

LETTER

A novel marine bioinvasion vector: Ichthyochory, live passage through fish

Tamar Guy-Haim ^{1,2*}† Orit Hyams-Kaphzan,³ Erez Yeruham,¹ Ahuva Almogi-Labin,³ James T. Carlton,⁴

¹Israel Oceanographic and Limnological Research, National Institute of Oceanography, Haifa, Israel; ²Marine Biology Department, The Leon H. Charney School of Marine Sciences, University of Haifa, Mt. Carmel, Haifa, Israel; ³Geological Survey of Israel, Jerusalem, Israel; ⁴Williams College - Mystic Seaport, Maritime Studies Program, Mystic, Connecticut

Scientific Significance Statement

Bioinvasions, the expansions of species into regions outside their native range, threaten biodiversity, and human livelihood worldwide. In the sea, international shipping has been considered the primary vector for the introduction of these non-indigenous species, although in many cases the specific vector is not known nor well understood. We present evidence for a novel bioinvasion vector that can explain the appearance and dispersal of dozens of benthic non-indigenous species in the Mediterranean Sea—that of live passage through fish digestive tracts (ichthyochory). This newly identified vector should be considered when evaluating both the history of prior invasions and the potential vectors of future invasions world-wide.

Abstract

Many species of Indo-Pacific holobenthic foraminifera have been introduced and successfully established sustainable populations in the Mediterranean Sea over the past few decades. However, known natural and anthropogenic vectors do not explain how these species were introduced long distances from their origin. We present evidence for a novel marine bioinvasion vector explaining this long-distance transport and introduction using both contemporary field and historical analyses. In 2015–2016, we found living specimens of 29 foraminiferal species in the fecal pellets of two Red Sea herbivorous rabbitfish—*Siganus rivulatus* and *Siganus luridus* in the Mediterranean. In our historical analysis, we found 34 foraminiferal species in preserved Red Sea rabbitfish specimens, dating between 1967 and 1975. In addition, we found congruent propagation patterns of the non-indigenous rabbitfish and foraminifera, lagging 4–11 yrs between discoveries, respectively. Predation of marine benthos by non-indigenous fish, followed by incomplete digestion and defecation of viable individuals, comprise the main introduction vector of these organisms into novel environments.

*Correspondence: tamar.guy-haim@ocean.org.il

†Present address: GEOMAR, Helmholtz Centre of Ocean Research Kiel, Marine Ecology, Germany.

Author Contribution Statement: The study was conceived by TGH and OHK. TGH led and designed the study. TGH and EY performed the experiments. OHK and AAL conducted the taxonomic analysis. TGH and OHK analyzed the data. TGH, OHK, EY, AAL and JTC developed the conceptual framework and drafted the manuscript.

Data Availability Statement: Data supporting the results are archived at doi:10.1594/PANGAEA.872632.

T.G.-H. and O.H.-K contributed equally to this work.

Additional Supporting Information may be found in the online version of this article.

This is an open access article under the terms of the Creative Commons Attribution NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

Non-indigenous species (NIS) are increasingly being discovered in terrestrial, freshwater, and marine habitats, altering community structure and ecosystem functions (Simberloff 2001; Sanders et al. 2003; Lowry et al. 2013). Nevertheless, the vectors of NIS introduction often remain obscure. In the sea, human-mediated transport mechanisms, primarily vessel hull fouling and ballast water, fisheries, aquaculture, and canals (Ruiz and Carlton 2003), are known to play important roles in NIS dispersal. However, none of these vectors explain the invasion of at least 68 benthic foraminifera NIS from the Red Sea into the Mediterranean Sea over the past decades (Zenetos et al. 2012; Weinmann et al. 2013).

Since the opening of the Suez Canal in 1869, hundreds of NIS from the Red Sea have been recorded in the Mediterranean Sea (Galil et al. 2015). The unidirectional advancement of Red Sea species via the canal is termed “Lessepsian migration” and the Red Sea NIS are termed “Lessepsian migrants,” after Ferdinand de Lesseps, the French diplomat who was in charge of the canal’s construction (Por 1978). The Lessepsian migrants moved with currents or under their own volition, as well as by vessel-mediated transport. Many benthic organisms are meroplanktonic, undergoing a larval planktonic phase, and thus are potentially capable of dispersing long distances, including travelling through waterways. Most benthic foraminifera, however, are holobenthic, being permanent bottom-dwellers in sediments, on rocks, or as epiphytes on seaweeds and seagrass, with no planktonic stage (Hyams-Kaphzan et al. 2008). Although capable of active movement across surfaces, benthic foraminifera speed-rates range between 1.8 mm h^{-1} and 8.4 mm h^{-1} (Kitazato 1988). It would thus take a persistent foraminiferal species about 4000 yrs to “walk” the 164 km long Suez Canal.

Several mechanisms have been proposed to explain the range expansions of benthic foraminifera (Alve 1999): ballast water taking up suspended foraminifera stirred up from sediments (McGann et al. 2000), passive dispersal by currents and sediment transport (Alve and Goldstein 2010), attachment to gastropod veliger shells (Nesbitt 2005), ship hull fouling (Gollasch 2002), rafting on marine plants or debris (Winston 2012), and movement with aquaculture products (Cohen 2012). To date, no data have been found to support any of these hypotheses to explain new invasions of rocky substrate or epiphytic foraminifera. First, while foraminifera are known from ballast water and ballast sediments, these are in large part species associated with soft-sediment habitats, as are the few other foraminifera invasions in other regions of the world (McGann et al. 2000). Second, an extensive 10-yr survey of ballast protist communities of cargo vessels arriving in Israeli Mediterranean ports did not reveal any of the known benthic foraminifera NIS (Galil and Hülsmann 1997). Third, dispersal by juvenile drifting or rafting are less probable vectors as the westward propagation of benthic foraminifera NIS in the Mediterranean is both clockwise and



Fig. 1. A marbled spinefoot rabbitfish *Siganus rivulatus* grazing on turf algae near Mikhmoret, Israel. The arrow points to a large epiphytic non-indigenous Indo-Pacific foraminifera, *Sorites orbiculus*, magnified at bottom right. Other benthic foraminifera species, smaller than can be seen by the naked eye, are plentiful in the shallow rocky reefs of the Eastern Mediterranean.

anti-clockwise, inconsistent with the Levantine anti-clockwise longshore current (Robinson et al. 1992). Therefore, it is necessary to consider alternate mechanisms of introduction for foraminifera NIS invasion, particularly for the Mediterranean. One phenomenon that has been overlooked is the potential of other non-indigenous species to act as biotic vectors.

In the Mediterranean Sea, the majority of foraminifera NIS inhabit the rocky subtidal, attached to carbonate-rich hard substrates and seaweeds (Hyams-Kaphzan et al. 2014). Over the past decades, these habitats have undergone a profound phase-shift from algal forests to turf barrens, due to over-grazing by invasive Indian Ocean herbivorous rabbitfish [*Siganus rivulatus*, first observed in 1924 (Steinitz 1927), and *Siganus luridus*, first observed in 1955 (Ben-Tuvia 1964)] found in the entire eastern basin (Fig. 1). Rising seawater temperature over the past several decades may have facilitated their expansion westward toward the Atlantic and northward into the Ionian, Tyrrhenian, Aegean, and Adriatic Seas (Vergés et al. 2014) (Fig. 2). These and other herbivorous fish may incidentally ingest living epiphytic foraminifera and then defecate them unharmed, although their calcareous tests may be destroyed in those fish with an acidic digestion phase (Debenay et al. 2011).

In this study, our objective was to compile evidence for the ability of invasive herbivorous fish to transport the large number of benthic foraminifera species from the Red Sea to the Mediterranean Sea and to facilitate their long-distance westward dispersal. We addressed this objective by: (1) testing the viability of benthic foraminifera species in fecal pellets of invasive rabbitfish in the Mediterranean Sea, (2) examining the presence of foraminifera species in the digestive tracts of museum specimens of Red Sea rabbitfish

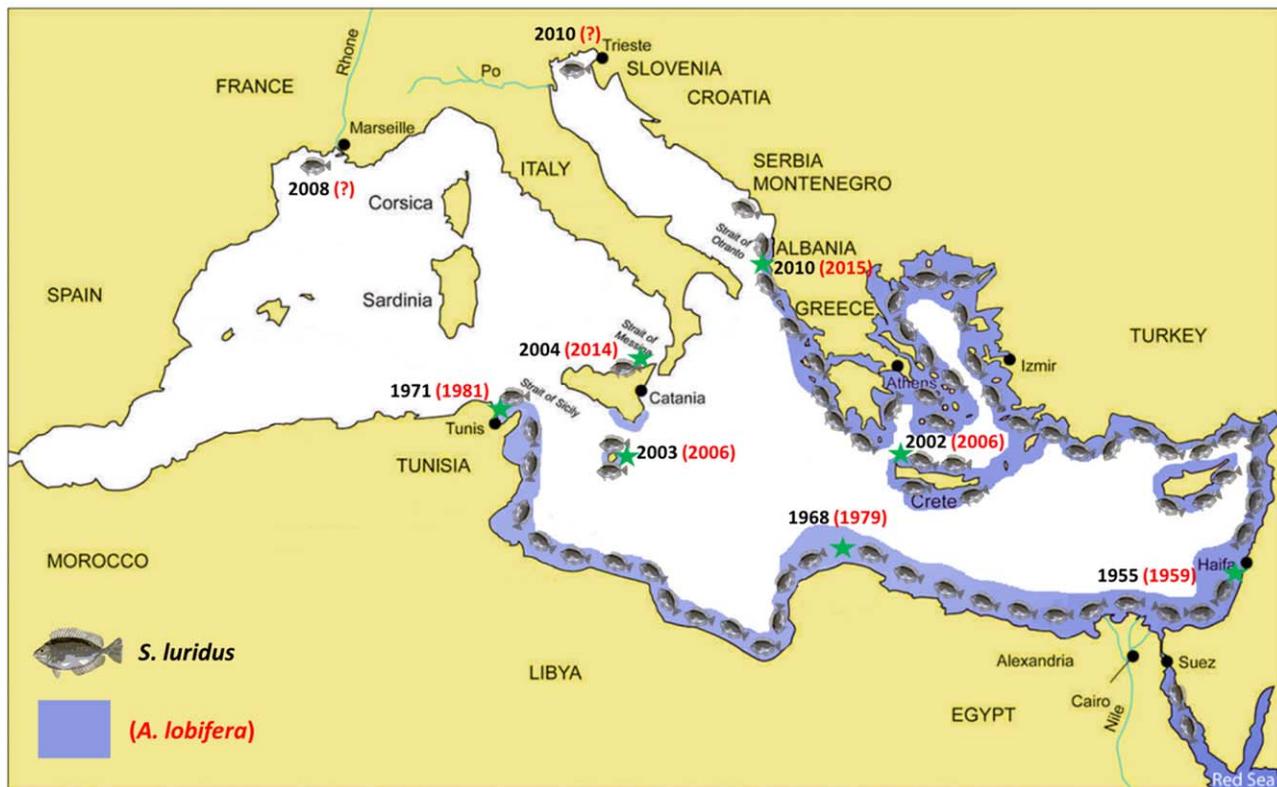


Fig. 2. Distribution and propagation map of the non-indigenous foraminifera *Amphistegina lobifera* (marked by blue filled area) and the invasive rabbitfish *Siganus luridus* (fish symbols). First record years of *S. luridus* are in black, and of *A. lobifera* in red brackets. Sites of observation are marked by green stars. Modified from Langer et al. (2012). All related references are presented in Supporting Information Table S3.

collected from the Gulf of Suez, and (3) compiling both temporal and spatial records of rabbitfish and benthic foraminifera introductions in the Mediterranean Sea.

Materials and methods

Rabbitfish fecal pellet analysis

Fifty-five specimens of *Siganus luridus* ($n = 20$) and *S. rivulatus* ($n = 35$) were collected by hand at night while free-diving between August 2015 and August 2016 off the coast of Haifa (depth of 2–3 m; 32.8333°N, 034.9738°E), and transferred to the nearby IOLR facilities. The fish were individually placed for 12 h in 5 L circular tanks with a funnel bottom. Seawater was pumped in directly from the Mediterranean at a flow rate of 70 L·h⁻¹ and sand-filtered to eliminate contamination. The fish were removed from the tanks, and the fecal pellets were funnelled out and taken for analysis.

The number of fecal pellets obtained per fish was 8–45, yielding a defecation rate of 36.2 ± 22.3 fecal pellets·d⁻¹ (average \pm SD). Overall, 1350 fecal pellets were analyzed. Each pellet was isolated, rinsed in filtered seawater, and placed in a 500 mL glass jar. Fecal infauna were manually separated from algal debris and organic material, identified, and counted under a dissecting microscope. Test integrity

(the lack of physical damage to the calcareous shell) and symbiont presence in the symbiont-bearing foraminifera species were visually examined using a dissecting microscope and a scanning electron microscope (SEM). The fecal infauna were kept in individual glass jars per pellet for an additional 48 h, to test their movement [using a negative geotaxis assay following Bernhard (2000)]. The foraminifera attached to the glass walls were then manually removed using a fine paintbrush, identified to species, counted under a dissecting microscope, and photographed with a SEM.

Historical data analysis

Forty-six preserved specimens of *Siganus luridus* ($n = 24$) and *S. rivulatus* ($n = 22$) collected from the Gulf of Suez, Red Sea, during 1967–1975 (Supporting Information Fig. S1) were obtained from the Hebrew University Zoological Museum Fish Collection. Upon collection, the fish were fixed in 10% formalin for 7 d and then transferred and stored in 70% ethanol. The preserved fish were dissected and their gastrointestinal tract (gut) was removed, weighed, and volume measured. Gut contents were placed in Rose-Bengal (2 g L⁻¹ ethanol 95%) for 14 d to ensure coloring of the entire sample. Foraminifera were examined under a stereomicroscope and SEM and were morphologically identified to species.

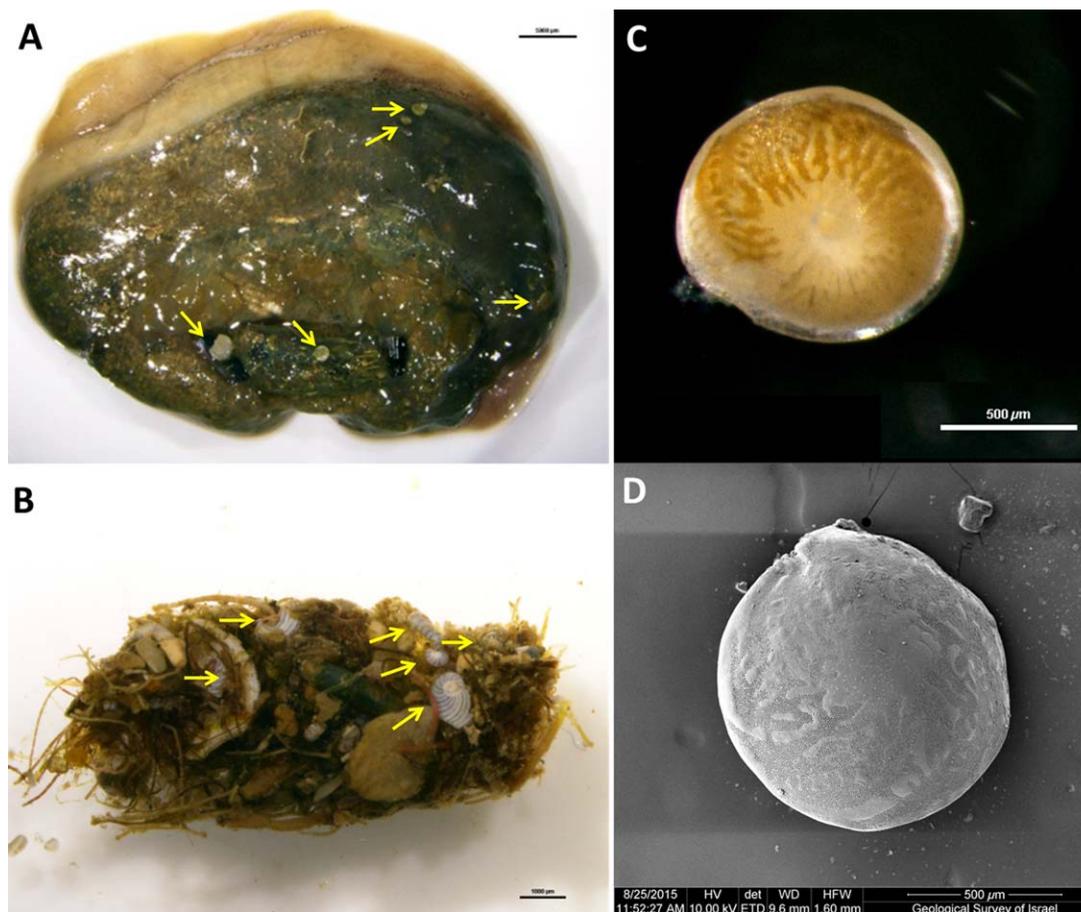


Fig. 3. Living foraminifera in rabbitfish gut and fecal pellets. **(A)** Gastrointestinal tract of *Siganus luridus*. The arrows point to benthic foraminifera, detected through the thin wall. **(B)** Fecal pellet of *S. rivulatus*. The arrows point to benthic foraminifera. **(C)** Live *Amphistegina lobifera* isolated from a fecal pellet by negative geotaxis assay. Endosymbiotic algae appear in dark. **(D)** *A. lobifera* isolated from fecal pellet. Scanning electron microscopy shows intact test. Scale is 5 mm **(A)**, 1 mm **(B)**, and 0.5 mm **(C, D)**.

pH analysis of rabbitfish gut

To assess the gastrointestinal pH microenvironment of the rabbitfish, digestive tracts of fresh fish were removed, unfolded, spread horizontally, and then immediately placed in a micro-profiling system (Unisense A/S, Denmark), including MM33-2 micromanipulator, microsensor multimeter amplifier, temperature sensor (TP-2000), and a membrane pH electrode (pH-100, tip diameter 90–110 μm, < 10 s response time, precision ± 0.01) with an external reference electrode, and SensorTrace Profiling software. Measurements were taken throughout the length and width of the gastrointestinal tract. All electrodes were calibrated with commercial pH solutions (Sigma-Aldrich, U.S.A.).

Experiments

Animal experiments were performed in compliance with the relevant laws and ethics guidelines.

Results and discussion

Classically recognized natural and anthropogenic dispersal vectors of marine organisms fail to explain how scores of

Indo-Pacific holobenthic foraminifera species have rapidly invaded the Mediterranean Sea, successfully establishing sustainable populations. In this study, we examined and tested ichthyochory, live passage of organisms via fish guts, as an alternate mechanism explaining the non-indigenous foraminifera introductions, using analyses of rabbitfish gut and fecal pellet contents, gut analyses of rabbitfish museum specimens collected from the Gulf of Suez, and comparisons of distributions and first records of rabbitfish and foraminifera species in the Mediterranean Sea, since their first appearance there.

Rabbitfish gut content and fecal pellet analyses

Gut content analysis of *S. rivulatus* and *S. luridus*, collected from south-eastern Mediterranean rocky reefs, revealed a high abundance and diversity of live foraminifera, predominantly NIS (Fig. 3A; Supporting Information Table S1). Low gastrointestinal pH ranging from 2.5 to 4.5, is expected in herbivorous fish (Lobel 1981) and may have a detrimental effect on benthic foraminifera, whose tests are characterized

by high calcium carbonate concentration. It was therefore important to assess both the rabbitfish gut pH levels and the viability of ingested foraminifera. We measured gut pH levels ranging between 7.05 and 8.41, possibly due to high inorganic carbonate concentration (Wilson et al. 2009). Further analysis of rabbitfish fecal pellets (Fig. 3B) revealed a variety of empty foraminifera tests (2–80 tests-fecal pellet⁻¹) as well as live foraminifera (1–50 individuals-fecal pellet⁻¹). Overall 29 foraminifera species were present in the fecal pellets, 11 of which are known Lessepsian migrants. Most live individuals were found in good physiological condition (Supporting Information Table S1), containing endosymbiotic algae in the symbiont-bearing species (Fig. 3C), and presenting intact tests (Fig. 3D), likely due to the considerably high pH levels in the rabbitfish gut.

We found a variety of additional taxa in the gut and feces of the rabbitfish, with several still being motile, including gastropods, bivalves, copepods, polychaetes, ostracods, and brittle stars (Supporting Information Table S1); as all of these have planktonic larvae (with the possible exception of the gastropods and ophiuroids, not identified to species), determining the possible role of fish predation as a dispersal mechanism of these organisms is challenging. Live gammarid amphipods, which lack larval stages, were also found, but these are typical of tychoplankton and rafting, and thus present the same challenges of distinguishing ichthyochory from drift. Microplastic filaments were also abundant in the gut and feces of the rabbitfish, reflecting a global trend (Cózar et al. 2014).

Viability of ingested benthic foraminifera

We used a locomotion assay to distinguish live from dead foraminifera. Benthic foraminifera move by means of their pseudopodial network, extending from the test along flat surfaces (Travis and Bowser 1991). Many species present a negative geotactic behavior, crawling upwards on substrates (Murray 2006). In this study, over 20% of foraminifera isolated from feces climbed upwards. However, because not all foraminifera species exhibit this behavior, our assessment of the diversity of live benthic foraminifera transferred via rabbitfish ingestion is probably an underestimate.

Historical data

The historical data that we obtained from preserved museum specimens of siganid fish collected in the Gulf-of-Suez and Cyprus, dating back to 1967 (Supporting Information Fig. S1), revealed a large assortment of 34 benthic foraminifera species (Supporting Information Table S2; Figs. 4, 5), seven of which are Lessepsian migrants. The foraminifera, included large symbiont-bearing species, originated from both Mediterranean and Red Sea fishes. Prominent among them was *Amphistegina lobifera* Larsen (Fig. 3C,D), the most abundant Lessepsian migrant in the Mediterranean Sea (Weinmann et al. 2013). It is among the most prolific and ubiquitous foraminifera on coral reefs, seagrass beds, and

carbonate shelves, and is known to be a major carbonate producer, with a contribution of at least 260 g CaCO₃ m⁻² yr⁻¹ (Hyams-Kaphzan et al. 2014). *A. lobifera* was first observed on the Israeli shelf during the late 1950s in low numbers (Reiss 1961). Today, up to 90% of the rocky reef foraminifera assemblage off northern Israel is comprised of *A. lobifera* (Hyams-Kaphzan et al. 2014).

While recent geological studies have shown that *A. lobifera*, at least as a morphospecies, was present in the Mediterranean Sea up until the Middle Pleistocene (Meriç et al. 2016), its modern day presence in the Mediterranean is due to its dispersal in the 20th century through the Suez Canal. There is no evidence to suggest that prehistoric populations of *A. lobifera* in the Mediterranean persisted into modern times: detailed studies documenting the Mediterranean foraminiferal fauna have been conducted since the 1800s, and no living *A. lobifera* were detected until the 1950s, even as many very rare foraminifera were reported. No environmental triggers are known that would have led a previously unknown species of foraminifera to suddenly become abundant at the end of the 20th century, nor do we have evidence that any known native, but previously extraordinarily rare, species, has now become a predominant member of the Mediterranean biota. Indeed, geological or prehistoric occurrences of species that went extinct and then reappeared in modern times (due to anthropogenic dispersal or natural expansion) is not uncommon. A well-documented marine example is the end-of-Pliocene extinction of the clam *Mya arenaria* in the North Pacific Ocean, followed by its introduction in the 1870s by human activity from the North Atlantic to the Pacific coast of North America (MacNeil 1965).

Non-indigenous rabbitfish and foraminifera propagation pattern

Based on parasitological data, the invasion of the Mediterranean rabbitfish involved actively swimming adults, rather than passively dispersed larvae (Diamant 2010). Adult rabbitfish can swim long distances (Kaunda-Arara and Rose 2004), and in doing so we suggest that they spread benthic foraminifera from the Red Sea, via the Suez Canal, to the Levantine basin and westward. Assuming that passive dispersal by rabbitfish is a major vector in determining the distribution of benthic foraminifera NIS into the Mediterranean Sea, we can expect that the propagation of both will be reflected in one another. Indeed, when we compare the propagation of *S. luridus* with that of *A. lobifera* (Fig. 2; Supporting Information Table S3) we find an overall correspondence in the extent and timing of first reported sightings in new biogeographic regions.

Ichthyochory – dispersal by live passage via fish guts

Dispersal of organisms by “hitchhiking” in the digestive tract of another species is well-known in terrestrial and freshwater habitats (Darwin 1859). Seed dispersal via ingestion by vertebrates (mostly birds and mammals), termed

Plate 1



Fig. 4. Assortment of benthic foraminifera isolated from gastrointestinal tracts of preserved *S. luridus* and *S. rivulatus* collected at the Gulf of Suez between 1967 and 1975 (the Hebrew University Zoological Museum, Jerusalem). Living specimens are indicated by Rose Bengal stain. Possible Lesepian species (Red Sea species that are found in the Mediterranean Sea) are marked by asterisk. **1–2.** *Ammonia convexa*, **1.** spiral side, **2.** umbilical side; **3–4.** *Amphistegina lobifera*, **3.** spiral side, **4.** umbilical side; **5–6.** *Challengerella bradyi*, **5.** spiral side, **6.** umbilical side; **7.** *Elphidium advenum* subsp. *limbatum*, lateral view; **8.** *Elphidium fichtellianum*, lateral view; **9.** *Elphidium striatopunctatum*, lateral view; **10–12.** *Neorotalia calcar*, **10–11.** spiral side, **12.** umbilical side; **13–14.** *Pararotalia* sp., **13.** spiral side, **14.** umbilical side; **15.** *Affinetrina planciana*, lateral view; **16.** *Hauerina diversa*, lateral view; **17.** *Peneroplis pertusus*, lateral view; **18.** *Peneroplis planatus*, lateral view; **19.** *Pseudoschlumbergerina ovata*, oblique lateral view; **20.** *Sigmoihauerina bradyi*, lateral view; **21.** *Sorites orbiculus*, lateral view; **22.** *Spiroloculina communis*, lateral view; **23.** *Triloculina trigonula*, lateral view. Scale bar: 3–4, 9, 18, 21 = 500 μm ; 19 = 300 μm ; 1–2, 5–7, 10–17, 16, 20, 22–23 = 200 μm ; 8 = 100 μm .

Plate 2

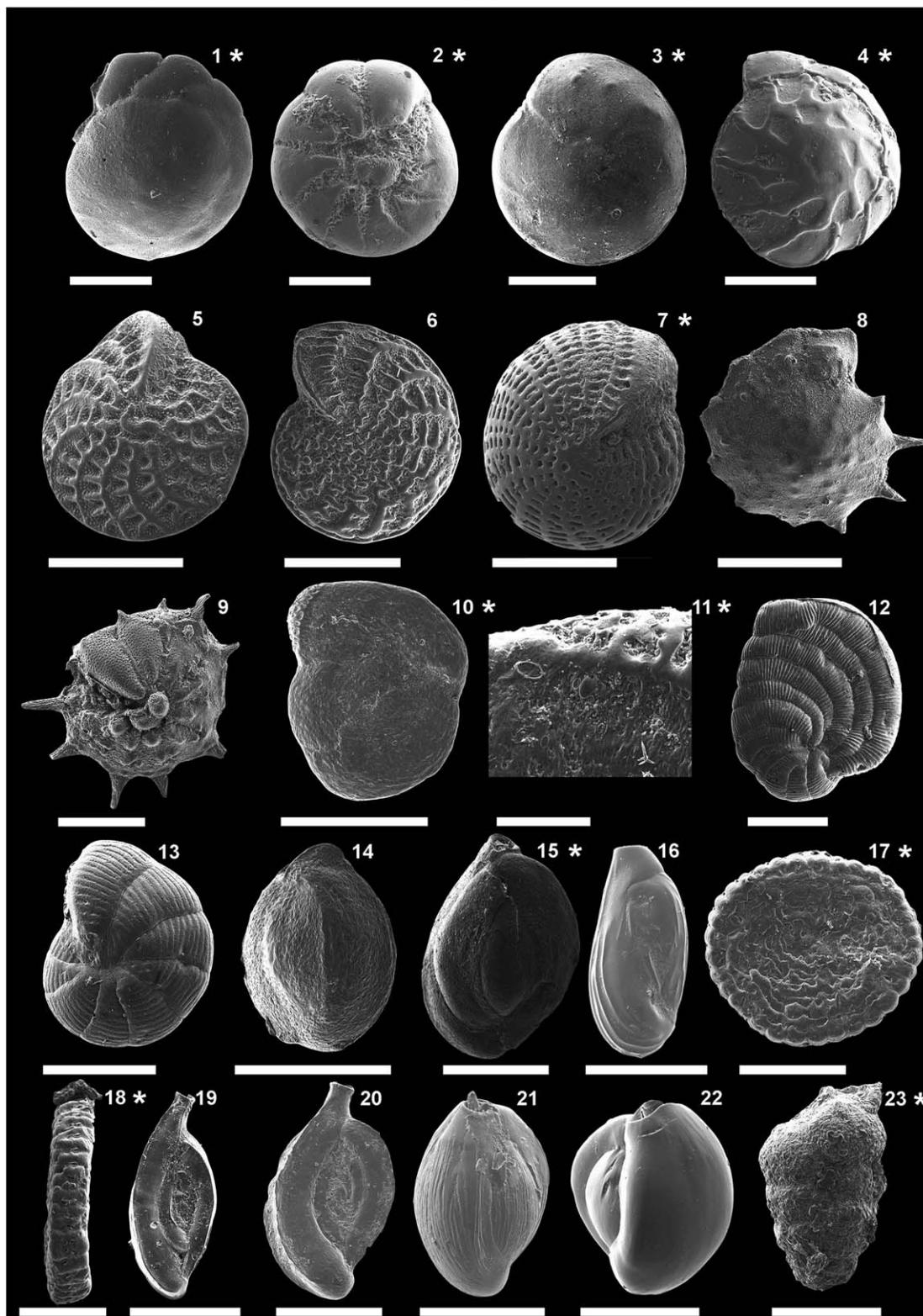


Fig. 5. Scanning electron micrographs of benthic foraminifera isolated from gastrointestinal tracts of preserved *S. luridus* and *S. rivulatus* collected at the Gulf of Suez between 1967 and 1975 (the Hebrew University Zoological Museum, Jerusalem). Possible Lessepsian species (Red Sea species that are found in the Mediterranean Sea) are marked by asterisk. **1–2.** *Ammonia convexa*, **1.** spiral side, **2.** umbilical side; **3.** *Amphistegina lobifera*, spiral side; **4.** *Challengerella bradyi*, oblique spiral side; **5.** *Elphidium advenum* subsp. *limbatum*, lateral view; **6.** *Elphidium fichtellianum*, lateral view; **7.** *Elphidium striatopunctatum*, lateral view; **8–9.** *Neorotalia calcar*, **8.** spiral side, **9.** umbilical side; **10–11.** *Hauerina diversa*, **10.** lateral view, **11.** enlargement of the apertural view, showing diatoms; **12.** *Peneroplis planatus*, lateral view; **13.** *Peneroplis pertusus*, lateral view; **14.** *Pseudomassilina* sp., lateral view; **15.** *Pseudoschlumbergerina ovata*, oblique lateral view, **16.** *Pseudotriloculina* sp. lateral view, **17–18.** *Sorites orbiculus*, **17.** lateral view, **18.** profile view; **19.** *Spiroloculina communis*, lateral view; **20.** *Spiroloculina* sp., lateral view; **21.** *Triloculina terquemiana*, oblique lateral view; **22.** *Triloculina trigonula*, oblique lateral view; **23.** *Textularia agglutinans*, lateral view. Scale bar: 7, 12, 17, 23 = 500 μm ; 10, 14–15, 21–22, 18 = 400 μm ; 3–4, 8, 13, 16, 19–20 = 300 μm ; 1–2, 5–6, 9 = 200 μm ; 11 = 50 μm .

“endozoochory,” is the most common seed dispersal mechanism in trees. Ichthyochory, dispersal by fish, plays a significant role in the dispersal of seeds of freshwater and riparian plants (Pollux 2011). Survival of fish gut passage has been shown in numerous freshwater zoobenthic groups, and has been suggested to mediate NIS introductions (Gatlin et al. 2013). In marine environments, little is known about the role of ichthyochory in species dispersal and introduction. The evidence presented here suggests that this vector has a major role in structuring marine benthic communities and may accelerate “invasional meltdown,” whereby a group of NIS facilitates one another’s establishment, spread and impacts (Simberloff and Von Holle 1999). Interestingly, the time lag between the discovery of the fish and the later discovery of the foraminifera was about 4–11 yr (Fig. 2; Supporting Information Table S2). While this could be a consequence of the invasion of foraminifera in multiple time-steps (Arim et al. 2006), it is more likely attributable to the relative ease of discovering and identifying exotic fish vs. the much more intensive effort required to detect and identify non-indigenous foraminifera.

Implications of ichthyochory as a bioinvasion and dispersal vector

The invasion and subsequent dominance of *A. lobifera* in the rocky shores of the Eastern Mediterranean Sea, suppressing the native inhabitants of these environments (Hyams-Kaphzan et al. 2008, 2014), combined a prime example of how species migration from the Red Sea is drastically and rapidly changing the biota of the native invaded communities. High turnover rates make foraminifera tests a dominant component of sands worldwide. *Amphistegina* can account for up to 90% of sand biomass in certain locations (McKee et al. 1959). In the Aegean Sea, *A. lobifera* predominates on the rocky reefs at formidable densities of 230–310 K individuals·m⁻² (Yokeş and Meriç 2009). This overgrowth not only outcompetes the native foraminifera species (Hyams-Kaphzan et al. 2008; Zenetos et al. 2012), but it also dramatically changes the rocky reef habitats. The thickness of the deposited tests at multiple locations along the Turkish coast has reached 60–80 cm (Yokeş and Meriç 2009), with a consequent “desertification” of the rocky reefs and a shift in the biodiversity from hard- to soft-bottom-dwelling species. Biodiversity shifts and potential losses are inevitable results of such a process.

Benthic foraminifera are commonly used as paleogeographical proxies for models reconstructing ancient environmental conditions, including temperature, oxygen, pH, nutrients, productivity, organic matter flux, and ocean circulation (Sen Gupta 1999; Lea 2006). These models often correlate distinctive species assemblages with specific paleoconditions, assuming limited connectivity of foraminiferal communities. The fish-mediated long distance dispersal of benthic foraminifera suggested by our study may alter the

underlying assumptions behind paleogeographical modeling, and motivate integrating this vector in future revised models.

In August 2015, the newly expanded Suez Canal was opened. This project is designed to double the shipping capacity of the canal, thereby intensifying the inflow of Lessepsian migrants into the Mediterranean (Galil et al. 2015). Furthermore, a now-warming Mediterranean Sea increases habitat suitability for both invasive fish (Vergés et al. 2014) and Indo-Pacific benthic foraminifera (Langer et al. 2012), further facilitating their westward propagation.

The light shed here upon the mystery of the mechanisms of benthic foraminifera invasion and their rapid spread throughout the Mediterranean illustrates the importance of understanding the intricacies of species interactions and their role in species invasion. The discovery of ichthyochory as a new trans-provincial ocean vector signals a critical shift in thinking on the dispersal of marine species. The ingestion and egestion of live prey by highly mobile predators in the sea—noting that both prey and predators may represent, in modern times, combinations of native and introduced species—portends to be as global a phenomenon as the dispersal of viable plant seeds by birds and mammals on land. We argue that retrospective studies will reveal that the spatially and temporally linked biogeography of predator–prey patterns that we suggest here may in fact have already been manifested but gone unnoticed in other regions of the world. Ichthyochory has profound implications for the interpretation and re-interpretation of modern and historical biogeography, ecology, and evolutionary biology of the world’s seas.

References

- Alve, E. 1999. Colonization of new habitats by benthic foraminifera: A review. *Earth Sci. Rev.* **46**: 167–185. doi:[10.1016/S0012-8252\(99\)00016-1](https://doi.org/10.1016/S0012-8252(99)00016-1)
- Alve, E., and S. T. Goldstein. 2010. Dispersal, survival and delayed growth of benthic foraminiferal propagules. *J. Sea Res.* **63**: 36–51. doi:[10.1016/j.seares.2009.09.003](https://doi.org/10.1016/j.seares.2009.09.003)
- Arim, M., S. R. Abades, P. E. Neill, M. Lima, and P. A. Marquet. 2006. Spread dynamics of invasive species. *Proc. Natl. Acad. Sci. USA* **103**: 374–378. doi:[10.1073/pnas.0504272102](https://doi.org/10.1073/pnas.0504272102)
- Ben-Tuvia, A. 1964. Two siganid fishes of Red Sea origin in the eastern Mediterranean. Ministry of Agriculture, Department of Fisheries, Sea Fisheries Research Station.
- Bernhard, J. M. 2000. Distinguishing live from dead foraminifera: Methods review and proper applications. *Micropaleontology* **46**: 38–46. <http://www.jstor.org/stable/1486179>
- Cohen, A. 2012. Aquatic invasive species vector risk assessments: Live saltwater bait and the introduction of non-native species into California. California Ocean Science Trust.

- Cózar, A., and others. 2014. Plastic debris in the open ocean. *Proc. Natl. Acad. Sci. USA* **111**: 10239–10244. doi:[10.1073/pnas.1314705111](https://doi.org/10.1073/pnas.1314705111)
- Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray.
- Debenay, J.-P., A. Sigura, and J.-L. Justine. 2011. Foraminifera in the diet of coral reef fish from the lagoon of New Caledonia: Predation, digestion, dispersion. *Rev. Micropaléontol.* **54**: 87–103. doi:[10.1016/j.revmic.2010.04.001](https://doi.org/10.1016/j.revmic.2010.04.001)
- Diamant, A. 2010. Red-Med immigration: A fish parasitology perspective, with special reference to the Myxosporea, p. 85–97. *In* D. Golani and B. Appelbaum-Golani [eds.], *Fish invasions of the Mediterranean Sea: Change and renewal*. Pensoft Publishers, Sofia-Moscow.
- Galil, B. S., and N. Hülsmann. 1997. Protist transport via ballast water—biological classification of ballast tanks by food web interactions. *Eur. J. Protistol.* **33**: 244–253. doi:[10.1016/S0932-4739\(97\)80002-8](https://doi.org/10.1016/S0932-4739(97)80002-8)
- Galil, B. S., and others. 2015. ‘Double trouble’: The expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. *Biol. Invasions* **17**: 973–976. doi:[10.1007/s10530-014-0778-y](https://doi.org/10.1007/s10530-014-0778-y)
- Gatlin, M. R., D. E. Shoup, and J. M. Long. 2013. Invasive zebra mussels (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) survive gut passage of migratory fish species: Implications for dispersal. *Biol. Invasions* **15**: 1195–1200. doi:[10.1007/s10530-012-0372-0](https://doi.org/10.1007/s10530-012-0372-0)
- Gollasch, S. 2002. The importance of ship hull fouling as a vector of species introductions into the North Sea. *Biofouling* **18**: 1051–1121. doi:[10.1080/08927010290011361](https://doi.org/10.1080/08927010290011361)
- Hyams-Kaphzan, O., A. Almogi-Labin, D. Sivan, and C. Benjamini. 2008. Benthic foraminifera assemblage change along the southeastern Mediterranean inner shelf due to fall-off of Nile-derived siliciclastics. *Neues Jahrb. Geol. Paläontol. Abh.* **248**: 315–344. doi:[10.1127/0077-7749/2008/0248-0315](https://doi.org/10.1127/0077-7749/2008/0248-0315)
- Hyams-Kaphzan, O., L. Perelis Grossowicz, and A. Almogi-Labin. 2014. Characteristics of benthic foraminifera inhabiting rocky reefs in northern Israeli Mediterranean shelf. *Isr. Geol. Surv., Rep. GSI/36/2014*.
- Kaunda-Arara, B., and G. A. Rose. 2004. Long-distance movements of coral reef fishes. *Coral Reefs* **23**: 410–412. doi:[10.1007/s00338-004-0409-7](https://doi.org/10.1007/s00338-004-0409-7)
- Kitazato, H. 1988. Locomotion of some benthic foraminifera in and on sediments. *J. Foraminiferal Res.* **18**: 344–349. doi:[10.2113/gsjfr.18.4.344](https://doi.org/10.2113/gsjfr.18.4.344)
- Langer, M. R., A. E. Weinmann, S. Lötters, and D. Rödder. 2012. “Strangers” in paradise: modeling the biogeographic range expansion of the foraminifera *Amphistegina* in the Mediterranean Sea. *The Journal of Foraminiferal Research* **42**: 234–244. doi:[10.2113/gsjfr.42.3.234](https://doi.org/10.2113/gsjfr.42.3.234)
- Lea, D. 2006. Elemental and isotopic proxies of past ocean temperatures, p. 365–390. *In* J. I. Drever Ed., *Treatise on geochemistry*, v. **6**, Elsevier.
- Lobel, P. S. 1981. Trophic biology of herbivorous reef fishes: Alimentary pH and digestive capabilities. *J. Fish Biol.* **19**: 365–397. doi:[10.1111/j.1095-8649.1981.tb05842.x](https://doi.org/10.1111/j.1095-8649.1981.tb05842.x)
- Lowry, E., E. J. Rollinson, A. J. Laybourn, T. E. Scott, M. E. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2013. Biological invasions: A field synopsis, systematic review, and database of the literature. *Ecol. Evol.* **3**: 182–196. doi:[10.1002/ece3.431](https://doi.org/10.1002/ece3.431)
- MacNeil, F. S. 1965. Evolution and distribution of the genus *Mya*, and Tertiary migrations of Mollusca, 51 pp. United States Geological Survey Professional Paper 483-G.
- McGann, M., D. Sloan, and A. N. Cohen. 2000. Invasion by a Japanese marine microorganism in western North America. *Hydrobiologia* **421**: 25–30. doi:[10.1023/A:1003808517945](https://doi.org/10.1023/A:1003808517945)
- Mckee, E. D., J. Chronic, and E. B. Leopold. 1959. Sedimentary belts in lagoon of Kapingamarangi Atoll. *AAPG Bull.* **43**: 501–562.
- Meriç, E., and others. 2016. Did *Amphistegina lobifera* Larsen reach the Mediterranean via the Suez Canal? *Quat. Int.* **401**: 91–98. doi:[10.1016/j.quaint.2015.08.088](https://doi.org/10.1016/j.quaint.2015.08.088)
- Murray, J. W. 2006. Ecology and applications of benthic foraminifera. Cambridge Univ. Press.
- Nesbitt, E. A. 2005. A novel trophic relationship between cassid gastropods and mysticete whale carcasses. *Lethaia* **38**: 17–25. doi:[10.1080/00241160510013132](https://doi.org/10.1080/00241160510013132)
- Pollux, B. 2011. The experimental study of seed dispersal by fish (ichthyochory). *Freshw. Biol.* **56**: 197–212. doi:[10.1111/j.1365-2427.2010.02493.x](https://doi.org/10.1111/j.1365-2427.2010.02493.x)
- Por, F. D. 1978. Lessepsian migration: The influx of Red Sea biota into the Mediterranean by way of the Suez Canal. Springer.
- Reiss, Z. 1961. Recent foraminifera from the Mediterranean and the Red Sea coasts of Israel. *Bull. Geol. Survey Israel* **32**: 27–28.
- Robinson, A. R., and others. 1992. General circulation of the Eastern Mediterranean. *Earth Sci. Rev.* **32**: 285–309. doi:[10.1016/0012-8252\(92\)90002-B](https://doi.org/10.1016/0012-8252(92)90002-B)
- Ruiz, G., and J. Carlton. 2003. Invasive species: Vectors and management strategies. Island Press.
- Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. *Proc. Natl. Acad. Sci. USA* **100**: 2474–2477. doi:[10.1073/pnas.0437913100](https://doi.org/10.1073/pnas.0437913100)
- Sen Gupta, B. K. 1999. Modern foraminifera. Kluwer Academic Publishers.
- Simberloff, D. 2001. Biological invasions—how are they affecting us, and what can we do about them? *West. N. Am. Nat.* 308–315. http://scholarsarchive.byu.edu/wnan/vol61/iss3/7?utm_source=scholarsarchive.byu.edu%2Fwnan%2Fvol61%2Fiss3%2F7&utm_medium=PDF&utm_campaign=PDFCoverPages
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: Invasional meltdown? *Biol. Invasions* **1**: 21–32. doi:[10.1023/A:1010086329619](https://doi.org/10.1023/A:1010086329619)
- Steinitz, W. 1927. Beiträge zur Kenntnis der Küstenfauna Palästinas, p. 311–353. *In* U. Hoepli Ed., *Publicazioni della Stazione Zoologica di Napoli*, v. **8**.

- Travis, J. L., and S. S. Bowser. 1991. The motility of foraminifera, p. 91–155. *In* J.J. Lee, and O. R. Anderson Ed., *Biology of Foraminifera*. Academic Press.
- Vergés, A., and others. 2014. The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proc. R. Soc. Lond. B Biol. Sci.* **281**: 20140846. doi:[10.1098/rspb.2014.0846](https://doi.org/10.1098/rspb.2014.0846)
- Weinmann, A. E., D. Rödder, S. Lötters, and M. R. Langer. 2013. Traveling through time: The past, present and future biogeographic range of the invasive foraminifera *Amphistegina* spp. in the Mediterranean Sea. *Mar. Micropaleontol.* **105**: 30–39. doi:[10.1016/j.marmicro.2013.10.002](https://doi.org/10.1016/j.marmicro.2013.10.002)
- Wilson, R., F. J. Millero, J. R. Taylor, P. J. Walsh, V. Christensen, S. Jennings, and M. Grosell. 2009. Contribution of fish to the marine inorganic carbon cycle. *Science* **323**: 359–362. doi:[10.1126/science.1157972](https://doi.org/10.1126/science.1157972)
- Winston, J. E. 2012. Dispersal in marine organisms without a pelagic larval phase. *Integr. Comp. Biol.* **52**: 447–457. doi:[10.1093/icb/ics040](https://doi.org/10.1093/icb/ics040)
- Yokeş, M. B., and E. Meriç. 2009. Drowning in sand: Invasion by foraminifera. *In* C. P. Wilcox and R. B. Turpin [eds.], *Invasive species: Detection, impact and control*. Nova Science Publishers.
- Zenetos, A., and others. 2012. Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union’s Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterr. Mar. Sci.* **13**: 328–352. doi:[10.12681/mms.327](https://doi.org/10.12681/mms.327)

Acknowledgments

We thank Gil Rilov for the use of the research facilities in IOLR, Haifa, Dani Golani for access to fish specimens in the National History Collections of the Hebrew University of Jerusalem, Dan Tchernov for the use of microsensors, Jacob Silverman, Jonathan Erez, Arik Diamant, Gil Rilov, Martin Wahl, Dor Edelist, Eyal Rahav and Yair Achituv for providing insights on the study and valuable comments on the manuscript, Chana Netzer-Cohen for aid in processing the adapted map, Michael Kitin and Raanan Bodzin for technical aid and for acquiring the SEM images. We would also like to thank Isabelle Côté and the anonymous reviewer for their highly constructive review of the manuscript. We dedicate this paper to the memory of Dr. Nechama Ben-Eliyahu (1935-2014), marine biologist, invertebrate zoologist, and a pioneer in Lessepsian migration research.

Submitted 23 November 2016

Revised 21 February 2017

Accepted 27 March 2017