non-indigenous (first recorded in 1950 from the Aegean Sea by Kosswig, 1950)
Triglidae	*Chelidonichthys lucerna* (Linnaeus, 1758)	0	0	1	0	Native

(Continued)

Table 1. (Continued)

Family	Taxon	Abundances				Status in the Mediterranean
		SG10	SG20	SG30	SG40	
Sparidae	*Diplodus annularis* (Linnaeus, 1758)	0	0	1	0	Native
Sparidae	*Diplodus* sp.	0	0	1	0	Native
Sparidae	*Pagellus acarne* (Risso, 1827)	0	0	2	0	Native
Sparidae	*Pagellus bogaraveo* (Brünnich, 1768)	1	0	2	0	Native
Sparidae	*Pagellus erythrinus* (Linnaeus, 1758)	1	0	1	0	Native
Sparidae	*Pagellus* sp.	1	0	1	0	Native
Sparidae	Sparidae indet.	0	0	3	0	Native
Sparidae	*Spicara flexuosa* (Rafinesque, 1810)	0	1	5	2	Native
Sparidae	*Spicara maena* (Linnaeus, 1758)	0	0	8	0	Native
Sparidae	*Spicara smaris* (Linnaeus, 1758)	2	0	11	0	Native
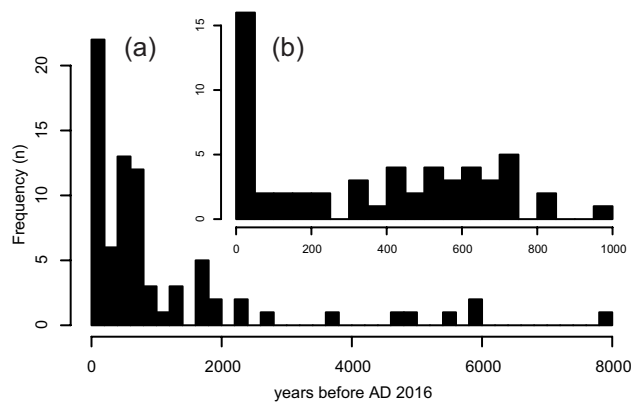
Figure 2. (a) Age-frequency distribution of the otoliths at stations SG10, SG30, and SG40 (*n* = 77) based on radiocarbon measurements in 200-year bins calibrated in years before AD 2016. The death assemblages have a maximum and median age of ca. 8000 and 559 years before AD 2016, respectively. The inset plot (b) displays the AFD of otoliths from the most recent 1000 years.


Figure 3. Non-metric multidimensional scaling plot of otolith abundances. Assemblages from 10 to 30 m cluster according to depth, whereas those at 40 m depth show larger dispersion.

The records of *Amblygobius albimaculatus* and *Callogobius* sp. are the first in the Mediterranean Sea. We assign three otoliths to *Amblygobius albimaculatus* (Table 1), one from SG30 (length = 1.82 mm, height = 1.29 mm) and two from SG40 (length 1 = 1.43 mm, height 1 = 1.18 mm; length 2 cannot be measured because the otolith is broken, height 2 = 1.47 mm). These otoliths (Figure 5.32) are clearly distinguished by the anterodorsal area, which protrudes mostly dorsally and less toward the anterior side, as seen also in the Indo-Pacific specimens of this species (coll. W. Schwarzhans; and figured by Rivaton and Bourret, 1999). In contrast, the specimens of *Thorogobius macrolepis* (Kolombatovic, 1891), both presented here and figured by Lombarte et al. (2018), have an anterodorsal area that protrudes toward the anterior side only. Compared to the adult specimens figured by Rivaton and Bourret (1999) with length = 3.6 mm and height = 2.5 mm, but considering the fact that the morphological features of their otoliths are fully developed, we can estimate that our specimens belong to young adults.

Three otoliths from SG30 belong to *Callogobius* sp.: length 1 = 1.86 mm, height 1 = 1.20 mm; length 2 = 1.75 mm, height 2 = 1.06 mm; length 3 = 1.75 mm, height 3 = 1.21 mm. These specimens (Figure 5.36) resemble those of *Chromogobius zebratus* (Kolombatovic, 1891) also identified in these sediments and figured by Lombarte et al. (2018) and *Chromogobius quadrivittatus* (Steindachner, 1863) figured by Nolf (2013). In addition, they resemble the *Nematogobius* otoliths from the Azores coastal sediments figured by Schwarzhans (2013a) in terms of the overall shape. However, *Nematogobius* otoliths have a relatively small sulcus and lack a crista inferior. On the other hand, in our

specimens, the sulcus is wide and the crista inferior very strong. Therefore, we assign these specimens to the Indo-Pacific genus *Callogobius*, which exhibits resemblance in both shape and sulcus morphology (Nolf, 2013). Based on the relationships between fish size and otolith size of other gobies (Froese and Pauly, 2019) and the samples figured by Rivaton and Bourret (1999), we suggest that these otoliths belong to adult individuals.

In terms of climatic affinity, the DAs are dominated by subtropical species (Table 2). Nevertheless, tropical and temperate taxa participate as well in small abundances (Supplemental Table S5, available online). The tropical taxa are all non-indigenous, namely *Bregmaceros nectabanus*, *Amblygobius albimaculatus*, *Callogobius* sp., and *Oxuyrichthys petersii*, and they contribute to the DAs at the 30- and 40-m stations. Therefore, the native Mediterranean assemblages are considered almost purely subtropical.

Trophic composition

There are no true herbivores (trophic group H) in the DAs (Figure 6 and Supplemental Tables S3 and S7, available online). Omnivores preferring plants (OV) are represented by *Bregmaceros nectabanus*, *Sardina pilchardus*, *Amblygobius albimaculatus*, and *Chromogobius zebratus*. Carnivores preferring decapods and fish (CD) are represented by *Arnoglossus laterna*, *Arnoglossus* sp., *Ariosoma baleari-cum*, *Pagellus acarne*, and *Chelidonichthys lucerna*. Higher carnivores (CC) are represented by *Tylosurus* sp., *Arnoglossus rueppelii*, *Citharus linguatula*, *Conger conger*, *Scophthalmus rhombus*, *Saurida undosquamis*, and *Trachinus draco*. The DAs at all depths
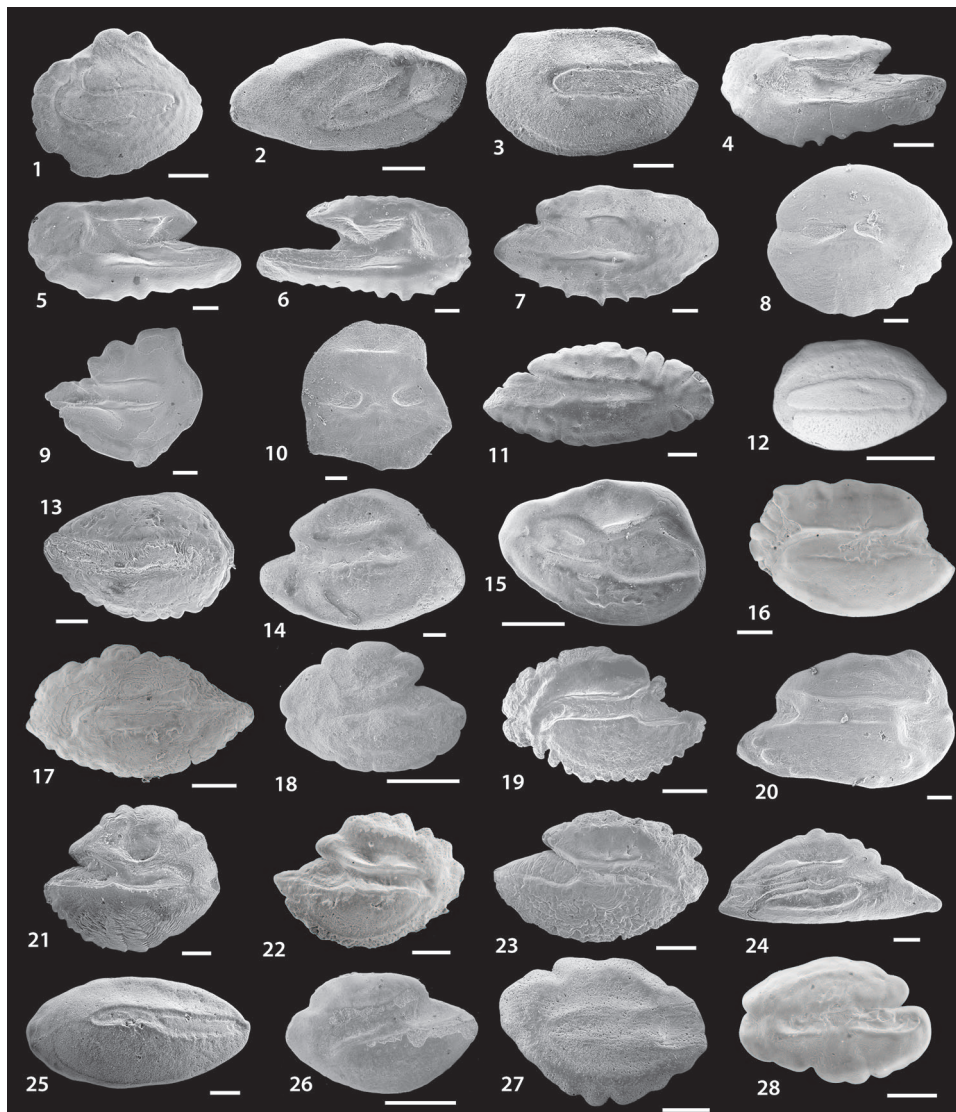
Figure 4. SEM photographs of the fish otoliths recovered from the surficial sediments off the Israeli coast. 1. *Ariosoma balearicum* SG10, 2. *Conger conger* SG30, 3. *Panturichthys* sp. SG30, 4. *Sardina pilchardus* SG30, 5. *Sardinella aurita* SG10, 6. *Sardinella maderensis* SG30, 7. *Engraulis encrasicolus* SG30, 8. *Cyclothone braueri* SG30, 9. *Vinciguerria poweriae* SG30, 10. *Bregmaceros nectabanus* SG40, 11. *Saurida undosquamis* SG30, 12. *Ophidion rochei* SG30, 13. *Tylosurus* sp. SG10, 14. *Chelidonichthys lucerna* SG30, 15. *Apogon imberbis* SG30, 16. *Diplodus annularis* SG30, 17. *Trachurus mediterraneus* SG30, 18. *Pagellus acarne* SG30, 19. *Pagellus erythrinus* SG10, 20. *Upeneus pori* SG30, 21. *Spicara flexuosa* SG40, 22. *Spicara maena* SG30, 23. *Spicara smaris* SG30, 24. *Callionymus filamentosus* SG20, 25. *Trachinus draco* SG30, 26. *Chromis chromis* SG30, 27. *Citharus linguatula* SG30, 28. *Scophthalmus rhombus* SG30. Scale: 1 mm for #12; 500 μm for #1, 15, 18, 19, 26; 200 μm for #2, 3, 5–7, 9–11, 13, 16, 17, 20–25, 27, 28; 100 μm for #4, 8, 14.

comprise mostly omnivores favoring animal food items (OA), which include all the remaining taxa. Nevertheless, carnivores feeding mostly on decapods and fish are present in high abundance at the 10-m station.

Discussion

The baseline eastern Mediterranean fish fauna

The studied DAs range from the mid-Holocene to the present and mostly predate the major anthropogenic impacts affecting the basin such as the Lessepsian invasion and climate warming. The Lessepsian invasion started in 1869 AD with the opening of the Suez Canal, but it has accelerated since the 1960s with the salinity reduction of the Bitter Lakes (El-Serehy et al., 2018). The Israeli shelf has experienced a 3.6°C sea surface temperature increase during the last 30 years (Ozer et al., 2017) and the last century recorded a warming that exceeds the natural variability of the last millennium (Sisma-Ventura et al., 2014). Accordingly, the contribution of Lessepsian species is negligible in terms of both abundance (overall only 2.8% of individuals) and diversity (only 7 out

of the 57 identified taxa, 12%; Tables 1 and 2). In fact, these DAs show similar taxonomic composition as modern fish faunas of the northern and western Mediterranean at similar depths and substratum setting, which have not been affected by the Lessepsian invasion (e.g. Demestre et al., 2000; Karachle and Stergiou, 2017; Stergiou and Karpouzi, 2002). As in these living assemblages, the most abundant trophic groups in the DAs are omnivores preferring animals (OA) and carnivores preferring decapods and fish (CD), whereas higher carnivores (CC) and omnivores preferring plants (OA) follow in abundance (Figure 6). Therefore, we consider that these DAs represent well the Holocene, pre-impact, native fish fauna of the Israeli coastal waters, because previous studies have indicated that anthropogenic impacts and climate change degrade the trophic structure of the Mediterranean ecosystem (Albouy et al., 2014; Coll et al., 2008).

Paleobiogeography

Fish species distributions are controlled by environmental (including climatic) factors and connectivity changes today as
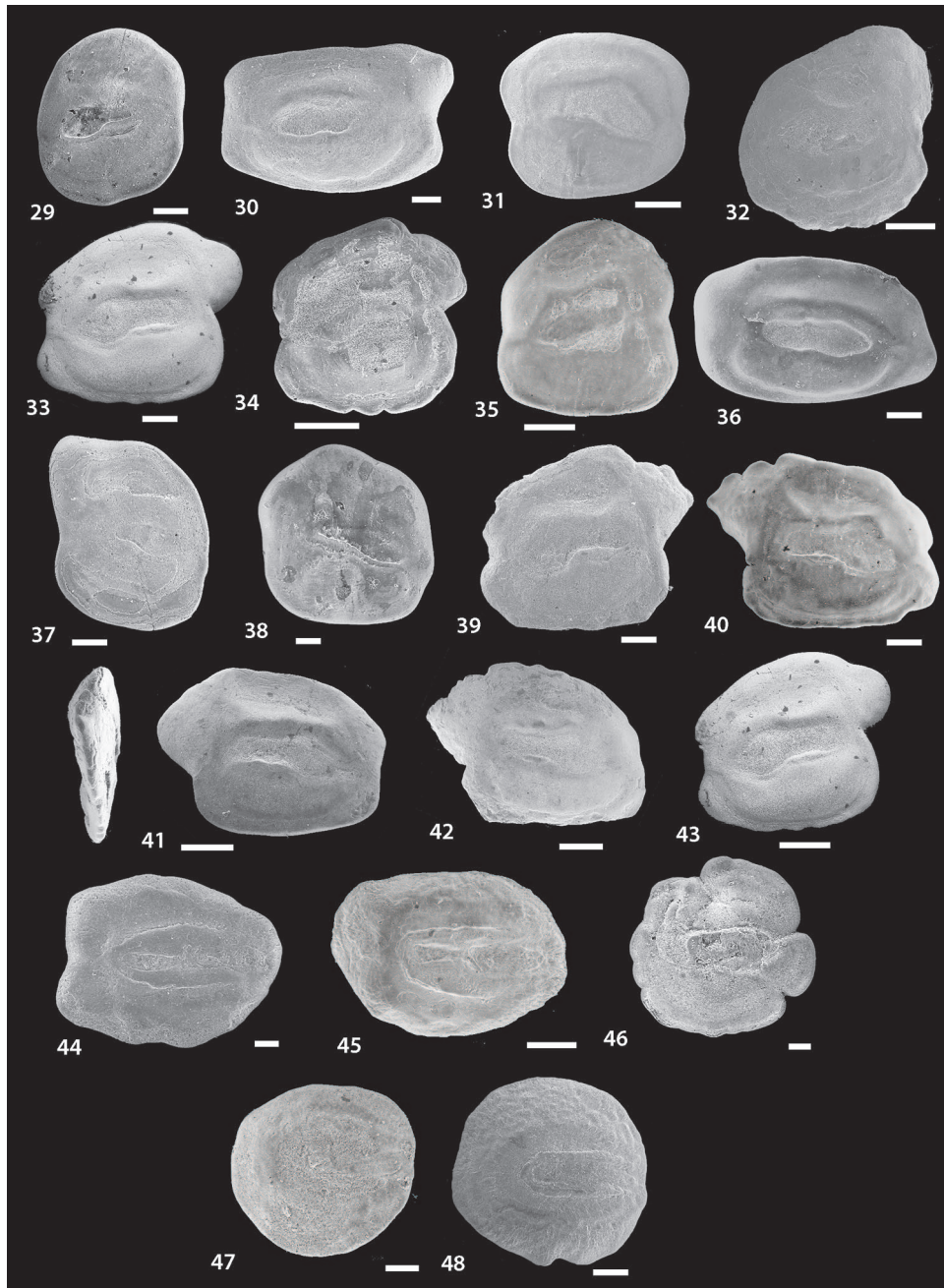
Figure 5. SEM photographs of the fish otoliths recovered from the surficial sediments off the Israeli coast (continuing from Figure 2). 29. *Aphia minuta* SG10, 30. *Chromogobius zebratus* SG30, 31. *Deltentosteus quadrimaculatus* SG30, 32. *Amblygobius albimaculatus* SG40, 33. *Gobius niger* SG30, 34. *Lesueurigobius friesii* SG30, 35. *Lesueurigobius suerii* SG30, 36. *Callogobius* sp. SG30, 37. *Oxyurichthys petersii* SG30, 38. *Pomatoschistus marmoratus* SG20, 39. *Gobius auratus* SG40, 40. *Gobius cobitis* SG30, 41. *Gobius paganellus* (perpendicular view and inner face) SG30, 42. *Thorogobius macrolepis* SG40, 43. *Zebrus zebrus* SG30, 44. *Arnoglossus laterna* SG30, 45. *Arnoglossus rueppelii* SG30, 46. *Symphurus nigrescens* SG30, 47. *Microchirus ocellatus* SG30, 48. *Solea solea* SG10. Scale: 200 μm for #29–37, 39–43, 45; 100 μm for #38, 44, 46–48.

well as in the past. The opening of the Suez Canal broke a long-standing barrier between the Atlantic-Mediterranean and Indo-Pacific biogeographic provinces, which had been established in the middle Miocene, around 13.8 Ma (Bialik et al., 2019). As a result, many Red Sea species have invaded the Mediterranean Sea, with disruptive consequences for the native fauna (Galil et al., 2015; Goren et al., 2016). Reviewing the paleobiogeography of the non-indigenous species found in the DAs informs us on why these particular species invaded the Mediterranean Basin and reveals the characteristics of the native and the non-indigenous fish species inhabiting the Mediterranean today. In contrast to native species, these non-indigenous species have not been present in the Mediterranean in the geological past (Agiadi et al., 2018, 2019, 2020; Girone et al., 2006, 2010; Landini and Sorbini,

1992; Nolf, 2013). We distinguish four groups of non-indigenous taxa based on their paleobiogeographic distribution.

The first group includes genera with representative species in the Mediterranean Sea during extended warm periods in the geological past, which disappeared afterward, only to re-enter the basin today through the Suez Canal as Lessepsian invaders. We found two non-indigenous tropical taxa in this category: *Oxyurichthys petersii* and *Callogobius* sp. *Oxyurichthys petersii* is a Red Sea endemic species, evolved after the Pliocene, which was first reported in the Mediterranean by Ben-Tuvia (1983). *Callogobius* sp. first appeared in the late Eocene (Thacker, 2015). *Callogobius weileri* was also recorded in the Miocene of the east Atlantic and the Pliocene of the Mediterranean Sea (Schwarzhans, 2013b). There are 26 valid species of *Callogobius* today in

Table 2. Species richness in the DAs. Contribution of native and non-indigenous species and individuals in the death assemblages. Relative abundance of the taxa identified at each depth station grouped based on their climatic affinity. Tropical zone is 0°–23.5°N and S; subtropical zone is 23.5°–40°N and S; and temperate zone is 40°–60°N and S. Ratio of pelagic versus demersal (benthic and benthopelagic) species' relative abundance as an index of nutrient inflow in oligotrophic environments.

Composition	Depth station			
	SG10	SG20	SG30	SG40
Diversity				
Total number of otoliths (individuals)	56	25	463	56
Sample coverage	0.810	0.804	0.964	0.845
Observed species richness	17	7	54	16
Coverage standardized species richness	17	7	24	14
Native versus non-indigenous				
Number of native taxa (relative)	17 (100%)	6 (86%)	48 (89%)	14 (88%)
Number of non-indigenous taxa (relative)	0 (0%)	1 (14%)	6 (11%)	2 (13%)
Total number of native individuals (relative)	56 (100%)	24 (96%)	451 (97%)	52 (93%)
Total number of non-native individuals (relative)	0 (0%)	1 (4%)	12 (3%)	4 (7%)
Climatic affinity				
Tropical	0	0	2	9
Subtropical	95	100	95	89
Temperate	3	0	3	2
Nutrient inflow				
Pelagic species abundance	40.35	72	34.16	26.32
Demersal species abundance	59.65	28	65.84	73.68
Pelagic/demersal ratio	0.68	2.57	0.52	0.36
Otoliths dated	20	0	47	10
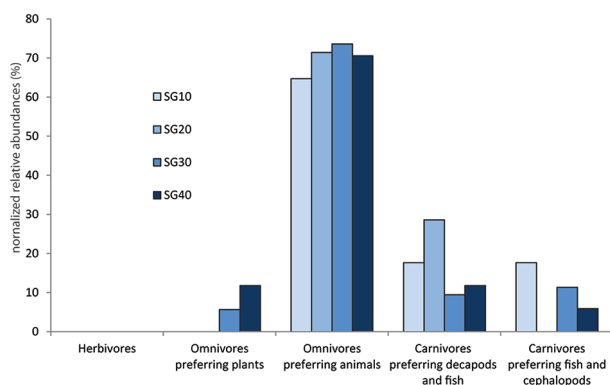
Figure 6. Trophic structure of the death assemblages (DAs); normalized relative abundances of each trophic group to the DAs. The DAs have a trophic structure that is typical in marine ecosystems.

the Indian and Pacific Oceans, including the Red Sea (Golani and Fricke, 2018). Overall, it is possible that the distribution of this first group of taxa has been mostly controlled by climate, suggesting that the Suez Canal opening enabled the re-entrance of these lineages into the eastern Mediterranean, bringing the ecosystem closer to deep-time warm geologic periods.

The second group includes non-indigenous species belonging to genera with representatives native to the Mediterranean. This is for example the case of *Callionymus*; the Mediterranean today is occupied by the native temperate species *Callionymus lyra*, while the tropical Red Sea species *C. filamentosus* was first reported in the Mediterranean off Israel in 1953 (Ben-Tuvia, 1953). As a fossil, in the Mediterranean, *Callionymus pusillus* was recorded in the Messinian of Italy and Algeria (Gaudant et al., 1997; Landini and Menesini, 1984). *Callionymus* has also been recorded from the Miocene of the eastern Atlantic (Schwarzhans, 2013b), but its oldest record is from the Lower Oligocene of western Germany (Schwarzhans, 1973). Overall, *Callionymus* has been present throughout the geological history of the basin.

Three Lessepsian non-indigenous taxa belong to lineages that were never found in the Mediterranean before. *Amblygobius albimaculatus* is a small Indo-Pacific goby, with known records from the Red Sea, including the Gulf of Suez (Golani and Fricke, 2018). *Upeneus pori* is an endemic Red Sea species (Bogorodsky and Randall, 2019) with no fossil record and first reported in the Mediterranean by Kosswig (1950). However, *Upeneus* sp. has been reported from the Neogene of the West Atlantic (Aguilera et al., 2011). This implies that the genus *Upeneus* was distributed in both the Indo-Pacific and the Atlantic realms, and possibly therefore in the Mediterranean, before the closure of the Mediterranean–Indian Ocean connection in the Middle Miocene (Bialik et al., 2019), considering the Indo-Pacific biodiversity hotspot as the center of origin for the dispersal of Teleost fishes (Worm and Tittensor, 2018). *Saurida undosquamis* is known to inhabit the oxygen minimum zone off Yemen (Gallo and Levin, 2016), but again there is no fossil record of this species anywhere. It was first found in the Mediterranean in 1962 (Ben-Tuvia, 1966). *Saurida caribbaea* has been reported from the Neogene of Panama (Aguilera et al., 2011), again implying a circumglobal distribution of the genus *Saurida* in the early Neogene. The presence of these three species demonstrates that the Lessepsian invasion favors tropical taxa that simply gain access to new grounds.

The fourth group includes taxa considered Lessepsian introductions, which however had representatives in the Mediterranean during the Pleistocene. The status of such taxa is therefore doubtful, because they may have remained in Mediterranean refugia until the present-day climate warming presented favorable conditions for the expansion of their population in the basin. *Bregmaceros nectabanus* is the only species in the DAs that falls under this category.

Bregmaceros

Bregmaceros nectabanus is the only non-indigenous species identified in our DAs, whose status in the Mediterranean has ever been debated (Goren and Galil, 2008). It was first reported in the basin as *Bregmaceros atlanticus* by D'Ancona and Cavinato (1965) from the Sicily Straits, without actual documentation of

the specimen. Since then, it has been reported throughout the eastern Mediterranean and all the way into the north Aegean and the Ionian Sea (Aydin and Akyol, 2013; Chartosia et al., 2018; Dogrammatzi and Karachle, 2015; Goren and Galil, 2008; Yılmaz et al., 2004). Goren and Galil (2008) doubted its status as an invader because of its scarce and patchy records in the Mediterranean; instead, they proposed that it was introduced in ballast water. Harold and Golani (2016) reviewed these identifications and argued that all previous records of *Bregmaceros* belong in fact to *B. nectabanus*, which is a Red Sea species, and not *B. atlanticus*, which is an Atlantic species.

Nevertheless, the origin of *Bregmaceros* in the present-day Mediterranean is still enigmatic, considering the paleobiogeographic history of this genus. The earliest record of the genus *Bregmaceros* is in the middle Eocene (Přikryl et al., 2016), when it had an almost global distribution that persisted in the Miocene. The Mediterranean was inhabited by the extinct endemic species *Bregmaceros albyi* (Sauvage, 1880) from the Burdigalian (Arambourg, 1927) until at least the Zanclean (Landini and Menesini, 1986). However, *Bregmaceros* remains have also been found in the eastern Mediterranean until the middle Pleistocene. Although not yet identified to the species level (Agiadi and Karakitsios, 2012; Cornée et al., 2019), these fossils suggest that this taxon never entirely disappeared from the Mediterranean Sea and the otoliths we found here belong to a Pleistocene relict. However, this hypothesis is not supported by our results: the two *Bregmaceros* otoliths dated here were modern, likely post-dating the first reported occurrence in the Mediterranean Sea.

Death assemblages support the detection of non-indigenous species

Despite the importance of early detection of non-indigenous species (Simberloff et al., 2005), imperfect detectability hampers their timely recognition (Kéry and Schmid, 2004). Small-sized fishes or those with cryptic lifestyles can be particularly hard to detect. All *Callogobius* species from the Red Sea, the most likely origin of the new introduced species reported here, are cryptobenthic and range in maximum size from 22 to 76 mm (median 38.5 mm; Delventhal et al., 2016). *Amblygobius albimaculatus* is an Indo-Pacific epibenthic species that builds burrows in the substrate and attains a size of just 18 mm (Hoese, 1986; Maugé, 1986; Randall, 1995). Both are thus difficult to intercept in visual censuses or trawl surveys, which have provided most of the data on benthic fishes on the Israeli shelf (e.g. Edelist et al., 2011, 2013).

Otolith death assemblages can facilitate the detection of non-indigenous fishes due to the virtues of time averaging. Otoliths are durable remains and we showed that their assemblages span decades to millennia (Figure 2). Otoliths are degraded by a two-stage taphonomic process: the first and faster occurs in surficial sediments and has half-lives of 4–200 years, whereas the second and slower occurs after burial with half-lives of 30–500 years (Albano et al., 2020). Consequently, young otoliths, as are those that belong to Lessepsian species, have high chances of preservation and enable non-indigenous species detection beyond the limitations of species small body size, cryptic lifestyle, and restricted seasonality. Death assemblages have already proved to improve the estimates of detectability and occupancy of native and non-indigenous land snails (Albano et al., 2015), determine the native or non-indigenous status of plants (Van Leeuwen et al., 2005, 2008) as well as uncover long time lags in first detection of invasive species (Albano et al., 2018).

Conclusion

The fish otolith DAs analyzed here capture the last 8000 years and mostly predates the major anthropogenic impacts in the area, that is,

the Lessepsian invasion and climate warming. They represent well the Holocene native fish fauna of the Israeli shelf both taxonomically and functionally. The DAs are dominated by native Mediterranean species, both in terms of species richness and abundance. The trophic structure of the DAs is similar to those of the present-day western and northeastern Mediterranean coastal fish assemblages, suggesting that these DAs form a good baseline for investigating the impact of environmental and anthropogenic changes on the eastern Mediterranean fish fauna. Furthermore, we reviewed the paleobiogeographic distribution of the few non-indigenous species discovered in our DAs and specifically focused on *Bregmaceros nectabanus* whose status as a Lessepsian invasive species has been debated. The radiocarbon dating results indicated that the specimens we found are modern and do not provide support for the hypothesis that *Bregmaceros* is a Pleistocene relict. Finally, we demonstrated that otolith death assemblages contribute to non-indigenous species detection and record here for the first time in the Mediterranean Sea *Amblygobius albimaculatus* and *Callogobius* sp.

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Supplemental material

Supplemental material for this article is available online.

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