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ORIGINAL ARTICLE

Preliminary data on the genetic structure of a highly successful invading population of oyster suggesting its establishment dynamics in the Levant

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Abstract

Biological invasions in the marine environment are a worldwide threat to native communities. The opening of the Suez Canal, which connects the Red Sea with the Mediterranean, resulted in the most invaded marine system in the world, causing dramatic ecological changes to the East Mediterranean Sea. One of the most prominent rocky benthos invertebrate invaders is the Indo-Pacific oyster *Spondylus spinosus* (family Spondylidae), first recorded along the Israeli coast in 1988. The biology and ecology of *S. spinosus* have not been studied in its native range or in the newly invaded one. We used field surveys to uncover the invasive oyster's current status and molecular tools to characterize some aspects of its genetic population structure, in search of clues to its invasion dynamics. We found that *S. spinosus* forms dense populations along the Israeli Mediterranean coast and reaches large shell sizes. Using two mitochondrial DNA markers, we confirmed that the invading species is identical to that found in the Red Sea. The genetic structure of the population at five sites along the coast reveals a total of seven haplotypes. The most common haplotype was the only one found in the northern Red Sea population, whereas one Mediterranean site (Sdot Yam) was particularly variable (five haplotypes). We conclude that *S. spinosus* has become well established in the Mediterranean following more than two decades since its first record there. We suggest that the Sdot Yam site is where the oyster was first established and where repeated introductions may since have occurred.

Key words: *Mollusca, oysters, Lessepsian migrant, mitochondrial DNA*

Introduction

Biological invasions in the marine environment represent a recognized worldwide threat to native communities (Rilov & Crooks 2009). Marine invasions are often facilitated by environmental changes rooted in man-made activities (Roberts 2007). Between 300 and 400 multicellular species have been introduced into the eastern Mediterranean through the Suez Canal since its opening in 1869 (Rilov & Galil 2009; Zenetos et al. 2010), in what is known as the Lessepsian migration (Por 1978). Of these alien species, molluscs are the most common, with 190 species reported by 2010 (Zenetos et al. 2010). Some of these species have become highly abundant in their new environment, with the potential to change community structure and even function. For example, in the rocky intertidal, the Red Sea mussel *Brachidontes pharaonis* Fischer, 1870 (family Mytilidae), has been shown to dominate the community at many sites along the shore, and has become the favourite prey of a local predatory whelk (Rilov et al. 2002, 2004).

In the subtidal, one of the most dominant bivalve invaders is the large Indo-Pacific oyster *Spondylus spinosus* Schreibers, 1793 (family Spondylidae), along with the other well-established invading oyster *Chama pacifica* Broderip, 1934 (family Chamidae; Zurel 2011). The former species was first recorded along the Israeli East Mediterranean coast in 1988 by local fishermen. Subsequently, Mienis et al. (1993) recorded the species there at a depth range

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of 15–20 m, with densities of up to ~15 oysters/m^2. A decade later, this oyster was also recorded from Turkey and Cyprus (Çeviker & Albayrak 2006; Zenetos et al. 2009). Our preliminary observations suggested that the species now forms dense populations all along the Israeli coast, with a potentially large ecological impact. Little is known about the oyster's biology, ecology, or the mode of introduction, neither in its original habitat nor in the newly invaded one. The current study is the first step in understanding these issues by focusing on its population and genetic structures.

The main vectors of alien species introduction include the transport of larvae in ballast water, fouling organisms on ship hulls, inadvertent introductions associated with mariculture, or the direct connection of two bodies of water, as has been accomplished by the Suez Canal (Carlton & Geller 1993). It is not an easy task to distinguish between these vectors, but genetic and molecular methods can come to our aid in understanding species dispersal and the invasion process (e.g. Kyle & Boulding 2000; Kalisz et al. 2001; Le Roux & Wieczorek 2009). For example, a basic genetic study of the invading *B. pharaonis* has shown that its introduction into the eastern Mediterranean was carried out by dispersal of its early life stages from the Red Sea through the Suez Canal (Shefer 2003). Similarly, analysis of the genetic structure of populations of invasive species has yielded information that could not have been achieved by any other method (see Dlugosch & Parker 2008; McGlashan et al. 2008; Muirhead et al. 2008; Estoup & Guillemaud 2010). Fundamental questions regarding the geographic sources of the invasive species (e.g. Muirhead et al. 2008; Freshwater et al. 2009; Hoos et al. 2010) and the time of invasion (Provan et al. 2008) have been answered by means of molecular tools. The latter can also provide information regarding the taxonomic affiliation of the invasive populations (e.g. McGlashan et al. 2008; Saunders 2009), the introduction modes or vectors (Holland 2001; Gaither et al. 2010) and population dynamics (e.g. Bax & Thresher 2009; Pysek & Richardson 2010; Teske et al. 2011).

In this study we examined the distribution of *S. spinosus* along the Israeli Mediterranean coast and the genetic structure of its population. We used both classical taxonomic identification of the oyster, along with molecular typing. By applying multiple mitochondrial DNA (mtDNA) gene sequence analysis, we confirmed the invading species' identity, based on genetic features, and revealed the genetic variability of *S. spinosus* along the Israeli Mediterranean coast. These findings have enabled us to suggest the original site of establishment and the mode of invasion of this oyster into the Mediterranean Sea.

Methods

Data collection

Populations of *Spondylus spinosus* were studied at six sites along the Israeli Mediterranean coast, from Akhziv in the north to Palmahim in the south, and in the suspected area of origin, Eilat (Gulf of Aqaba, northern Red Sea) (Figure 1). Field data and sampling were carried out by SCUBA diving (2009–2011).

Oyster population size was examined by two methods: density counts, using the quadrat method, and number-per-unit-effort surveys. Density counts were done in Sdot Yam (3 m depth) and Tel Aviv (9 m), by conducting dive surveys along 25-m long transects, one on horizontal bedrock and one on vertical walls. Live oysters were counted on hard substrate along the transect using a 1 m^2 quadrat ($n = 46$ quadrats per site; 4 quadrats that landed on sandy patches were excluded from the analysis). Each counted oyster was also measured for shell

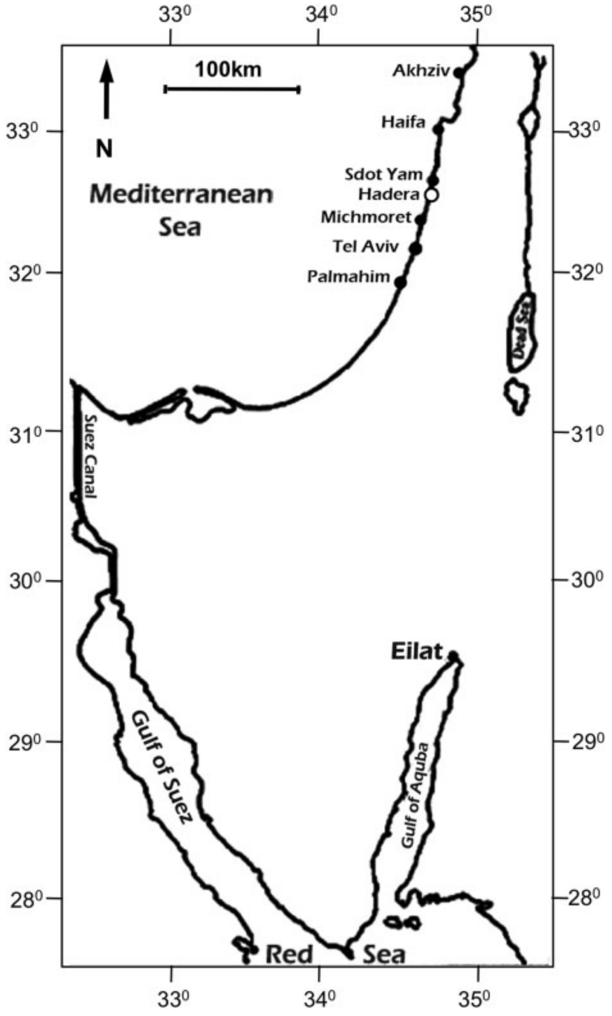

Figure 1. Study sites along the Israeli Mediterranean coast and Eilat (Gulf of Aqaba, northern Red Sea).

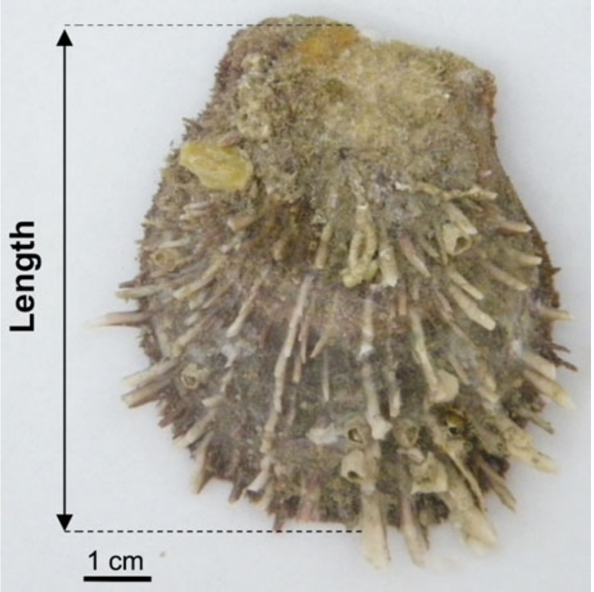

Figure 2. Length measurement of *Spondylus spinosus* shell.

length in order to compare the size structure of the populations in the Mediterranean to that found in the Red Sea. The oysters were measured with a ruler (precision 0.5 cm), from their umbo to the margins of the upper valve (Figure 2), and scored into five size groups: <3, 3–6, 6–9, 9–12 and > 12 cm. The size frequency distribution of the oysters was similarly calculated and compared using the Kolmogorov–Smirnov (K-S) two-sample test (Sokal & Rohlf 1995).

An independent-sample *t*-test was conducted in order to compare the average oyster density per m^2 between the horizontal and vertical surfaces and between sites. Due to the low occurrence of *S. spinosus* in Eilat (see Results), its abundance was determined there as the number of oysters found per unit effort (NUE) during 1 h of dive-search (adopted from McClanahan & Muthiga 1992; Rilov et al. 2000). The same method was also applied at the Akhziv, Michmoret and Palmahim sites (Figure 1), where density transects could not be conducted due to unfavourable sea conditions. Using the NUE survey method at some of the Mediterranean sites and the Red Sea site allowed for a direct comparison of population densities at both locations.

Molecular analyses

In order to study the genetic features of *Spondylus spinosus*, oysters were collected from five Mediterranean sites: Akhziv (30 oysters), Haifa (34), Sdot Yam (30), Tel Aviv (26), Palmahim (19) and Eilat (14), totalling 153 animals. Oysters were removed from the substrate using hammer and chisel and transported live to Tel Aviv University (TAU). They were then opened, and a tissue sample (1 cm^3) was removed from the adductor muscle of each, preserved in 100% ethanol, and stored at −20°C. Total genomic DNA of the samples was extracted using a DNA extraction kit (QIAGEN). Two segments of the mtDNA genes, *16S* and *12S*, were PCR-amplified, using the primer sets following Puslednik & Serb (2008) (Table I). These primers are based on Palumbi et al. (1991) with minor changes.

PCR was performed for each sample in a total volume of 25 μl, containing 1X reaction buffer, 0.2 mM dNTPs, 1 μM of each primer, 5–10 ηg/μl DNA and 1 unit of Super-Therm Taq DNA polymerase (JMR Holdings, London). Amplification was performed in a PTC-200 DNA Engine thermal cycler (MJ Research Inc., USA), with an initial denaturation step of 94°C for 4 min, 32 cycles of 94°C for 45 s, 55°C for 45 s, 72°C for 45 s, followed by a final elongation at 72°C for 3 min. PCR products were electrophoresed on 1.5% (w/v) agarose gels in TBE buffer, ethidium bromide stained, and visualized on a digital Bio Imaging System, BIS-202D (Pharmacia Biotech, USA). PCR products were sequenced from both directions by Macrogen Inc. Seoul, Korea. Sequencing results were edited and aligned using CLUSTAL W following Thompson et al. (1994).

NCBI BLAST was used to locate *12S* sequences available in GenBank for the congeners of *S. spinosus*, and three other bivalves were chosen as a distinct species for distances reference (Table II). A maximum likelihood tree of all haplotypes was constructed using BioEdit v. 7.0.5.3. The probability for each branch to equal zero length was calculated for the generated tree by DNAml-DNA maximum likelihood program. The phylogenetic tree reconstruction approach was used to test the proximity between the Mediterranean and the Red Sea oysters in comparison to the proximity to their congeners and to distinct species.

The *16S* gene of the mtDNA was found to be the more variable of the two sequences, and was chosen for the haplotype analysis within the Mediterranean Sea sites. Pairwise F_{st} was computed using the Tamura–Nei model (Tamura & Nei 1993) of sequence substitution using Arlequin 3.5. The data were visualized and adjusted using Network v. 4.6 software.

Table I. Primers used for amplification and sequencing of *12S* and *16S* mtDNA of *Spondylus spinosus* oysters following Puslednik & Serb (2008).

Locus	Primer name	Sequence (5′–3′)
12S	12S F	AGA CAT GGA TTA GAT ACC C
12S	12S R	ACC CCT ACC TTG TTA CGA CTT
16S	16S arL	CGC CTG TTT AAC AAA AAC AT
16S	16S rbH	CCG GTT TGA ACT CAG ATC ACG T

Table II. Species used in maximum likelihood analysis and GenBank accession number for *12S* mitochondrial DNA.

Species	Author	Localities	Accession number
Spondylus gaederopus	Linnaeus, 1758	Mediterranean Sea	AJ571607.1
Spondylus nicobaricus	Schreibers, 1793	Indo-West Pacific	EU379424.1
Spondylus squamosus	Schreibers, 1793	Indo-West Pacific	EU379425.1
Spondylus victoriae	Sowerby, 1843	Indo-Pacific	JF339047.1
Spondylus ictericus	Reeve, 1856	West Atlantic	EU379423.1
Propeamussium alcocki	Smith, 1894	Indo-Pacific	JF339046.1
Mirapecten mirificus	Reeve, 1853	West Pacific	EU379401.1
Ostrea edulis	Linnaeus, 1758	North Atlantic, Europe, Wadden Sea, Mediterranean Sea	HQ259072.1

Results

Oyster abundance

Spondylus spinosus was the only species of the genus found at the study sites, as no individuals of the indigenous congeneric *Spondylus gaederopus* Linnaeus, 1758 were spotted. The oysters were found on hard substrates at 0.5–16 m at all 5 study sites along the Israeli Mediterranean coast, from Akhziv in the north to Palmahim in the south (Figure 1). Their average density at the Sdot Yam and Tel Aviv sites was 3.4 ± 2.5 per m^2 and 4.4 ± 1.8 per m^2, respectively. The density of *S. spinosus* did not differ significantly between the two sites ($n = 46$ quadrates at each site, $t_{45} = -1.47$, $P > 0.05$), or between vertical surfaces and horizontal ones ($n = 30$ and 16 for Sdot Yam and 25 and 21 quadrates for Tel Aviv, respectively, $t_{26} = 2.47$, $P > 0.05$). The average size of an oyster shell was 7.43 ± 3.1 cm ($n = 100$) for Sdot Yam and 8.6 ± 3.7 cm ($n = 74$) for Tel Aviv sites ($t_{173} = 2.5$, $P > 0.05$). Size frequency distribution of *S. spinosus* oysters in Sdot Yam and Tel Aviv (Figure 3) did not differ significantly between the two sites (K-S two-sample test, $Z = 1.108$, $P > 0.05$).

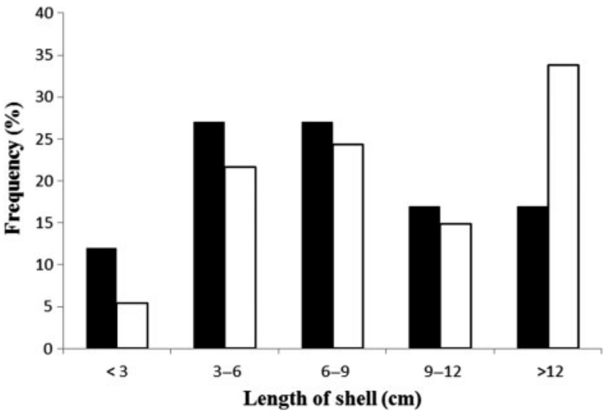

Figure 3. Size frequency distribution of *Spondylus spinosus* oysters at the Sdot Yam (black, $n = 100$ oysters) and Tel Aviv sites (blank, $n = 74$ oysters).

Although our field search was intensive, only a few oysters were found at the Eilat coral reefs and on some artificial substrata, such as metal nets in the area. We only observed one or two oysters during each 60-min dive, compared to 67.5 ± 8.63, 22.73 ± 1.46 and 11.43 oysters found in Akhziv (northern coast), Michmoret (central coast) and Palmahim (southern coast, single sampling), respectively ($\chi^2_2 = 70.83$, $P < 0.01$). Eilat oysters were significantly smaller than those at the Israeli Mediterranean sites, with an average shell length of 5.2 ± 1.8 cm ($n = 13$) and a range of 2–7.7 cm ($t_{50} = -6.9$, $P < 0.05$).

Genetic population structure

The maximum likelihood analysis of *12S* sequences (GenBank numbers KC821504–KC821505) revealed that all *Spondylus spinosus* oysters collected from both the Israeli Mediterranean and Eilat sites belonged to one monophyletic group (Figure 4). Other species of *Spondylus* were classified as separate units, with

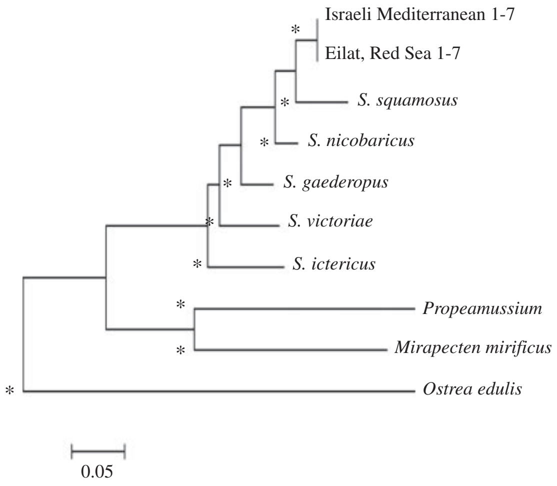

Figure 4. Maximum likelihood tree for *12S* mtDNA. *Spondylus spinosus* oysters from the Mediterranean and Red Sea compared to congeners, *Propeamussium alcocki*, *Mirapecten mirificus*, and *Ostrea edulis* (transition/transversion ratio = 2; ln likelihood = − 1741). Asterisks indicate branch length significantly > zero ($P < 0.01$).

Table III. *Spondylus spinosus*. Pairwise F_{st} values among sites in the Mediterranean based on model of Tamura & Nei (1993). Asterisk indicates value significantly > zero ($P < 0.01$).

	Akhziv	Haifa	Sdot Yam	Tel Aviv	Palmahim
Akhziv	0				
Haifa	0.0001	0			
Sdot Yam	0.00713	0.0001	0		
Tel Aviv	0.01105	0.0001	0.00672	0	
Palmahim	0.125	0.17642 *	0.024	0.17264	0

Propeamussium alcocki Smith, 1894, *Mirapecten mirificus* Reeve, 1853 and *Ostrea edulis* Linnaeus, 1758 being used as a distance reference.

Pairwise F_{st} values for all study sites in the Mediterranean showed no significant pattern of differentiation between sites, as the only significant values were for Palmahim-Haifa (Table III).

Seven haplotypes categorized the haplotype network of *S. spinosus* on the Israeli Mediterranean coast (Figure 5) based on *16S* sequences (GenBank numbers KC821506–KC821513). Out of the total number of oysters ($n = 139$), haplotype 2 was the most common, featuring in 76% of all oysters and was found at all Mediterranean sites. Haplotype 1, which differed from haplotype 2 by a single mutation, was also found at all sites and was the second most common, while haplotypes 3–7 were each represented by only one oyster. The Sdot Yam site was the most variable, featuring five of the seven haplotypes. The Tel Aviv and Palmahim sites were the second most variable, featuring three haplotypes, while the Akhziv and Haifa sites featured two haplotypes. All oysters from Eilat were characterized as haplotype 2 and were not included in the haplotype network.

Discussion

The current study presents for the first time data on the abundance and genetic structure of the invasive oyster *Spondylus spinosus* population along the Israeli Mediterranean coast, and also refers to its indigenous conspecific population in Eilat, the northern Red Sea. Its relatively high densities in the former region emphasize its successful establishment in just over two decades since it was first recorded in its new environment. Using abundance surveys and DNA comparison, we show that the *Spondylus* species dominating the eastern Mediterranean rocky reefs is indeed *S. spinosus*. The genetic structure of the Mediterranean populations may indicate its origin and route of dispersion.

Although we used different methods to assess oyster abundance, due to either extremely low density (Eilat) or harsh sea conditions (some Mediterranean sites), the data clearly demonstrate that *S. spinosus* is abundant along the Israeli Mediterranean shores and its density is several-fold (Palmachim), to more than an order of magnitude (Akhziv), higher than in Eilat. This finding highlights the importance of future studies, including a survey of additional populations along the Red Sea to determine whether densities are low everywhere in this oyster's native home range compared to the eastern Mediterranean, or whether Eilat may represent a northern-edge population, often characterized by relatively smaller densities and size (Lawton 1993). *Spondylus spinosus* was equally abundant on vertical and horizontal hard surfaces at both the Sdot Yam and Tel Aviv sites, suggesting that the oyster is successfully utilizing both types of surface along the Israeli Mediterranean coast, and that the high

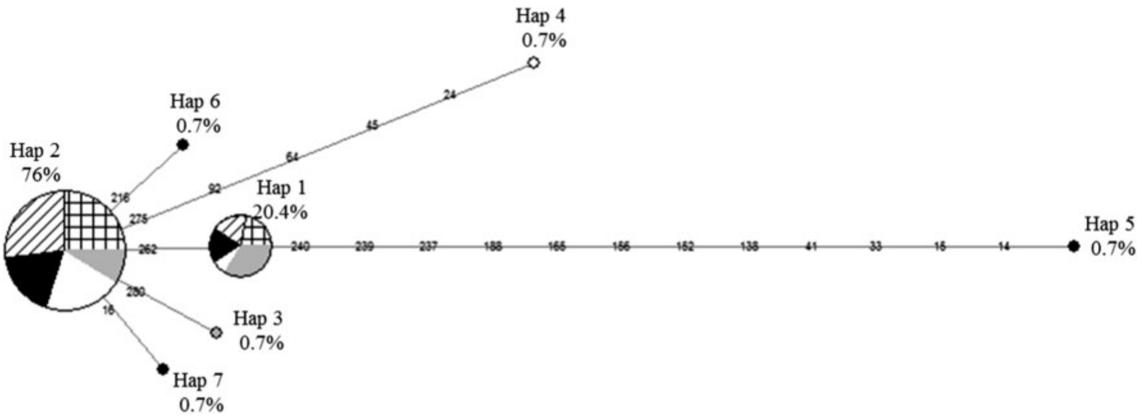

Figure 5. Haplotype network for *16S* mtDNA sequences from the Israeli Mediterranean coast S*pondylus spinosus* oysters. Circles represent haplotypes, line represents genetic distance with mutation location indicated, circle diameter represents their relative frequency, and patterns represent sampling sites: ▦, Akhziv; ▨, Haifa; ■, Sdot Yam; □, Tel Aviv; ▩, Palmahim sites. Line length represents number of mutations between haplotypes. Haplotype relative frequency in the Mediterranean population in indicated with haplotype number.

sedimentation on horizontal surfaces (pers. obs.) is not a limiting factor for the oyster.

The size frequency distribution of the oysters at the Sdot Yam and Tel Aviv sites did not differ significantly (Figure 3), which may imply a lack of size gradient along the Israeli Mediterranean coast. However, additional surveys at more distant sites are required in order to conclude this issue. Nevertheless, at both sites oysters with shell length greater than 12 cm were abundant (17% of Sdot Yam and 34% of Tel Aviv populations). Oliver et al. (1992) reported shell lengths of *S. spinosus* in the Indo-Pacific of up to 7 cm, whereas Mienis et al. (1993) reported lengths up to 12 cm in the Mediterranean. The relatively high densities and larger shell size of *S. spinosus* at our Mediterranean sites indicate a thriving population of the Indo-Pacific oyster in the newly invaded region (see also Gutowsky & Fox 2011). The mechanism behind its success could be that of low competition, or even a lack of competition, with indigenous benthic organisms, as its main potential competitor, the native oyster *Spondylus gaederopus*, was completely absent in the surveys. Furthermore, reduced predation pressure and the absence of parasites most probably lead to high fitness and increased fecundity in this invasive species (see Smith et al. 2009; Hänfling et al. 2011).

The high abundance of large oysters, both *S. spinosus* (this study) and *Chama pacifica* (Zurel 2011), where they did not exist previously, suggests that they play substantial ecological roles in their new environment. One ecological role for large three-dimensional extensive space utilizers is to serve as ecosystem engineers (Jones et al. 1994), adding considerably to substrate complexity and possibly also to niche and species diversity. Their second role is as effective plankton feeders (Haven & Morales-Alamo 1970), which in the ultra-oligotrophic Levant basin (Azov 1991) may greatly affect food availability for other benthic organisms. Extensive faeces and pseudo-faeces deposition by the invasive oysters may also affect the nutrient cycling by altering the nutrient composition available for benthic organisms (e.g. Griffiths 1993). These issues should be examined in future studies in order to determine the ecological impact of the invasive oyster species in their shared new environment.

The present study is the first to present mtDNA sequences for *S. spinosus*. The *12S* sequences of oysters from both the Mediterranean and the northern Red Sea were applied along with classical taxonomy in order to identify the oyster. The *16S* sequences of oysters from several sites were used in order to acquire a preliminary insight into their genetic variability and haplotype structure in the newly invaded Mediterranean environment. Comparing *12S* sequences of oysters from the Mediterranean and Eilat to the same locus sequences of congeners, including *S. gaederopus* which is indigenous to the Mediterranean (Figure 4), revealed that *S. spinosus* is indeed the same species in both seas. The monophyletic group obtained from the Mediterranean and the northern Red Sea oysters differed significantly from the other *Spondylus* species. The genetic findings thus support the suggestion that the species is indeed *S. spinosus*, as indicated by classical taxonomy (Mienis et al. 1993). Undoubtedly, correct identification of an invasive species has great importance for constructing an appropriate population management policy (Saunders 2009).

Once an invasive species has been found in a new environment, its native range usually implies the invasion routes and vectors (McGlashan et al. 2008). *S. spinosus* was first recorded in the Mediterranean in 1988 off the coast of Haifa, Israel (Figure 1; Mienis et al. 1993). There was no record of the oyster at any site to the west of the Israeli coast until a decade later (Çeviker & Albayrak 2006), which implies that its dispersal along the Mediterranean coast has been northwestward. Such a dispersal pattern is common among Lessepsian migrants (Galil & Zenetos 2002). It can therefore be concluded that our molecular findings, along with the westward dispersal featured by *S. spinosus* in the Mediterranean Sea, validate the hypothesis that part of the *S. spinosus* population in the Mediterranean Sea originates from the Red Sea and may be a Lessepsian migrant, although some haplotypes may originate from elsewhere in the Indo-Pacific.

Sequencing of the *16S* of all Mediterranean *S. spinosus* oysters revealed seven haplotypes (Figure 5). Although the most common haplotype was the only one also found in the northern Red Sea, it should be noted that all the oysters there were from a single area. Thus, it is assumed that a low density population at a given site does not reflect the true genetic variability of *S. spinosus* throughout the entire Red Sea, or in the Gulf of Aqaba. In addition, we suggest that the use of multiple genetic markers, rather than *16S* solely, will contribute to the understanding of the invasion process. It should also be noted that while the current study does not seek to provide a conclusive comparison of the genetic variability of these oysters between the Mediterranean and the Red Sea, the genetic variability and structure found along the Israeli Mediterranean coast offers an indication of the invasion process and its vectors.

The haplotype network, which allows multifurcations, is a more accurate and realistic model than the haplotype tree in cases of invasion into a vast marine area (Shefer et al. 2004). The haplotype network of

S. spinosus along the Israeli Mediterranean coast (Figure 5), together with pairwise F_{st} test statistics (Table III), provides important information regarding the invasion process of *S. spinosus*. Pairwise F_{st} values confirm the pattern featured in the haplotype network that there is no spatial gradient of haplotypes, which implies a high degree of connectivity between Mediterranean sites. Although F_{st} values were low, *P*-values for F_{st} were found to be significant for the Palmahim–Haifa sites. We assume that this value showed significance due to the relatively small sample size at the Palmahim site ($n = 19$) compared to the other Mediterranean sites ($n = 26$–34), and no obvious haplotype gradient was observed. This emphasizes the need to study population genetic structure using multiple markers with a relatively large sample size.

The highest number of haplotypes was found at the Sdot Yam site (Figure 5). The relatively high genetic variation at this site may imply multiple introduction events which occurred at different times and/or from multiple sources. We suggest that haplotype 2, which was found at all Mediterranean sites and in Eilat, was among the first to invade the new environment and to expand to other sites along the Israeli Mediterranean coast, while uncommon haplotypes were found only at the Sdot Yam site. The multiple mutations, which separate some of these haplotypes from the most common one (haplotype 2), verifies the assumption of multiple introduction events, as two decades may not be a long enough period for these mutations to arise.

In order to determine whether population genetic variability is indeed greater at the Sdot Yam site compared to other Mediterranean sites, the use of multiple genetic markers should be applied together with larger sample sizes. Nevertheless, these preliminary results support Lamprell's (1998) assumption that *S. spinosus* was introduced into the Mediterranean by marine traffic. Since 1981, a massive import of coal shipped via the Suez Canal has been routinely taking place at the Hadera power plant, which is only 2 km south of Sdot Yam (Figure 1), making these coal vessels a probable vector of the invasive oyster as well as of other Lessepsian migrants (Fine et al. 2005). Although shipping is only considered as the second largest vector for marine species in the eastern Mediterranean, after Erythrean invasions (Galil & Zenetos 2002), it is still a considerable pathway. Many successful invaders to this region were transported in ballast water or as fouling biota (Galil & Zenetos 2002; Zenetos et al. 2010). However, the mode of transport for many Lessepsian migrants is assumed to be based on dispersal patterns and not on population genetic structure. Our results reveal a genetic structure which points to the less common way of introduction, by shipping, emphasizing the need for prospective management of this pathway.

We conclude that *S. spinosus* is a highly successful invader into the East Mediterranean Sea, and most probably will disperse further. Shabtay (2011) suggested that among the properties which enhance *S. spinosus*'s successful invasion are high reproductive intensity and low predation pressure, due to the high biomechanical strength of its shell in the Mediterranean compared to the Red Sea. Along with *Chama pacifica* (see Zurel et al. 2011), both invasive species flourish and form oyster clusters (and sometimes reefs) in a region where none existed before. Previous studies have indicated that it is almost impossible to eradicate an invasive species once it is established (Thresher & Kuris 2004); therefore, a management strategy should focus on the prevention of further dispersal of the species. In this study, we suggest the site of first establishment, which supports the assumption that *S. spinosus* was most probably transported into the Mediterranean in the ballast tanks of coal ships. This enables us to suggest a basic management strategy in order to prevent further arrivals of the oyster and its further dispersal in the Mediterranean. At present, the oyster *S. spinosus* is already abundant along the Israeli Mediterranean coast (Mienis et al. 1993; this study). Consequently, it should be monitored across the entire Mediterranean Sea, along with an examination of its effects on both the biological and physical components of the habitat.

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