Alleged Lessepsian foraminifera prove native and suggest Pleistocene range expansions into the Mediterranean Sea

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ABSTRACT: Biogeographical patterns are increasingly modified by the human-driven transloca-tion of species, a process that accelerated several centuries ago. Observational datasets, however, rarely range back more than a few decades, implying that a large part of invasion histories went unobserved. Small-sized organisms, like benthic foraminifera, are more likely to have been re-ported only recently due to their lower detectability compared to larger-sized organisms. Recently detected native species of tropical affinity may have thus been mistaken for non-indigenous spe-cies due to the lack of evidence of their occurrence in pre-invasion records. To uncover the unob-served past of the Lessepsian invasion — the entrance of tropical species into the Mediterranean through the Suez Canal — we collected sediment cores on the southern Israeli shelf. We deployed state-of-the-art radiocarbon techniques to date 7 individual foraminiferal tests belonging to 5 alleged non-indigenous species and show that they are centuries to millennia old, thus native. Two additional species previously considered non-indigenous occurred in centennial to millen-nia-old sediments, suggesting their native status. The evidence of multiple tropical foraminiferal species supposed to be non-indigenous but proved native in the eastern Mediterranean suggests either survival in refugia during the Messinian Salinity Crisis (5.96–5.33 million years) or, more likely, dispersal from the tropical Atlantic and Indo-Pacific during the Pleistocene. In the inter-glacials of this epoch, higher sea levels may have allowed biological connectivity between the Mediterranean and the Red Sea for shallow-water species, showing that the Isthmus of Suez was possibly a more biologically porous barrier than previously considered.

KEY WORDS: Isthmus of Suez · Lessepsian invasion · Historical biogeography · Connectivity · Foraminifera · Mediterranean Sea · Radiocarbon dating

1. INTRODUCTION

Biogeographical patterns are the outcome of the processes of evolution, dispersal and extinction that acted over geological time scales. Such patterns are increasingly modified by the human-driven trans-location of species around the globe over the past decades to few millennia (Ojaveer et al. 2018). How-ever, observational datasets of most biota are limited to yearly or decadal scales, implying that a large

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part of the history of biological invasions went unrecorded. Therefore, early invasions may have gone undocumented and the non-indigenous species involved erroneously assumed native. Conversely, poorly detectable native species may have been recorded only in recent times and falsely considered as non-indigenous if biogeographically related to other regions. Both scenarios may obscure natural patterns and hamper the full understanding of the magnitude and rate of invasions, as well as their ecological consequences.

The paleontological record is increasingly becoming a fundamental source of information on unobserved past ecosystem states, enabling the reconstruction of patterns of diversity, dispersal and extinction, and thus uniquely contributing to the process of disentangling natural from human-modified biogeographical patterns (Kidwell & Tomašových 2013, Dietl et al. 2015, Yasuhara et al. 2020). The study of fossil pollen allowed the recognition of early translocations of plants by humans, e.g. by Norse settlers in southern Greenland in the 10th century (Fredskild 1978) or by European settlers in North America in the 16th and 17th centuries (McAndrews 1988) (see Jackson 1997 for a review). The absence from the local fossil record of synanthropic land snail shells found exclusively in urban areas on San Salvador Island (Bahamas) suggested their non-indigenous origin (Yanes 2012). Moreover, fossil pollen data have indicated that alleged non-indigenous plants are instead native in North America (Betancourt et al. 1984), the Galapagos Islands (van Leeuwen et al. 2008, Coffey et al. 2011) and on Easter Island (Flenley et al. 1991). Also in the marine environment, the paleontological record has proved useful in reconstructing the unobserved history of biological invasions (Yasuhara et al. 2012). For example, it has provided evidence of possible early translocations of dinoflagellates (McMinn et al. 1997, Irwin et al. 2003, Amorim & Dale 2006, Marret et al. 2009) and of the timing of the arrival of non-indigenous benthic foraminifera (McGann et al. 2012, Guastella et al. 2021), and has been helpful in quantifying time lags in the detection and identification of the drivers of invasion success of an introduced bivalve (Albano et al. 2018).

The Mediterranean Sea is a biodiversity hotspot (Coll et al. 2010) with an endemicity rate of 45% (Costello et al. 2017) shaped by its peculiar geological and paleoclimatic history (Taviani 2002, Sabelli & Taviani 2014). A west-to-east gradient of declining diversity and abundance is apparently related to decreasing nutrient availability and increasing tem-

perature and salinity (Tortonese 1951, Coll et al. 2010). The magnitude of this decline remains uncertain due to the lower sampling effort in the eastern and southern sectors (Morri et al. 2009, Idan et al. 2018, Achilleos et al. 2020, Albano et al. 2020). This gradient is currently being disrupted by biological invasions, particularly through the opening of the Suez Canal in 1869, which broke a long-standing biogeographic barrier between the temperate Northern Atlantic and the Indo-West Pacific realms. This so-called 'Lessepsian invasion' (Por 1978, Galil 2009) has an opposite east-to-west gradient related to the location of the Suez Canal (Galil 2012, Nunes et al. 2014). Additionally, climate-driven native diversity collapses in the eastern Mediterranean Sea are further disrupting natural patterns (Rilov 2016, Albano et al. 2021, Steger et al. 2021).

The low sampling effort in the eastern Mediterranean implies that we know little about what its biodiversity looked like before and during the first century of the Lessepsian invasion, between the mid-19th and mid-20th centuries. Reliable and quantitative data have only become available in the last few decades (e.g. Galil & Lewinsohn 1981, Tom & Galil 1991, Edelist et al. 2011, Guarnieri et al. 2017). This knowledge gap has led to the assumption that each newly recorded species of tropical affinity in the eastern Mediterranean is a non-indigenous one.

Benthic foraminifera are single-celled marine eukaryotes, often with calcareous tests, that are commonly preserved in marine sediments. They are good indicators of environmental health and global change of marine ecosystems (Sabbatini et al. 2014). Hundreds of non-indigenous foraminifera have been reported from the Mediterranean Sea (Zenetos et al. 2008), but their status has rarely been assessed based on a historical baseline. In this study, we report the occurrence of tests of benthic foraminifera previously considered non-indigenous in deep sections of sediment cores collected off the Mediterranean coast of Israel and we thus question their non-indigenous status. Similarly, Stulpinaite et al. (2020) and Meriç et al. (2016, 2018) corrected the non-indigenous status of some foraminifera species based on occurrences in pre-Lessepsian (pre-AD 1869) sediments. In order to assess whether our tests are post-Lessepsian, we deployed state-of-the-art radiocarbon techniques to date them individually and ascertain their exact age. We show that all tests are of Holocene age — thus representing native species — and discuss the consequences of these results for the biogeography of the Mediterranean Sea.

2. MATERIALS AND METHODS

2.1. Core and sample collecting and analysis

Two ~1.2 to 1.5 m long sediment cores were collected at each of 2 sites at ~30 m (SC30, replicates SC30_1 and SC30_3) and ~40 m (SC40, replicates SC40_3 and SC40_4) depth off Ashqelon, on the Mediterranean shelf of southern Israel, with a gravity corer aboard the RV 'Mediterranean Explorer' in 2016 (Table S1, Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m700p065_supp1.pdf). From a visual inspection, differences in grain size distribution along the cores were obvious but no sedimentary structures could be recognized. Cores were cut into 1 cm thick slices, which were air dried for at least 96 h.

One core each was used for foraminiferal analysis and sieved with a 150 µm mesh, which is a typical sieve size for the study of benthic foraminifera (e.g. Fontanier et al. 2002, Duros et al. 2011) and balances the need for intercepting small-sized tests with the time to process the samples. Sediments were then dried at 40°C for 48 h. One slice every 5 cm was used for foraminiferal analyses. This resolution is considered sufficient for marine sediments in areas with relatively low sedimentation rates as studied here, which are effectively mixed by physical and biological processes at decimeter scales (e.g. Tomašových et al. 2017, Gallmetzer et al. 2019). This strong degree of time-averaging is also nicely indicated by the presence of shells of *Corbula gibba* of very different ages in the same layers in our cores (see Fig. 1). Samples were split into aliquots containing at least 300 tests, which were subsequently picked, identified and counted. The foraminiferal data were standardized and the occurrence of species reported as non-indigenous in the literature recorded (Table 1).

The replicate core was used to determine the sediment grain size, again each fifth 1 cm thick slice. The fraction finer than 63 µm was analyzed with a Micromeritics SediGraph III 5120, after mixing with 5 ml of 2% sodium pyrophosphate ($Na_4P_2O_7$). Coarser fractions were sieved and weighed. Sediment classification follows Folk (1954).

2.2. Core age models

From each target increment — the top 5 cm of the cores, layers with major changes in sediment grain size and the core bottom (see Table 2) — 3 to 5 valves of the native bivalve *C. gibba* with a minimum mass of 1 mg were selected for radiocarbon dating, yielding a total of 29 and 28 valves for cores SC30_1 and SC40_4, respectively. *C. gibba* was the only macrofossil common enough throughout both cores and of sufficient mass to be dated with standard radiocarbon methods. To avoid dating individual bivalves twice, only right valves were used whenever possible. If a sufficient number was available within an increment, right valves to be dated were selected by random drawing; otherwise, all right valves within the increment were used, and randomly drawn, non-matching, left valves were added until a sufficient sample size was achieved. Selected valves were pre-cleaned by manually removing sediment and encrustations visible under a stereomicroscope.

Valves were dated by accelerator mass spectrometry (AMS) using powdered carbonate targets (Bush et al. 2013, Bright et al. 2021), with a typical analytical precision better than 0.6% (1 σ). Mollusk shells were subsampled by gently breaking and then selecting a small fragment. All samples were cleaned by sonicating and rinsing 3 times in deionized distilled water (DDI; 16.3 MΩ-cm). Samples were leached with 2 M HCl, with the extent of leaching dependent on sample mass: samples larger than 1 mg were leached to remove about 30% by mass and samples between ca. 0.5 and 1 mg were leached to remove about 15%. Samples were ultimately rinsed 3 times with DDI water then dried in a 50°C oven overnight. They were then ground to a fine powder using a small clean agate mortar and pestle. Between 0.15 and 0.50 mg of the carbonate powder of each sample was transferred to sterilized (3 h at 500°C) borosilicate glass culture tubes (6 mm outer diameter [OD] × 50 mm). The sample carbonate was combined with 6 to 7 mg of niobium (Nb Puratronic, −325 mesh, 99.99%) powder using a spatula. The tubes were flushed with N_2 gas and capped with Supelco plastic column caps (1/4" [ca. 6.35 mm] OD) to reduce atmospheric exposure until the powder was pressed into targets. The metal and carbonate mixture was pressed into pre-drilled (0.160" [ca. 4.1 mm] depth) aluminum targets at 400 psi, rotated 90° and pressed again at 400 psi. The targets were sent to the Keck Carbon Cycle AMS Laboratory at the University of California Irvine for ^{14}C analysis.

Radiocarbon ages were converted to calibrated ages or calendar years (cal. yr BP, i.e. before AD 1950) using the OxCal program v. 4.4.2 (Bronk Ramsey 2009) and the Marine20 data (Heaton et al. 2020) with a constant regional marine reservoir correction (ΔR) of −142 ± 66 yr, which is the weighted mean of 8 published pre-bomb ΔR values from Israel and Lebanon (Table S3).

Table 1. Native range and non-indigenous status in the Mediterranean Sea of the target foraminiferal species

Family	Species	Available data SC30	Available data SC40	Native range according to the literature	Non-indigenous status in the Mediterranean Sea
Hauerinidae	*Articulina alticostata* (Cushan, 1944)		Occurrence and age	Indo-Pacific (Cushman 1944, Loeblich & Tappan 1994, Langer & Lipps 2006, Debenay 2012, Mamo 2016)	Reported from Turkey (Meriç et al. 2004, 2008b) and on this basis considered non-indigenous (Zenetos et al. 2010) but identification questioned by Stulpinaite et al. (2020)
Hauerinidae	*Cribromiliolinella milletti* (Cushman, 1954)		Occurrence and age	Indo-Pacific (Cushman et al. 1954, Yim & He 1988)	A record as non-indigenous species is in the EASIN (European Alien Species Information Network) database without details. Considered not present in the Mediterranean Sea by Stulpinaite et al. (2020)
Hauerinidae	*Pseudotriloculina subgranulata* (Cushman, 1918)		Occurrence	Indo-Pacific including the Red Sea (Cushman 1918, Hottinger et al. 1993, Debenay & Cabioch 2007), possibly also Caribbean (Amergian 2019)	Reported from Israel (Yanko et al. 1998, Hyams-Kaphzan et al. 2008) and on this basis considered non-indigenous (Zenetos et al. 2012); unpublished records in sediment cores off Israel suggesting native status (Stulpinaite et al. 2020)
Hauerinidae	*Quinqueloculina erinacea* (Mikhlevich, 1976)		Occurrence	Indo-Pacific (Debenay 2012), Caribbean (Mikhalevich 1976)	New record for the Mediterranean Sea
Hauerinidae	*Quinqueloculina mosharrafai* (Said 1949)		Occurrence	Red Sea (Said 1949) and the Persian (Arabian) Gulf (Al-Enezi et al. 2020)	Reported from Israel (Hyams-Kaphzan 2014). Considered non-indigenous by Stulpinaite et al. (2020)
Hauerinidae	*Miliolinella fichteliana* (d'Orbigny, 1839)	Occurrence and age		Indian Ocean and the Red Sea (Hottinger et al. 1993, Thissen & Langer 2017)	Reported from Turkey (Meriç et al. 2008a,b). Considered non-indigenous by Stulpinaite et al. (2020)
Spiroloculinidae	*Spiroloculina antillarum* (d'Origny, 1839)	Occurrence and age		Stulpinaite et al. (2020) recognized 2 morphospecies: the typical one from Cuba (d'Orbigny 1839) to which our specimens belong, and another occurring in the Red Sea (Hottinger et al. 1993) and the Indian Ocean (Thissen & Langer 2017)	Stulpinaite et al. (2020) considered the Caribbean and the Red Sea/Indian Ocean morphospecies non-indigenous and native, respectively, in the Mediterranean Sea. They reported the former from Croatia (Wiesner 1923) and Libya (Martinotti 1920), the latter from Turkey (Meriç et al. 2008a,b) and Israel (Avnaim-Katav 2010)
Spiroloculinidae	*Spiroloculina nummiformis* (Said 1949)		Occurrence	Indo-Pacific including the Red Sea (Said 1949, Hottinger et al. 1993, Parker & Gischler 2011, Debenay 2012)	Reported from Israel (Hyams-Kaphzan 2000, Hyams-Kaphzan et al. 2008). Considered non-indigenous by Stulpinaite et al. (2020)
Nubeculariidae	*Nodophthalmidium antillarum* (Cushman, 1922)	Occurrence	Occurrence and age	Indo-Pacific including the Red Sea (Hottinger et al. 1993, Makled & Langer 2011, Langer et al. 2013), Caribbean (Cushman 1922) and north-western Atlantic (Culver & Buzas 1980)	Reported from Turkey (Alavi 1980, Meriç et al. 2012, 2014), Lebanon (Moncharmont Zei 1968) and Israel (Hyams-Kaphzan 2000). Considered non-indigenous by Stulpinaite et al. (2020)
Ophthalmidiidae	*Edentostomina cultrata* (Brady, 1881)		Occurrence	Indo-Pacific (Brady 1881, Langer & Lipps 2006), New Zealand (Hayward et al. 1999), north-western Atlantic to Caribbean (Culver & Buzas 1980, 1982, Sen Gupta et al. 2009), north-eastern Atlantic (Dorst & Schönfeld 2013)	Recorded from Turkey (Alavi 1980, Oflaz 2006) and on this basis considered non-indigenous (Zenetos et al. 2010); unpublished records in sediment cores off Israel suggesting native status (Stulpinaite et al. 2020)

We quantified the central tendency and spread of the shell age-frequency distributions with the median and the inter-quartile range (IQR), respectively. Finally, the core age model was obtained with Bayesian statistics using the R package rbacon 2.4.2 (Blaauw & Christen 2011) with the parameters as specified in Table S2.

2.3. Radiocarbon dating of foraminifera tests

Seven foraminiferal tests belonging to the allegedly non-indigenous miliolids *Articulina alticostata* (1 test), *Cribromiliolinella milletti* (1 test), *Miliolinella fichteliana* (1 test), *Spiroloculina antillarum* (1 test) and *Nodophthalmidium antillarum* (3 tests) (Figs. S2 & S3, Table 1) were dated individually. Tests were taken from the deepest layers in the cores where these species occurred (suggesting older ages and thus potential native status) and those in good preservation state were selected for dating.

Laboratory procedures followed Gottschalk et al. (2018). Foraminiferal tests were loaded into septum-sealed glass vials and the air was replaced with helium. The samples were weakly pre-leached using 0.01 M hydrochloric acid for 3 min at room temperature and the resultant CO_2 was again replaced with helium. The carbonate material was then dissolved in 85% orthophosphoric acid to form CO_2, which was measured directly in the AMS MIni CArbon DAting System (MICADAS) using the gas ion source at the University of Bern, Switzerland (Szidat et al. 2014, Gottschalk et al. 2018). The samples were measured together with 6 standards each of both IAEA-C1 and IAEA-C2 for background correction, ^{14}C normalization and $\delta^{13}C$ fractionation correction using the software Bats (Wacker et al. 2010). Afterwards, a constant contamination of $F^{14}C$ = 0.30 ± 0.04 with a carbon mass of 0.68 ± 0.10 µg C was applied to correct for the procedural blank, as previously determined for dating foraminifera in this laboratory (Gottschalk et al. 2018). Uncertainties of ^{14}C ages (see Table 3) include a full propagation of all contributions from AMS measurement, background correction, ^{14}C normalization and $\delta^{13}C$ fractionation correction, as well as the correction of the constant contamination, whereof the last contribution was the largest because of the small sizes of the samples (individual foraminiferal tests). Radiocarbon ages and their calibrated ages in cal. yr BP (see the age calibration procedure in Section 2.2) are reported in Table S4 in Supplement 2 at www.int-res.com/articles/suppl/m700p065_suppl2.xlsx for the mollusks and in Table 3 for the foraminifera.

3. RESULTS

3.1. Core age and sediment profiles

Cores SC30 and SC40 span millennia and centuries, respectively, as a consequence of markedly different sedimentation rates (0.2 and 2.4 mm yr^{-1}, respectively). The age model of core SC30 suggests a median age of ca. 5500 cal. yr BP at its maximum depth (Fig. 1). Time averaging, which quantifies the temporal mixing of the assemblages and here expressed as inter-quartile range, is several hundred years at most sediment depths and reaches 709 yr at the core bottom (Table 2). The age model of core SC40 suggests a median age at its maximum depth of ca. 600 cal. yr BP. Time averaging is generally limited to a few centuries in the upper 30 cm and to decades only in deeper sections. At 14 cm sediment depth, we detected a layer that contains the oldest shells (1427 cal. yr BP) with the highest time averaging (337 yr) of the core. Although we could not observe sedimentary structures, this strong age inversion and high degree of time averaging suggests transport of older shells from elsewhere (e.g. from shallower sites; at the SC30 station, the surficial death assemblage has a median age of 505 cal. yr BP and the age range is between 127 and 3043 cal. yr BP; Table 2).

Core SC30 comprises 3 zones with different sediment types (Fig. 1): a top layer down to ca. 40 cm sediment depth where sand to muddy sand prevails, a second interval down to ca. 110 cm sediment depth where clay prevails, and the bottom of the core where the sediment is coarser again. This latter sediment change, dated around 2600 cal. yr BP, may be related to a decrease in the Nile River discharge due to the onset of drier conditions in central Africa and consequent reduction in pelitic input relative to coarser sediments from coastal erosion (Hassan et al. 2012). Most of core SC40 is homogeneously muddy throughout; the top 5 cm contain slightly coarser sediment (Fig. 1).

3.2. Foraminiferal test ages

The dated foraminiferal tests span between 731 and 8261 cal. yr BP in calibrated median age (Table 3). With the single exception of a test of *Nodophthalmidium antillarum* (specimen F008) with a 95% confidence interval (CI) calibrated age range marginally overlapping with the opening of the Suez Canal (but a median age of 1111 cal. yr BP), all other 95% CI calibrated ages are much older.
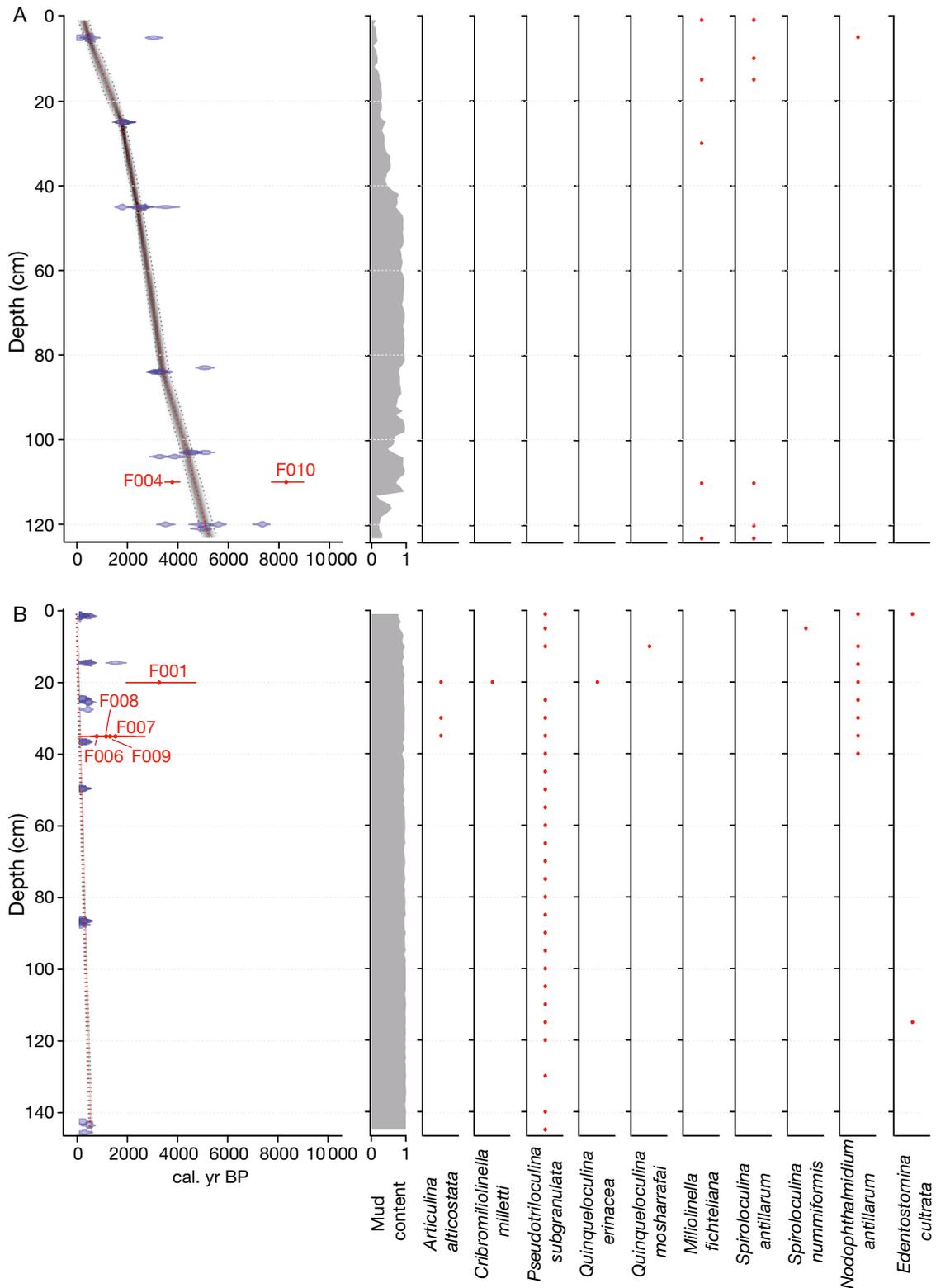
Fig. 1. Core age model (sloped lines, based on radiocarbon dating of *Corbula gibba* shells), age of foraminiferal tests (see Table 3), proportion of mud content (grains < 63 µm) and occurrence of foraminiferal species reported in the literature as non-indigenous in the Mediterranean Sea for 2 cores collected off Ashqelon, southern Mediterranean Israeli shelf, at (A) 30 (core SC30) and (B) 40 m (core SC40) depth. The probability distribution of the calibrated age of *C. gibba* shells is shown in blue violin plots. Calibrated ages (median and 95 % CI) of the foraminiferal tests are indicated by red dots and error bars, respectively. cal. yr: calibrated years

Table 2. Summary statistics for the age–frequency distributions of the bivalve *Corbula gibba* downcore. cal. yr: calibrated years

Core	Core slices (cm)	Number of dates	Median age (cal. yr BP)	Minimum median age (cal. yr BP)	Maximum median age (cal. yr BP)	Inter-quartile range (yr)
SC30_1	5	4	505	127	3043	863
SC30_1	25	5	1881	1768	1944	97
SC30_1	45	5	2557	1789	3531	228
SC30_1	83–84	5	3274	3079	5045	116
SC30_1	103–104	5	4451	3281	5054	721
SC30_1	120–121	5	4910	3533	7284	709
SC40_4	1	5	104	34	393	201
SC40_4	14	4	381	170	1427	337
SC40_4	24–27	5	290	122	358	131
SC40_4	36	3	176	123	249	63
SC40_4	49	3	139	96	168	36
SC40_4	86–87	5	147	80	204	70
SC40_4	142–145	3	181	123	359	118

Table 3. Sample details, measured ^{14}C ages with 68% uncertainties and calibrated ^{14}C ages with 95% confidence intervals of foraminiferal tests from sediment cores off Ashqelon, southern Israel

Species	Foraminiferal test code (University of Bern code)	Core	Sediment depth (cm)	Carbon mass (µg C)	^{14}C age (yr BP)	Calibrated median age (cal. yr BP)	Calibrated age at 95% CI (cal. yr BP)
Articulina alticostata	F006 (BE-12479.1.1)	SC40_4	35	19	1183 ± 130	731	464–1047
Cribromiliolinella milletti	F001 (BE-11692.1.1)	SC40_4	20	2	3335 ± 538	3243	1926–4688
Miliolinella fichteliana	F004 (BE-11695.1.1)	SC30_1	110	30	3823 ± 88	3784	3460–4103
Spiroloculina antillarum	F010 (BE-12483.1.1)	SC30_1	110	10	7798 ± 271	8261	7667–8967
Nodophthalmidium antillarum	F007 (BE-12480.1.1)	SC40_4	35	3	1851 ± 492	1486	504–2685
Nodophthalmidium antillarum	F008 (BE-12481.1.1)	SC40_4	35	2	1462 ± 567	1111	0–2300
Nodophthalmidium antillarum	F009 (BE-12482.1.1)	SC40_4	35	5	1704 ± 308	1271	629–1998

Additionally, *Miliolinella fichteliana* and *Spiroloculina antillarum* occur in SC30 at sediment depths greater than 1 m, where the core age model suggests ages between 4000 and 6000 cal. yr BP (Fig. 1). In SC40, *Edentostomina cultrata* occurs at 115 cm sediment depth, where the core age model suggests ages around 400 cal. yr BP (Fig. 1), and *Pseudotriloculina subgranulata* occurs in SC40 down to the core bottom at 145 cm sediment depth (ca. 600 cal. yr BP). Occurrences so deep below the seafloor and in layers dating to well before the opening of the Suez Canal suggest the pre-Lessepsian presence of these species in the Mediterranean Sea.

The non-indigenous *Quinqueloculina erinacea* and *Q. mosharrafai* occur at 20 and 10 cm sediment depth, respectively, and *S. nummiformis* occurs at 5 cm sediment depth in SC40 (Fig. 1). These depths, however, are too shallow to exclude reworking of young material from the surface and thus we have no evidence that *Q. erinacea*, *Q. mosharrafai* and *Spiroloculina nummiformis* occurred on the Mediterranean Israeli shelf before the opening of the Suez Canal.

4. DISCUSSION

4.1. Alleged non-indigenous foraminifera are native

The 7 foraminiferal tests we dated were all pre-Lessepsian (i.e. pre-AD 1869), suggesting that *Articulina alticostata*, *Cribromiliolinella milletti*, *Miliolinella fichteliana*, *Spiroloculina antillarum* (Caribbean morphotype, see Stulpinaite et al. 2020) and *Nodophthalmidium antillarum* are native Mediterranean species. Consistently, *M. fichteliana* has been reported from sediment cores collected between Rhodes and Crete, Greece, and dated between 4000 and ca. 25 000 cal. yr BP (Abu-Zied et al. 2008), and *S. antillarum* has been reported from Pleistocene sediments related to the last interglacial in Palma de Mallorca, Baleares (Spain) (Mateu 1972), from Holocene sediments in cores collected at the archeological site of Elaiussa Sebaste, Mersin (Turkey) (Melis et al. 2015) and in other Pleistocene to Holocene sediments in Turkey (Meriç et al. 2018) (but see discussion of its taxonomy in Section 4.2).

In our material, almost all foraminiferal tests are older than bivalve shells in the same layers. Such age offsets between different taxa in sediment cores are a widespread pattern in both shallow and deep waters. For example, a multi-phyla dating experiment on bivalves, foraminifera, echinoids, brachyurans and otoliths from Holocene sediment cores collected in the Adriatic Sea showed age offsets of 4000 yr between the benthic foraminifera *Adelosina intricata* and *Elphidium crispum*, and offsets of 1000 to 3000 yr between these foraminifera and the bivalves *Corbula gibba* and *Gouldia minima* (Nawrot et al. 2022). Relative differences in the likelihood of burial may be the primary cause of the age differences between bivalves and foraminifera. Foraminiferal tests can be rapidly incorporated into the sediment by burrowers such as callianassid shrimps and polychaetes that can actively mix the sediment down to more than 1 m (Dworschak & Rodrigues 1997, Pervesler & Hohenegger 2006). When buried, tests are protected from most destructive forces. Re-exhumation by bioturbators thus brings to surface tests that are significantly older than other skeletal remains such as bivalve shells that, due to their larger size, have a lower probability of taking part in these burial–exhumation cycles (Martin et al. 1996). The burial–exhumation dynamic also blurs the timing of production peaks and leads to skeletons of comparable durability being of different age despite their occurrence in the same horizon (Tomašových et al. 2019a,b).

Even if not individually dated, the occurrence of the foraminifera *Pseudotriloculina subgranulata* and *Edentostomina cultrata*, previously considered non-indigenous, at 115 and 145 cm sediment depths in our SC40 core suggests their native status. This result confirms the proposition of Stulpinaite et al. (2020) based on undated sediment cores collected off Israel. Further alleged non-indigenous foraminifera were found in sediments dating back from the middle Pleistocene to the Holocene (Meriç et al. 2016, 2018). The assignment of so many allegedly non-indigenous foraminifera species to native status requires a broader reassessment of our knowledge of this group in the Mediterranean Sea.

4.2. Consequences for marine ecology

Small-sized organisms like foraminifera are particularly prone to under- and misreporting. There is evidence for a variety of taxa that small body size delays their discovery (Blackburn & Gaston 1998), as early naturalists were biased towards collecting and describing large, conspicuous species (Blackburn & Gaston 1994). Indeed, 70% of the species analyzed here were first reported from the Mediterranean Sea in the last 20 yr, 2 were reported in the second half of the 20th century, and only *S. antillarum* was first reported in 1920. This last species is also an example of the challenges faced when treating very small-bodied taxa whose taxonomy is not settled. Stulpinaite et al. (2020) recognized 2 morphospecies: the *S. antillarum* s.s. and an undescribed species occurring in the eastern Mediterranean and the Red Sea, but their records in the literature are under the same name and not always illustrated, obscuring their geographic distribution and origin.

Our results also highlight how well-dated sedimentary sequences can support ecology. Direct observation of ecosystems is mostly limited to short time scales (years to decades), much shorter than the life span of many species and most habitats (years to decades and centuries to millennia, respectively) (Yasuhara et al. 2012, Kidwell & Tomašových 2013). Multi-decadal time series are limited to very few places (e.g. the North Sea, Schroeder 2005, and the Arctic fjords, Kortsch et al. 2012). Even when sampling and reporting took place early, data may be qualitative and based on serendipitous collecting events rather than on well-designed sampling (Dauvin 2010), and these early efforts may have been strongly biased in favor of large-sized organisms, as reported above. In these conditions, discriminating a natural from an anthropogenic pattern may not be possible. The occurrence of identifiable and individually dated (sub)-fossils in stratigraphic context complements available ecological datasets (e.g. Yasuhara et al. 2012, 2020, Cramer et al. 2017, Tomašových et al. 2019a, Gallmetzer et al. 2019, O'Dea et al. 2020). In this study, we showed that the Holocene record helps in discriminating the native vs. non-indigenous status of species, and may prove valuable in determining the origin of the so-called cryptogenic species, that is, those that are currently not demonstrably native or non-indigenous (Carlton 1996). Such cryptogenic species could have been introduced before any monitoring occurred and thus were not detected as newcomers.

4.3. Consequences for the biogeography of the Mediterranean Sea

We demonstrate that 3 foraminifera species of Indo-Pacific affinity (*A. alticostata*, *C. milletti* and *M. fichteliana*) and 3 species with a broad distribution in the tropical seas of the Caribbean and the Indo-

Pacific province (*P. subgranulata*, *N. antillarum* and *E. cultrata*) that were previously considered non-indigenous in the Mediterranean are instead native. Their Mediterranean distribution is limited to the eastern basin. The type locality of *S. antillarum* is in the Caribbean, but here it is shown to also be native to the Mediterranean, where it has a broad distribution. Additionally, the benthic foraminifer *Amphistegina lobifera* Larsen, 1976, which is currently considered an invasive species in the Mediterranean Sea, occurs both in the Pleistocene (Meriç et al. 2016) and at sediment depths slightly deeper than ours within undated sediment cores from Haifa Bay (Stulpinaite et al. 2020), suggesting a Holocene age and that the alleged non-indigenous status of this species merits further investigation. We consider it unlikely that these species could have occurred in the basin during the Holocene, become extinct and then been reintroduced through the Suez Canal, as the few extinctions of marine species during the Holocene are directly or indirectly ascribed to human action, and foraminifera are neither associated with direct human pressures nor with cascading effects strong enough to drive them to regional extinction (Dulvy et al. 2009).

The occurrence in the Mediterranean Sea of tropical foraminifera with broad global distributions may have 2 alternative explanations. In a first scenario, such distributions are the outcome of vicariance processes caused by the closure of the Tethyan Seaways during the Cenozoic (Harzhauser et al. 2007, Bialik et al. 2019, Straume et al. 2020). Populations of Tethyan species were geographically separated, leading to disjunct occurrences in both the present-day Caribbean and the Indo-Pacific. Some Tethyan species may have survived in the Mediterranean despite its quasi-complete desiccation during the Messinian Salinity Crisis (Hsü et al. 1977, Roveri et al. 2014), later evolving into closely allied species (Basso et al. 1996, Athanasiadis 1999).

An alternative scenario is that species which disappeared from the Mediterranean during the Messinian Salinity Crisis, or evolved later, (re)entered the basin upon normalization of marine conditions. The timing of their range expansion into the Mediterranean may be as early as the Pliocene for pan-tropical foraminifera, but strictly Indo-Pacific taxa may have entered only later, considering the lack of evidence of connections between the Mediterranean and the Red Sea during the Pliocene (Taviani 2002). Indeed, there is geological and evolutionary evidence of such connections in the late Pleistocene. During the Last Interglacial high stand (Marine Isotope Stage [MIS] 5e, ca. 125 000 kyr), the global sea level was 5 to 9 m higher than at present (Kopp et al. 2009, Dutton & Lambeck 2012, Rovere et al. 2016) and a shallow marine connection was probably in place across the Suez Isthmus enabling faunal exchanges between the Mediterranean and Red Sea (Plaziat et al. 1995). Such connections may have occurred in earlier times too, because populations of the benthic fish *Serranus cabrilla* that occur in both seas diverged approximately 194 000 yr ago at the end of the MIS 7 interglacial (Bos et al. 2020). More occurrences of sea levels higher than today in the Red Sea have been reconstructed for the last 500 kyr (Siddall et al. 2003), suggesting significant opportunities for the dispersal of shallow water species. Such high sea levels suggest that the Isthmus of Suez was probably a more porous biogeographic barrier than previously thought. Still, it would have acted as a strong filter in favor of shallow water euryhaline species (e.g. the intertidal Mediterranean gastropod *Pirenella conica* that now occurs in the northern Red Sea, Plaziat et al. 1995; or the intertidal Indo-Pacific bivalve *Brachidontes pharaonis* that has been recently hypothesized to have occurred in the Mediterranean before the opening of the Suez Canal, Belmaker et al. 2021), or species with particular ability to cross barriers. Fishes (e.g. *Serranus cabrilla*) can be easily perceived as effective dispersers, but foraminifera also have multiple dispersal pathways. Zygotes and embryonic juveniles are easily transported over large distances, with the latter capable of extending numerous filose pseudopodia that enhance flotation and thus the length of pelagic life (Alve 1999, Alve & Goldstein 2002, 2003). Additionally, foraminifera can be resuspended by storms or fish activity and then transported over long distances (Murray 2006). Last, the recently reported ichthyocory — the live passage of organisms through fish digestive tracts — for foraminifera (Guy-Haim et al. 2017) further increases their dispersal potential. An additional challenge for species entering the Mediterranean during interglacials is their survival during glacial times. However, although in the easternmost Mediterranean Sea summer sea surface temperatures during the last glacial maximum were 2°C lower than today, winter temperature anomalies were close to zero (Hayes et al. 2005), suggesting the occurrence of a refugium for thermophilic species. Indeed, survival in winter is one of the main conditions for warm water species to persist in cooler conditions (Amarasekare & Simon 2020).

The permeability of the Suez Isthmus barrier and these favorable climatic conditions may be the most likely scenario to explain the occurrence of tropical species in the Mediterranean and show that the biogeography of the Mediterranean Sea is still far from well understood.

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