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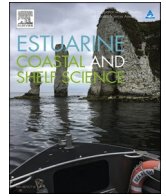
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New evidence of *Melithaea erythraea* colonization in the Mediterranean

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ABSTRACT

The Indo-Pacific gorgonian coral *Melithaea erythraea* (Melithaeidae, previously *Acabaria*) was first recorded in the Mediterranean in 1999 in the harbor of the Hadera power station, Israel. This species is the only octocoral known to have invaded the Mediterranean Sea. In the past two decades, it has demonstrated a stable population in this harbor, and never found outside this location, not even on the adjacent natural rocky reefs. Then, during 2015, several specimens of *M. erythraea* were found on a natural substrate at Nahsholim, Israel, about 23 km north of the power station. This is the first evidence of this coral's existence beyond the power plant harbor. The number of colonies there suggests that the population is sustainable, but further study is needed. Although no genetic differences were found among specimens from Nahsholim, Hadera, and the Red Sea, their bacterial epibiota has undergone change following migration. The carbon source and trophic position are similar between the Red Sea and the Mediterranean, suggesting that there is no nutritional barrier to migration for the coral. The larval connectivity model supports the hypothesis that the planulae that have settled in Nahsholim originated from the Port of Hadera, although other arrival scenarios are also possible. The spread of this species suggests that the eastern Mediterranean is becoming increasingly suitable for migrating corals, joining the many other Indo-Pacific migrants that have already established populations there.

1. Introduction

Lessepsian migration (Por 1978) refers to the migration of marine species via the Suez Canal (opened in 1869), usually from the Red Sea to the Mediterranean, and introducing Indo-Pacific into the Mediterranean Sea. The eastern Mediterranean Sea (Levant Basin) is continuously invaded by alien species from the Red Sea (Indo-Pacific distribution) and over 500 alien species have been recorded to date (Galil 2007; Por 2012; Galil et al., 2014). Many of these introduced species have established thriving reproductive communities (reviewed in Zibrowius 1992; Coll et al., 2010; Zenetos et al., 2010), such as the nudibranch *Goniobranchus annulatus*, the ascidian *Herdmania mums*, the crab *Portunus segnis*, and the finfish *Stephanolepis diaspros*. However, only one Indo-Pacific scleractinian coral, *Oulastrea crispata*, known to be a very cold-resistant (Lam 2000), has been observed to have introduced to the temperate waters of the Mediterranean (West Mediterranean records, Hoeksema and Ocaña Vicente, 2014; Mariani et al., 2018).

The octocoral *Acabaria erythraea* Ehrenberg 1834, currently classified as *Melithaea erythraea* (see Reijnen et al., 2014), is indigenous to the

Indian Ocean and is common along the East-African coast and in the Red Sea. The first occurrence of this species in the Mediterranean was noted in 1999 in the harbor of the power station at Hadera (32.47 °N, 34.88 °E) (Fine et al., 2005). In the Red Sea, it is rare both on natural reefs and artificial structures and found mostly in shaded habitats and on vertical reef walls. In the Hadera power plant harbor it features extremely high numbers and is most abundant on artificial structures (Fine et al., 2005). To date, no other colonies of *M. erythraea* have been reported along the surveyed Mediterranean coast, including on the surrounding natural sandstone reefs located only 200 m north of the harbor (Fine et al., 2005). Fine et al. (2005) discussed the hydrographical conditions of the harbor and the power plant cooling system turbines, which create a "larvae trap" preventing *M. erythraea* planulae from leaving the harbor.

During September 2015, a colony of *M. erythraea* was found in the rocky bay of Nahsholim (32.61 °N, 34.91 °E), at a depth of 3.5 m, inverted beneath a crevice (see Figs. 1 and 2). Further observations revealed a stable population comprising many colonies, all in shaded locations on either vertical walls or in crevices.

Fine et al. (2005) contended that *M. erythraea*'s arrival at the power

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Fig. 1. Colony of *Melithaea erythraea* in Nahsholim bay, 19 September 2015. Photo: M. Grossowicz.

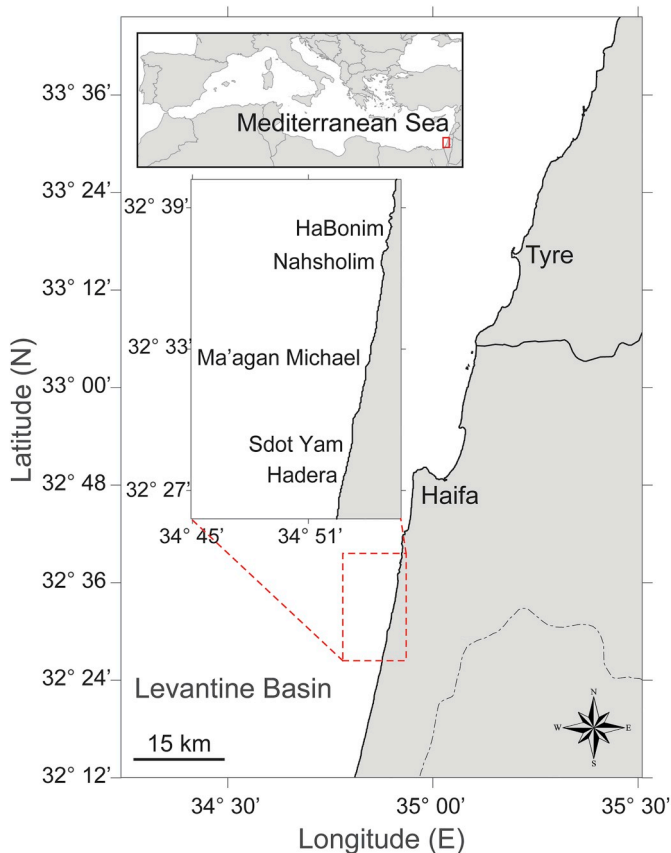


Fig. 2. Map of the northern Israeli coast of the Mediterranean, showing the relative locations of Hadera and Nahsholim.

plant harbor had probably occurred as planulae released from the ballast water of a ship docking there. Several hypotheses have been posited for *M. erythraea*'s colonization of the Nahsholim rocky bay: (1) planulae reached the bay from Hadera, e.g., when the power plant cooling system was temporarily shut down; (2) the vacuum-removed sand from the bottom of the port's harbor, discharged in front of Ma'agan Michael, may have contained planulae; and (3), an additional unrelated arrival took place of planulae from the Red Sea via ballast water (Galil 2007) or another human-mediated transfer.

The introduction of species into new environments that are not within their home range is recorded in almost every ecosystem (Vitousek

et al., 1997). However, when an introduced species becomes invasive, this has both ecological and financial consequences (Pimental et al., 2000). Furthermore, an invader may possess microbial pathogens or mutualists that can affect its survival and the establishment of a successful population with the potential to infect local communities. However, it is still not clear whether the co-invasion of a host and its microbiota does indeed occur (Roterman et al., 2015). Although not invasive so far, the population expansion of *M. erythraea* may yet occur (Crooks and Soulé 1999; Rilov et al., 2004). Understanding the expansion of alien species, especially that of corals, in the Levant in general and along the Israeli coast in particular (the nearest coast downstream to the Suez Canal opening), is important in order to understand the ecological impacts on the local biodiversity and community structure, during a time of global changes and bioinvasions. It is especially important to determine their diet and their ecological behavior. Here, we explore *M. erythraea*'s spread along the East-Mediterranean coast through observations, genetic analysis, bacterial epibiota composition, trophic level, and carbon source analyses, and larval connectivity modeling, and question its invasiveness potential. We hypothesize that the survival of this octocoral in the temperate waters of the Mediterranean is due to beneficial changes in temperature regime, lack of competition with algae, and absence of a nutritional barrier; while the slow spread of the coral may be due to a lag in observed population expansion caused by an integrated effect of environmental and genetic changes (Crooks and Soulé 1999).

2. Material and methods

This study of the population dynamics of *M. erythraea* employed several ecological methodologies: density surveys, genetic analysis, bacterial epibiota composition, trophic level, and carbon source stable-isotope analysis, and larval dispersal modeling.

2.1. Study sites and distribution of *M. erythraea*

As the coral was found on a natural rocky sub-tidal reef in Nahsholim bay (see Fig. 2) and colony density was surveyed. Preliminary observation revealed a relatively lower density compared to that reported by Fine et al. (2005), and most of the observed colonies were found aligned in a particular crevice, thwarting the traditional 'line'-transect as performed by Fine et al. (2005). Consequently, the area in which the population was found, at depths of 2–4 m, was measured using a measuring tape, a '10-min-search' transect was conducted, and the height of each colony was measured with a ruler.

To compare our findings with those from 1999 (following the work by Fine et al., 2005), a search for colonies of this species in the port of Hadera port was performed. To explore dispersal along the Mediterranean shores of Israel we carried out general observational surveys, searching in optimal locations such as rocky bays at shallow depths and under similar conditions to those in Nahsholim. Our dispersal model findings (see Modeling subsection) revealed a potential coral presence as follows: at Pigeons Island in front of Ma'agan Michael, HaBonim Nature Reserve, Sdot-Yam, and Nusani Island near Sdot-Yam (Fig. 2).

2.2. Specimen collection for genetic, bacterial epibiota, and stable-isotope analyses

Specimens for laboratory analyses were collected during the surveys. A branch was removed from a selected colony using scissors and placed in absolute ethanol prior to examination. In Nahsholim bay, specimens were collected in November 2015, June 2016, and May 2017, and a specimen from the survey in Hadera port was collected in June 2016. Finally, a specimen from Fine et al. (2005) study (collected by Y. Aluma in 2002 and stored in the Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, Tel Aviv, Israel), was also examined. For comparison with native populations in the Red Sea,

specimens were collected from the Kisosky pier in Eilat in May 2017. *Melithaea biserialis* was also collected in Eilat (it has never been recorded in the Mediterranean) for concomitant genus comparison.

2.3. Population genetic analysis

Three specimens were analyzed: from Nahsholim bay, Hadera port, and the 2002 specimen from Fine et al. (2005) study. Total genomic DNA was extracted from each preserved specimen using the Wizard SV Genomic DNA Purification System kit (Promega) according to the manufacturer's instructions. The partial sequence of the mitochondrial cytochrome c oxidase I (COI) gene was amplified using the Folmer primers (Folmer et al., 1994). Nuclear ribosomal 28S rDNA gene was amplified using a primer pair Acabaria28SR, TTTCCGCTGGCTTACCCTATTCAGGC and Acabaria28SF, TTGAAAGGAAGCGAATGGAGTTAGC, NADH dehydrogenase subunit 2 (ND2) with the primer pair AcabariaNADHR, TTGCTTCTTTATTA-TATTTTACTAC, and AcabariaNADHF, GGCTAATAA-TATGGCCCTATCATGGC, and Acabaria-mtMutS with the primer pair msh-2761F, TATGAACTTTGGCATGAGCC and msh-3270R, TGCCCAAATTACTATTTCTCTAATACG (Reijnen et al., 2014). PCR products were purified using Wizard SV Gel and PCR Clean-Up System (Promega). The sequencing was performed by HyLabs (Israel). The sequences were submitted to GeneBank with accession numbers MH325079 to MH325094.

2.4. Bacterial epibiota abundance

Six specimens of *M. erythraea*, one from Hadera port (hereafter Ha), two from Nahsholim (hereafter Na 16 and Na 17), and three from Eilat (hereafter Ei S1-3), and one of *M. biserialis* were analyzed using next-generation 16S. Total genomic DNA was extracted from the corals using the DNeasy PowerSoil Kit (Qiagen) according to the manufacturer's instructions. The template DNA was amplified using GoTaq Green Master Mix (Promega) with T100 thermal cycler (Bio-Rad). Partial sequence of the 16S genes were amplified using the following primers:

CS1_515F: **ACACTGACGACATGGTTCTA-CAGTGCCAGCMGCCGCGGTAA**, and CS2_806R: **TACGGTAGCAGAGACTTGGTCTGGACTACHVGGGTWCTAAT** for the former (Caporaso et al., 2012). Illumina Tags are in bold text. PCR products were sent to Hylabs laboratories for Next-generation sequencing. Samples were checked by Qubit and TapeStation, and were loaded on the Illumina Miseq, using the V2-500 cycle kit, sequenced for 2×250 cycles, generating paired-end reads.

2.5. Stable isotope analysis

Understanding the trophic interactions of a coral with its environment enables us to understand its establishment in a new habitat. We, therefore, compared the carbon source and trophic level between corals found in the Red Sea and in the Mediterranean with a compound-specific stable-isotope (SI) analysis of carbon (C) and nitrogen (N) in amino acids. The ethanol-preserved samples were dried overnight in the oven at 60 °C prior to hydrolyzation. Approximately 70 mg of each coral (tissue + skeleton) was acid hydrolyzed in 1 ml of 6 mol L⁻¹ HCl at 150 °C for 75 min (Cowie and Hedges 1992) under nitrogen atmosphere inside a 4 ml glass vial with PTFE cap. Samples were cooled to room temperature and then filtered through a 0.22 µm PTFE filter to remove all undissolved particles. HCl was evaporated under a gentle stream of nitrogen. Acid hydrolyzes sampled were derivatized using EZfaast amino acid analysis kit (Phenomenex) with slight modification, using dichloromethane in place of reagent 6 of the kit. For carbon analysis we injected 1.5 µl in split mode (1:15) at 250 °C and for Nitrogen we injected 2 µl in split mode (1:5) at 250 °C. The amino acids were separated on a Zebron ZB-50 column (25 m, 0.25 mm, and 0.25 µm) in

Thermo Scientific Trace 1300 GC. Gas chromatography (GC) conditions were set to optimized peak separation for the desired amino acids as follows: Initial temperature 110 °C ramped to 240 °C at 8 °C per min and then ramped to 320 °C at 20 °C per min and held for 2.5 min. Helium was used as a carrier gas with flow set to 1.5 ml min⁻¹. The separated amino acids were split into two direction flows: one toward Thermo Scientific ISQ quadruple for amino acid identification and the second toward Thermo Scientific Delta V advantage for C and N isotope analysis. The ISQ conditions were set to: transfer line 310 °C ion source 240 °C and scanned range 43–450 mass range. To define the isotopic ratio of carbon and nitrogen the separated amino acids were combusted in a Thermo scientific GC isolink II at 1000 °C for CO₂ and N₂. For N₂ analysis sample was subjected to a liquid nitrogen cold trap to freeze down all other gases, before entering to Delta V advantage (Thermo Scientific). From each sample duplicates were injected for carbon and triplicates for nitrogen.

Stable isotope ratios were expressed in standard δ notation, where the standard for carbon was Vienna PeeDee Bel-lemnite (VPDB) and for atmospheric nitrogen N₂ (Air). To account for the carbons incorporated during the derivatization process we found the correction factor for each amino acid using the equation: $n_{CD}\delta^{13}C_{CD} = n_C\delta^{13}C_C + n_D\delta^{13}C_{Dcorr}$, where n is the number of moles of carbon, C_C the compound of interest (amino acids), C_{CD} the derivatized compound, and C_{Dcorr} the empirically determined correction factor (Docherty et al., 2001). We used a standard containing our seven desired amino acids with a known isotopic ratio (Alanine, Valine, Leucine, Isoleucine, Methionine, Glutamic acid, and Phenylalanine) to set C_{Dcorr} for later calculation of the isotopic ratio of our sample. Since nitrogen was not added in the process of derivatization, corrections for nitrogen addition were not required. To confirm the reproducibility of the nitrogen isotope measurements the same standard mixtures of seven amino acids were used with an isotopic range for the nitrogen of -6.69 to +43.25‰. The standard of amino acids was injected 3 times for carbon and 3 times for nitrogen following oxidation of the reactor, and again after 18 sample injections.

2.6. Larval distribution modeling

Lagrangian particle tracking has become an important tool in the study of the ocean and encompasses many applications, including the determination of larval dispersion and population connectivity (Batchelder 2006; Paris et al., 2007; Lett et al., 2008; Velo-Suarez et al., 2010). A larval dispersal model was formulated using a Lagrangian algorithm model performed with MatLab tool-box 'PaTATO' (Fredj et al., 2016), in which particles representing larvae were treated as passive and devoid of inertia. The 2D velocity field utilized by the Lagrangian simulation was taken from the south-east Levantine Israeli Prediction System (SELIPS) forecast (Goldman et al., 2015). SELIPS is a forecasting system developed and operated by the Israel Oceanographic and Limnological Research Institute (IOLR), with a resolution set to $0.01^\circ \times 0.00833^\circ$, and depicts the water depth from the surface to 10 m depth. Eighty-six particles representing virtual planulae were followed from the settlement area in Nahsholim using back-trajectory analysis, i.e., tracking the origin of the planulae. The trajectories of the virtual planulae were followed for 10 d, representing the period of *M. erythraea* planula settlement (Fine et al., 2005). The simulation started on 1st August (0000 h), going back to 22nd July 2013, the full-moon period when *M. erythraea* is reported to release planulae (Fine et al., 2005). A first-order stochastic diffusivity of $K = 2 \text{ m}^2 \text{ s}^{-1}$ was incorporated in the trajectory calculation to represent sub-grid processes that are not resolved by observational systems or by numerical models. K was based on Okubo (1971), for a grid size of ~ 0 (1 km).

2.7. Uni- and multivariate analysis

A comparison of trophic position (TP) between the Mediterranean and the Red Sea was performed with Mann-Whitney U -test (small

number of samples). Principal Components Analysis (PCA) is a data analysis tool frequently used to reduce the dimensionality (or number of variables) from a large number of interrelated variables, while retaining as much of the information as possible (Ter Braak 1986). We implemented this analysis for two data-sets: the bacterial epibiota and carbon source results. For the bacterial epibiota, the OTU's given as fractions were arcsine-square-root transformed and then grouped by habitat. The carbon source data (amino acids $\delta^{13}\text{C}$ composition) were compared according to habitat, along with those from other organisms such as jellyfish (from both the Red Sea and Mediterranean), different Holothuroidea member family, zooplankton, and algae (all from the Mediterranean, data from S. Martinez, unpublished). PCAs were followed by PerMANOVA permutation multivariate test for statistical significance, with 1×10^4 permutations. All values are presented at a confidence interval of 95%. *U*-test, PCA analyses, and PerMANOVA were performed with R i386 3.3.3 using Vegan and lmpm packages.

3. Results

3.1. Distribution

The first observation of *M. erythraea* in Nahsholim was in September 2015. Colonies were found in one crevice, 16 m in length, and on several small crevices on rocks in front of the long one. The entire occupied area was 6 m wide. In a '10-min-search'-transect 18 colonies were counted, with an average colony height of 3.029 ± 1.538 cm. Colonies were observed at this site throughout the year. In a survey in the Hadera port only four colonies were found, due to site restrictions on a broader search that may have prevented finding more colonies. The number in Hadera port was much lower than that previously reported by Fine et al. (2005). In the adjacent HaBonim Nature Reserve park in February 2016, in Sdot-Yam and Nusani Island near Sdot-Yam in November 2017, no colonies were found. A photograph taken in 2014 by an underwater photographer at Pigeons Island in front of Ma'agan Michael suggested the presence of colonies there. In our surveys in October 2016 and July 2017, no colonies were found.

3.2. Population genetics and bacterial abundance analysis

The molecular analysis clearly presents 100% similarity in all examined gene (COI, 28S, NADH, mtMutS) sequencing among all the Mediterranean specimens and with the Red Sea one.

PCA multivariate analysis ordination of the bacterial composition of each coral specimen categorized according to its location indicates that

corals found in Eilat present a different bacterial composition to that of the Mediterranean ones (PerMANOVA, pseudo $F = 3.22$, p -value = 0.018). The bacterial composition of *M. erythraea* in Hadera and Nahsholim is similar, while differing from that of *M. biserialis* (Fig. 3). The most dominant bacteria in the Mediterranean samples were Cyanobacteria (order Stramenopiles), while for the Red Sea samples were Bacteroidetes (order Cytophagales). The latter group was not found at all in the Mediterranean specimens but was present in a small percentage in *M. biserialis*. Stramenopiles were present at both sites, but in greater number in the Mediterranean. Members of the Proteobacteria (order Rhodobacterales) were present at both sites in similar numbers (details of the bacterial composition are provided in the Supp. Info.).

3.3. Trophic level and carbon source

Fig. 4 presents the $\delta^{13}\text{C}$ variation of the amino acid content in the discussed corals, as well as for several other organisms: jellyfish (predators from the same phylum, Cnidaria), detritivores (sea cucumbers, class Holothuroidea), zooplankton (mostly herbivores), and some algae (primary producers). The results indicate that there is no significant difference in carbon source between the corals from Eilat and those from the Mediterranean (PerMANOVA, pseudo $F = 1.68$, p -value = 0.26); and that there is some similarity to the findings for jellyfish, cnidarian predators. However, the *M. biserialis* specimen differs in carbon source to *M. erythraea* and the jellyfish group. The detritivores are grouped separately, with no observable pattern among the different algae and zooplankton, which all differ from the coral and jellyfish groups. Differences among specimens are due to methionine, valine, and leucine amino acid $\delta^{13}\text{C}$ content.

Table 1 presents the TPs of the different specimens. Variation in $\delta^{15}\text{N}$ among specimens from Eilat and the Mediterranean is similar, with a slightly higher average of specimens from Eilat (2.86 ± 0.29 , mean \pm SD) relative to those from the Mediterranean (Nahsholim and Hadera, 2.61 ± 0.51 , mean \pm SD) (Mann-Whitney *U*-test, $W = 2$, p -value = 0.8), where both are lower than, albeit similar to, that of the jellyfish (both corals and jellyfish are considered as predators). TP of *M. erythraea* from all sites was similar to that of *M. biserialis*; however, due to technical limitations, we only have one repeat from each amino acid of *M. biserialis*, and more samples are thus needed in order to verify the isotopic range of this species.

3.4. Larval connectivity simulation

The *in-silico* simulation traced a 10-days route that the virtual passive

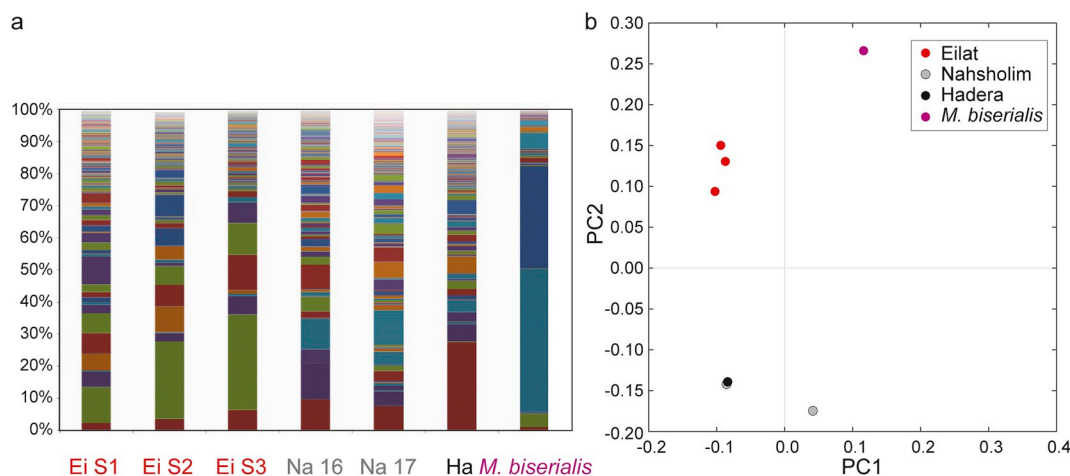


Fig. 3. 16S OTU bacterial epibiota composition. a – bacterial composition for each specimen. Ei S# - Eilat Specimen #, Na 16 – Nahsholim 2016 specimen, Na 17 – Nahsholim 2017 specimen, Ha – Hadera port specimen, *M. biserialis* – specimen of *Melithaea biserialis* from Eilat. The bacteria species composition is detailed in the Supp. Info. b – PCA multivariate analysis ordination of the bacterial composition categorized according to location of the coral habitat.

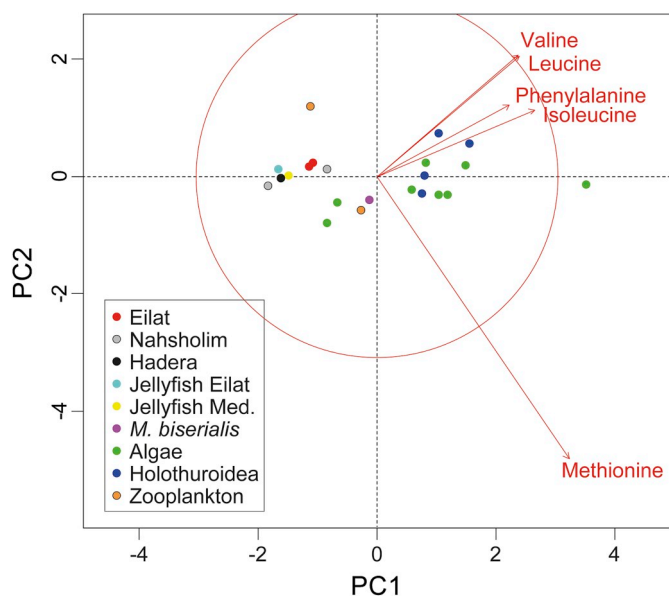


Fig. 4. PCA ordination of $\delta^{13}C$ variation of the amino acid content. The corals and jellyfish are clustered together, while *M. biserialis* is separated from this group.

Table 1

Trophic position (TP) of coral specimens calculated according to glutamic and phenylalanine amino acid $\delta^{15}N$.

Sample ID	Species	TP
Eilat S1	<i>M. erythraea</i>	3.07
Eilat S2	<i>M. erythraea</i>	2.65
Nahsholim (2017)	<i>M. erythraea</i>	2.47
Nahsholim (2016)	<i>M. erythraea</i>	3.19
Hadera (2016)	<i>M. erythraea</i>	2.19
Jellyfish Eilat	<i>Aurelia aurita</i>	3.71
Jellyfish Mediterranean	<i>Rhopilema nomadica</i>	3.57
EAPC	<i>M. biserialis</i>	2.96

particles representing planulae may have traversed before settling at the study site in Nahsholim bay. The number of days of the simulation matched those of a possible spawning event of this coral (Fine et al., 2005). The findings from the simulation suggest that the planulae may have arrived from the port, as in some parts of the simulation particles, resembling planulae, appeared to exit from the port itself (see Fig. 5).

4. Discussion

The findings from this study present evidence of expanding the colonization of an Indo-Pacific coral in the easternmost part of the Mediterranean. Initial evidence of colonization was recorded by Fine et al. (2005) inside a port, where colonies were found on an artificial substrate. The observed colonies we report here for the first time were found outside the shelter of the port, on a natural substrate in a relatively undisturbed environment.

The eastern Mediterranean is highly susceptible to the biological invasions that resulted from the opening of the Suez Canal in 1869, which enabled the entry of Indo-Pacific biota via ballast water and ship fouling (Galil and Zenetos 2002). Galil and Zenetos (2002) claim that corals were not considered to have invaded the Mediterranean, since scleractinian corals are not ordinarily considered members of ship fouling communities. However, in different areas than the Mediterranean, scleractinian are known to be transported on oil-platforms (Friedlander et al., 2014; Page et al., 2006; Wanless et al., 2010; Yeo et al., 2010), and as rafting animals on flotsam, like metal gas tanks (Hoeksema et al., 2012) and plastic debris (Hoeksema et al., 2018). Nevertheless, tropical coral invasion into the temperate waters of the Mediterranean is considered to be unlikely due to this sea's wide temperature range (low temperature in winter and very high in summer), which are not suitable for hermatypic corals (Veron, 1995). To date, only two indication of an Indo-Pacific scleractinian (*Oulastrea crispata*) having invaded the (western) Mediterranean has been reported (Hoeksema and Ocaña Vicente, 2014; Mariani et al., 2018), along with one report of an octocoral (Fine et al., 2005).

The invasive octocorals *Sansibia* sp. and *Clavularia* sp., of Indo-Pacific origin, have been found in the tropical waters of the Brazilian Atlantic (Mantelatto et al., 2018); however, water temperature ranges in these

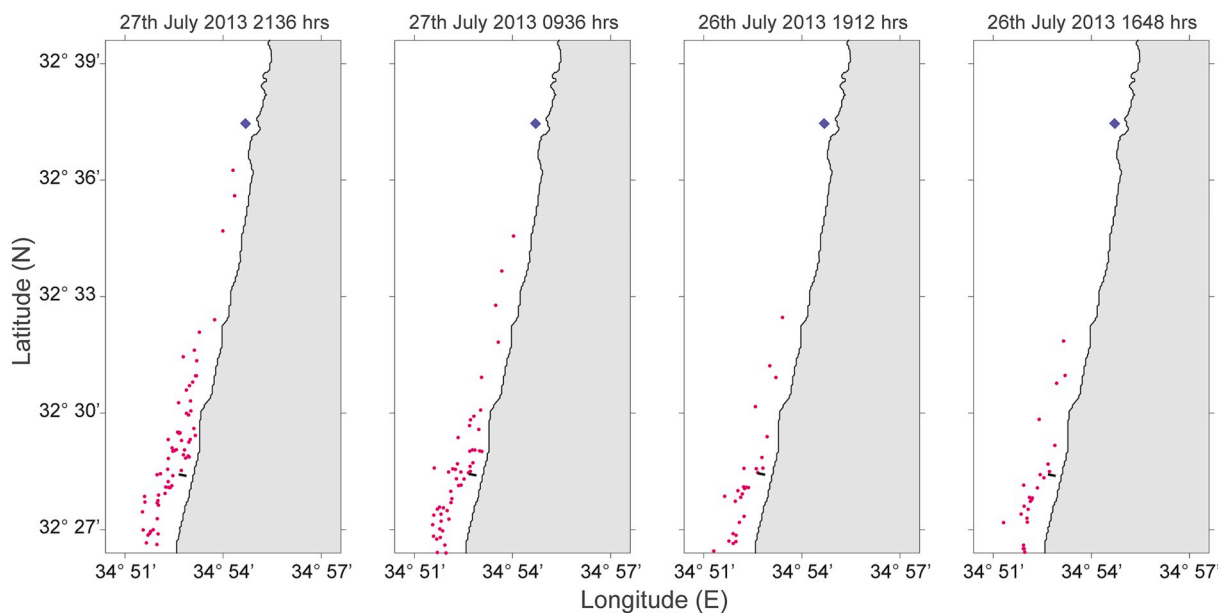


Fig. 5. Back-trajectory analysis suggests that the origin of the planulae settled in Nahsholim could be the Hadera port. The port's exit (northwards) is marked with a black line; the settlement site in Nahsholim with a blue diamond; and the virtual planulae in pink. The different panels represent different times from the beginning of the simulation, in which some simulated planulae seem to exit from the port. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

two oceans are similar and there is no temperature barrier to these species establishing successful populations. In recent years all the oceans, and the Mediterranean Sea in particular, have been experiencing a global sea-surface temperature (SST) increase (Takahashi et al., 2002; Occhipinti-Ambrogi 2007). A temperature time series from the offshore waters of Israel reveals an increase in SST of about 3 °C over the last three decades (Gertman et al., 2013). As global changes, such as a rise in temperature, affect biodiversity and species composition and facilitate bioinvasions (Hughes 2000), it is suggested that ocean warming has enabled the expansion range of tropical corals into the Mediterranean (Stachowicz et al., 2002; Por, 2009). Conditions favoring reef corals such as oligotrophy (Berman et al., 1984), reflected in clear water, and stable warm temperatures higher than 18 °C (Gertman et al., 2013), are becoming more common in the Levant basin. This trend of changing conditions is expected to continue, as predicted by several models (Stocker et al., 2013), alongside the oligotrophication processes caused by the construction of the Aswan Dam in the late 1960s, the major nutrient contribution to this area (Nixon 2003). Here, the evidence of the prolonged survival and expansion of an alien coral suggests that the current SST of the eastern Mediterranean no longer constitutes a barrier to tropical corals, at least for ahermatypic ones.

The competition that takes place between alien and native species (Davis 2003; Miranda et al., 2016) can result in a sudden change in reduced abundance of the latter (Galil and Zenetos 2002). Such competitive displacement could also be the reason for the establishment of the non-native *M. erythraea*. In a coral-reef environment, corals and macroalgae compete for a free substrate. Coma et al. (2011) suggested that coral invasion can be supported when macroalgae grazers are abundant, making the substrate available for coral recruitment. In the latter study, the grazer was the sea urchin *Paracentrotus lividus*, which had become the most abundant invertebrate in the shallow waters of a marine reserve on the Mediterranean coast of Spain. Coma et al. (2011) findings are supported by Serrano et al. (2012), who reported a phase shift from macroalgal to coral (the previously considered non-Lessepsian scleractinian *Oculina patagonica*) dominance in the western Mediterranean. Along the Israeli coast, the sea urchin *P. lividus* shows an opposite trend, with its population having collapsed, and today it is an extremely rare species (Yeruham et al., 2015). Two invasive herbivore fish in this area (the rabbitfish *Siganus rivulatus* and *S. luridus*) owe their successful establishment to the almost zero presence of other herbivores (Lundberg and Golani 1995), and they are contributing to the continuing depletion of the native canopy (Sala et al., 2011). Although this depletion may not directly contribute to coral recruitment, since this coral inhabits crevices and shaded niches where algae rarely grow, general changes in the environment, such as native canopy depletion, may cause a shift in competitors, including those organisms that compete for this coral's niche.

Some alien species affect the local fauna by acting as host for native associated fauna (Hoeksema and Ten Hove, 2017). If the alien species outcompetes a native species, presence or absence of epifauna may affect the local fauna even more. *M. erythraea* found in the Red Sea possess associated wing-oysters (*Pteria* sp.), however, these oysters were not observed on any Mediterranean specimen, as well as no other associated native bivalve. Different kind of epibiota is the microbial one. A comparison of the bacterial epibiota composition between the Mediterranean and the Red Sea specimens revealed that the epibiota has undergone change following migration. Similar changes in their microbiota were reported for the Lessepsian bivalves *Chama pacifica* (Zurel et al., 2011) and *Spondylus spinosus* (Roterman et al., 2015) when compared with specimens collected in their native environment of the Red Sea. Roterman et al. (2015) suggested that either only part of the microbiota had co-invaded together with their host into the Mediterranean Sea, or that there are species-specific selective constraints on microbial composition. In the present study, representatives of the two orders Stramenopiles and Rhodobacterales were present at both sites, in different numbers for Stramenopiles and in a similar number for

Rhodobacterales. However, the dominant order Cytophagales was found only in the Red Sea and not in the Mediterranean, supporting Roterman et al. (2015) hypothesis. Regarding the trophic aspects, no clear difference in both trophic position and carbon source of the isotope was revealed in the analyses between corals from the Red Sea and the Mediterranean. This carbon source similarity suggests that there is no trophic barrier to this coral to prevent its migration, as its food source is similar in both seas. The differences between the two *Melithaea* species' food carbon source can be explained by different diet compositions (Grossowicz and Benayahu 2012): *M. biserialis* is probably feeds on passive suspension particles (Zeevi-Ben Yosef and Benayahu 1999); while similarity of *M. erythraea* $\delta^{13}C$ to that of the jellyfish suggests that they probably feed on similar prey. Although there is no published study on *M. erythraea* diet composition, the Mediterranean jellyfish *Rhopilema nomadica* feeds on particles as small as, or smaller than, invertebrate larvae (Kuplik 2017).

Unlike many successful Lessepsian migrants, *M. erythraea* has not shown a dispersal among the rocky habitats along the Mediterranean shoreline, and has not been recorded in any of the surveys performed by the LTER program of the Morris Kahn Marine Research Station (<http://med-lter.haifa.ac.il/>) along the Israeli coastline at depths from 8 to 45 m. Its invasiveness characteristics are thus arguable, since only one stable population has been found to date outside the port. Nevertheless, whereas some alien species exhibit a rapid population growth rate, others appear to display a lag between initial introduction and population explosion (Rilov et al., 2004). Therefore, the presence of a stable population in Nahsholim bay may signify the first foot in the doorstep prior to its later spread along the south-eastern coast, as has been observed in many migrant species. For example, the Red Sea mussel *Brachidontes pharaonis* was first recorded in the Mediterranean seven years after the opening of the Suez Canal in 1869 (Safriel et al., 1980). In the 1970s this mussel was still considered rare and it was predicted not to establish similar dense populations to those of the native *Mytilaster minimus* (Safriel and Sasson-Frostig 1988). Safriel and Sasson-Frostig (1988) demonstrated, however, that *B. pharaonis* has had a negative effect on the survival and growth of the native species. Studies in the 1990s found that the invader had established extensive beds on platform formations along the Israeli coast (Rilov et al., 1996). Today *B. pharaonis* can be found as far north-west as Sicily (Rilov et al., 2004; Sarà et al., 2008). Therefore, it is possible that *M. erythraea* too will spread along the Levantine basin, with changes in the environment possibly contributing to the delayed population explosion (Crooks and Soulé 1999). The identity in the gene sequences between the Red Sea and the Mediterranean species also supports the existence of a genetic lag on the way to a population explosion, as a lag caused by the relative lack of fitness of the alien species in its novel environment (Crooks and Soulé 1999).

Following the opening of the Suez Canal, an increasing number of alien species have been documented in the Mediterranean (Galil and Zenetos 2002; Galil 2007), having arrived there not only in ballast water but also via the direct transport of larvae by currents (Agur and Safriel 1981; Zibrowius 1992). Abundance surveys of alien corals are important in order to understand the ecological consequences for the local biodiversity and community structure, especially since no natural competitor and/or predator of *M. erythraea* are known in the Mediterranean. Since we still do not understand the vectors of arrival of this tropical coral into the Mediterranean, additional surveys are needed, also south of the Hadera port. While back-trajectory Lagrangian model results support the arrival of the planulae from the port, this finding does not contradict a possible scenario of an independent arrival of new larval stock in ballast water (for example, on a ship entering Hadera port, the nearest port south of Nahsholim), or elsewhere. As the findings from the genetic analysis did not enable determination of whether the colonies in Nahsholim are descendants of the colonies in Hadera port (following power shut-down or sand removal), or whether their origin lies elsewhere, more specific population genetic studies are needed, such as

microsatellite (no primers available for any species of the Melithaeidae family) or Single-Nucleotide Polymorphism (SNPs) analyses. To conclude, *M. erythraea* seems to have slowly spread out from a shipping port to the natural reef, or at least to have successfully established a new habitat along the Mediterranean coast of Israel. Following water temperature rise, ultra-oligotrophy, and the Suez Canal expansion, the East Mediterranean is becoming increasingly tropicalized and thereby suitable for tropical coral settlement.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Michal Grossowicz: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Writing - original draft, Writing - review & editing. **Eli Shemesh:** Data curation, Investigation, Project administration, Writing - review & editing. **Stephane Martinez:** Formal analysis, Writing - review & editing. **Yehuda Benayahu:** Writing - review & editing. **Dan Tchernov:** Funding acquisition, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.106652>.

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