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The Indo-Pacific oyster *Spondylus spinosus* Schreibers, 1793 in the Eastern Mediterranean Sea: reproductive features

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Populations of the Indo-Pacific invasive bivalve *Spondylus spinosus* in the Eastern Mediterranean occur at high densities and occupy vast areas of the rocky habitats along the Israeli coast where they are cemented to hard substratum in an oyster-like fashion. We studied the reproductive features of this bivalve in part of the area where it has invaded and found it to be gonochoric, featuring a reproducing population with a sex ratio of 1:1, annual gonad development and an inferred spawning period coinciding with the seasonal rise in seawater temperature. It is suggested that these reproductive features support high fertilisation rates and fecundity, thus contributing to the maintenance of its populations in the new environment.

Keywords: bivalve; invasive species; Lessepsian species; reproduction

Introduction

Among the most important traits of a successful invader are its abilities to reproduce, recruit and spread in the new environment (Ruiz *et al.* 2000; McMahon 2002). Numerous aquatic invasive species possess features that enhance their expansion, such as time of onset of first reproduction and high fecundity (see Sakai *et al.* 2001). Consequently, an investigation of the reproductive features of an invader such as *Spondylus spinosus* Schreibers, 1793 which have not been studied before, can contribute to our understanding of its remarkable expansion in the Eastern Mediterranean.

There have been very few studies on the biology and ecology of the family Spondylidae, the so-called thorny oysters, which comprises over 65 species and subspecies (Huber 2010), many of them large, distributed in the Indo-Pacific, Caribbean, West Africa and the Mediterranean seas, and all of which are filter-feeders that adhere to rocky substrates (Cox *et al.* 1969). Of the 65 species of *Spondylus* Linnaeus, 1758, very few have been studied in relation to their reproductive biology. Research has been conducted mostly on species with commercial value as seafood or ornamentation. For example, in the Gulf of California *Spondylus princeps* Borderip, 1833 was found to spawn during July–October (Villalejo-Fuerte *et al.* 2005), whereas *Spondylus leucacanthus* Broderip, 1833 from the same area has a shorter spawning period, coinciding with maximum seawater temperature (Villalejo- Fuerte and Garcia-Dominguez 1998; Rodriguez-Astudillo *et al.* 2002).

Spondylus spinosus is native to the Indo-west Pacific and was first recorded from the Israeli Mediterranean coast in 1988. It has subsequently appeared there in many areas at a depth range of 1–40 m, occasionally reaching densities as high as 15 per 1 m^2 (Mienis *et al.* 1993). A decade later, it was also found in Turkey and Cyprus (Çeviker and Albayrak 2006; Zenetos *et al.* 2009). The high abundance of *S. spinosus* in its invaded environment has motivated the study of the biological and ecological features of this bivalve (Shabtay 2011; Shabtay *et al.* 2013). Here we investigate several important features of its sexual reproduction in the invaded environment: sex ratio; annual gonad development; inferred spawning period; and size at onset of reproduction.

Materials and methods

Study sites

Spondylus spinosus was studied along the Israeli Mediterranean coast sites Sdot Yam (32°29′N, 34°53′E) and Tel Aviv (32°05′N, 34°45′E). Both sites are characterised by kurkar sandstone (Yaalon 1967) horizontal bedrock and vertical walls, surrounded by sandy bottom (1–7 m and 9–16 m depth for Sdot Yam and Tel Aviv, respectively). Collection was conducted by scuba diving (2009–2011).

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Reproductive features

To study the reproductive features of *S. spinosus*, monthly samples of 8–12 large individuals (6–12 cm shell length) were collected from the Sdot Yam site during December 2009–August 2011 and transferred live to the laboratory. Temperature data for the Israeli Mediterranean coast were obtained from loggers on the sea surface in Ashdod (see Shabtay *et al*. 2013), as supplied by the Coastal and Marine Engineering Research Institute, Technion, Haifa (Israel). The samples were thus assigned to one of four seasons: winter (December–February); spring (March–May); summer (June–August); and autumn (September–November).

Histological examination was used to determine the sex of the bivalves and their reproductive state. They were opened, the entire soft part was removed, fixed in 4% formaldehyde in seawater for 24 h,, rinsed in freshwater and then transferred to 70% ethanol. When gonads were detected under a compound microscope, a small section of the gonad tissue (c. 5 mm^2) was carefully removed from each specimen using a scalpel, dehydrated in a graded series of ethanol and buthanol, and embedded in paraffin (56 °C). From each sample c. 15 histological sections, 7 µm thick, were obtained (Microtome M1R, SHANDON), mounted on glass slides and stained with Ehrlich's haematoxylin and eosin. The sections were examined under a light microscope (Nikon OPTIPHOT) at ×10 and ×20 magnification for sex determination and reproductive stage of the gonads, using the scoring system of Dix and Ferguson (1984) where score 0 indicates sexual rest, 1 spent gonads, 2 early gametogenesis, 3 late gametogenesis, 4 ripe and 5 spawned gonads. An average monthly reproductive stage was calculated and presented as the population reproductive index (IR, score 0–5) following Dix and Ferguson (1984):

$$IR = \sum(fi \cdot xi) / \sum fi$$

where fi is number of individuals at a certain reproductive stage and xi is the reproductive stage.

To determine size at first reproduction, we used 10 specimens, shell length 20–50 mm, collected from the Sdot Yam site (June 2010), and specifically included the smallest observed in the field. The month of sampling coincided with the time when ripe gonads (i.e., stage 4) were observed (see Results).

Statistical analyses were performed using SPSS v.15.1 with statistical significance of $\alpha = 0.05$ for all tests.

All specimens obtained from the Sdot Yam site that featured gonads were used for calculating the sex ratio against the expected 1:1 ratio, using the chi-square test.

Results

Reproductive features

Spondylus spinosus exhibits a reproductive population along the Israeli Mediterranean coast. It would appear to be gonochoric as no hermaphrodites were encountered in this study. The gonads surround the intestines and, in live specimens, the female ones are pink while those of the male are cream-white, with both featuring a granular texture. Of the 223 individuals collected at the Sdot Yam site, 24.2% (54) were males, 25.6% (57) females and the remaining 50.2% (112) had no gonads. Thus, a male to female sex ratio of 1.05:1 was found, exhibiting no significant deviation from the expected 1:1 ratio ($n = 103$, $\chi^2_1 = 0.01$, $P > 0.05$). The smallest male that featured gonads was 30 mm, and the smallest female was 32 mm; ripe gonads were found in all the larger specimens of both sexes.

The histological sections of the male and female gonads revealed the 0–5 developmental stages corresponding to the Dix and Ferguson (1984) score. At the sexual rest stage (score 0), neither male nor female gonads were visible and therefore sex could not be determined, even by histology. Among males, early gametogenesis (score 2) exhibited a cell layer on the thick follicle wall, undergoing spermatogenesis, and the follicles themselves were empty at that stage (Fig. 1A). The subsequent later spermatogenesis (score 3) exhibited a thick sperm follicle wall and follicles loaded with spermatocytes undergoing maturation (Fig. 1B). The following ripe stage (score 4) exhibited a thin sperm follicle wall and follicles packed with mature spermatocytes (Fig. 1C). The spawning stage (score 5) revealed partly empty sperm follicles with no or only a thin wall (Fig. 1D). The spent stage (score 1) featured a collapsed follicle wall with a few spermatocytes (Fig. 1E).

Among the females, the early gametogenesis (score 2) exhibited follicles with immature oocytes on their wall surface (Fig. 2A). Subsequently, later gametogenesis (score 3) featured mature oocytes filling most of the follicles, where walls could still be observed (Fig. 2B). The ripe stage (score 4) displayed swollen follicles packed with mature oocytes and only a small amount of connective tissue between them (Fig. 2C). At the spawning stage (score 5), some follicles were empty while others had retained some mature oocytes (Fig. 2D). The spent stage (score 1) featured empty follicles with a collapsed wall and a certain amount of connective tissue (Fig. 2E).

At early gametogenesis, the average diameter of the oocytes was 40 ± 8 µm ($n = 45$) for the April–May sampling, and this gradually increased to 56 ± 2.5 µm ($n = 12$) and 97 ± 41 µm ($n = 12$) for the late gametogenesis and ripe stage, respectively in May–June. At the spawning stage their size decreased to 67 ± 12

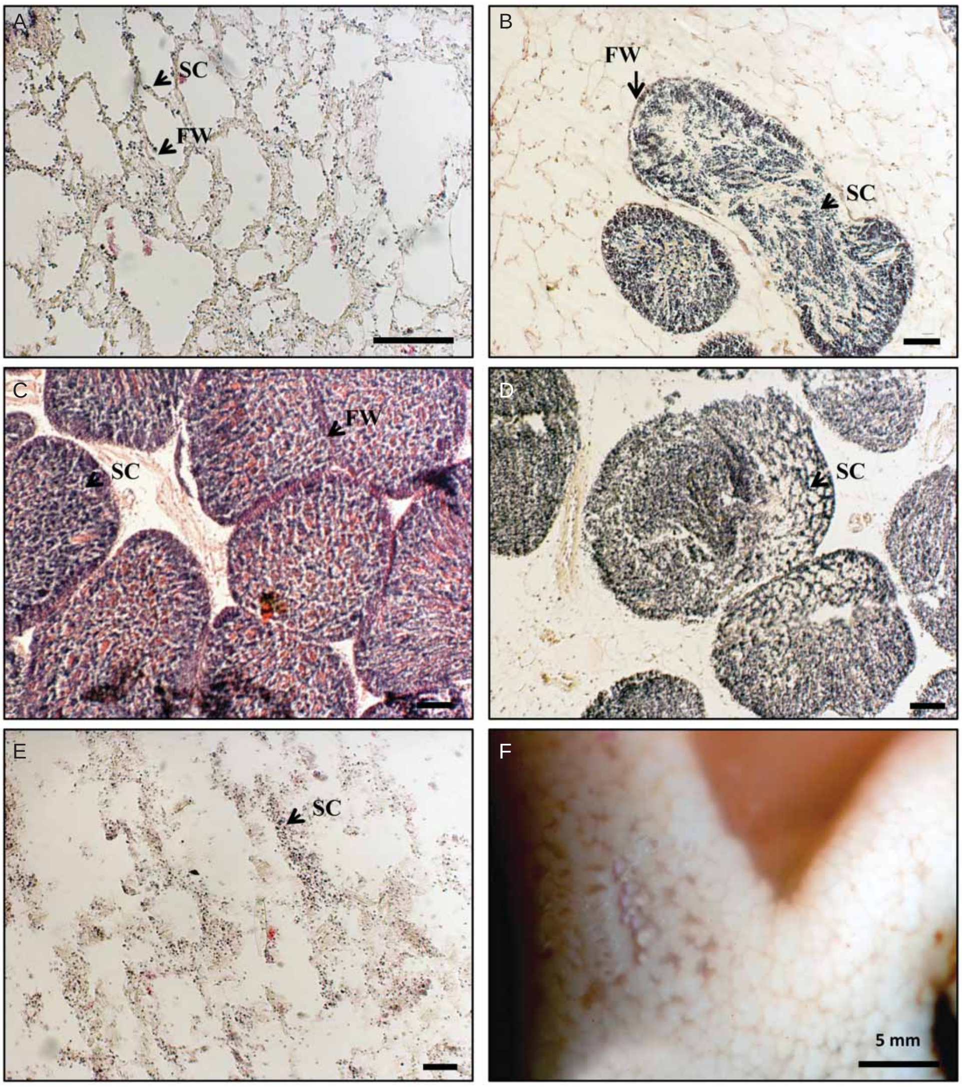

Figure 1. Images of male gonads of *Spondylus spinosus*. **A,** Early spermatogenesis; **B,** late spermatogenesis; **C,** ripe stage; **D,** spawning stage; **E,** spent gonads; **F,** ripe gonads of live dissected specimen. FW—follicle wall of spermatids; SC—spermatocytes. Scale bars at A–E = 100 μm, at f 5 mm.

μm ($n = 27$) in July–August. Notably, no significant differences were found between oocyte diameter of the different stages (ANOVA, $P > 0.05$), reflecting the large deviation around the latter average value.

The number of male and female *S. spinosus* at a given reproductive stage during the study is presented in Table 1. The results indicate the inferred timing of a synchronised spawning, as in June and July 2010 all males ($n = 15$) and females ($n = 10$) were at either the ripe or the spawning stage, and in July 2011 both sexes were at the spawning stage.

The reproductive stages (score) of the male and female gonads derived from the histological sections (Figs 1, 2) were used to calculate the respective average monthly reproductive index (IR), also in relation to the annual seawater temperature curve (Fig. 3). Gonad development (Figs 1, 2A) began in April (spring) 2010 and 2011 (IR = 0.5 and 1.2, respectively), when seawater temperature was c. 20 °C. In May most of the individuals featured ripe gonads (Figs 1, 2C) or well-developed ones (IR = 1.4 and 2.4 for 2010 and 2011, respectively, Figs 1, 2B). The inferred spawning (Figs 1, 2D) was noted in early summer (June, seawater c. 27 °C) and lasted until August (c. 30 °C, IR = 3–5). Between October-March (autumn to winter) 2010 and 2011 all were at the sexual rest stage (IR = 0), coinciding with seawater temperature range of c. 17–26 °C.

Discussion

Spondylus spinosus is a Lessepsian invasive bivalve in the Eastern Mediterranean, having spread rather swiftly

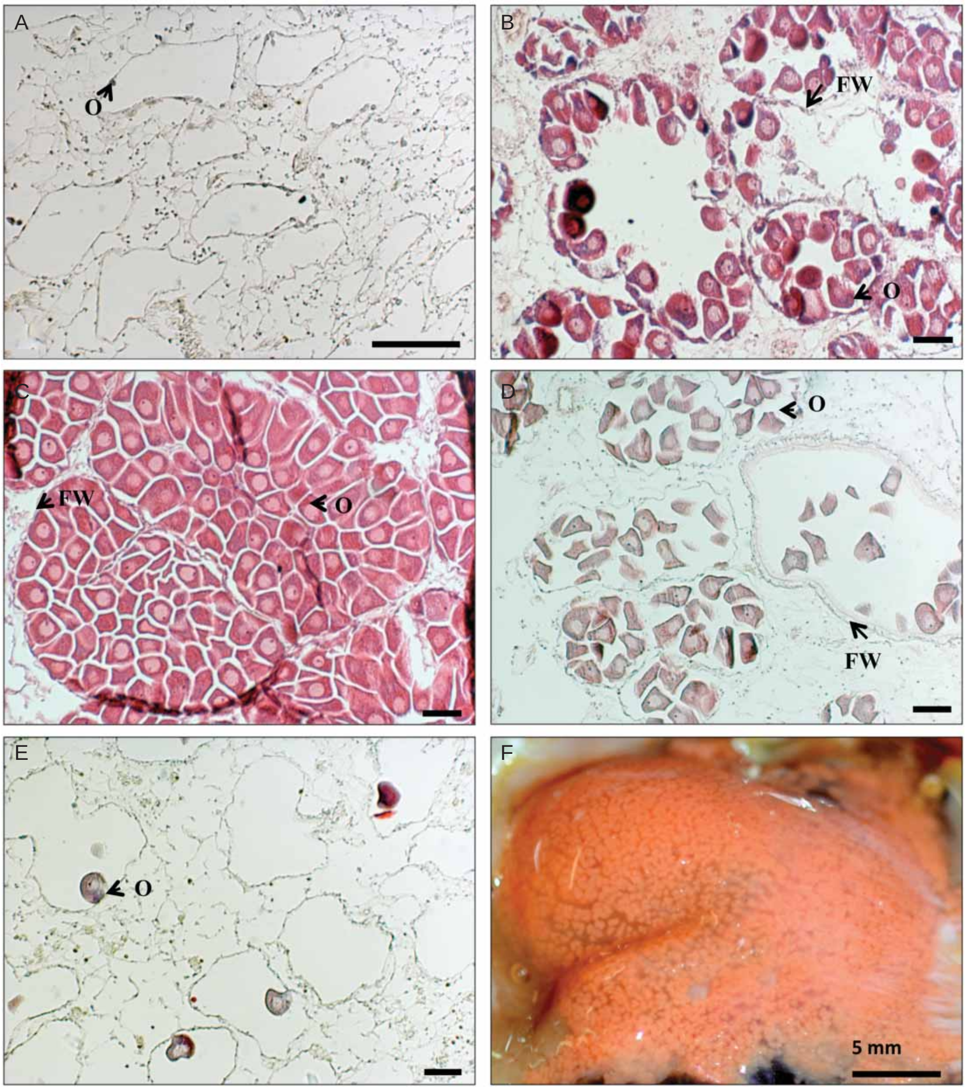

Figure 2. Images of female gonads of *Spondylus spinosus*. **A,** Early oogenesis; **B,** late oogenesis; **C,** ripe stage; **D,** spawning stage; **E,** spent stage; **F,** live ripe oocytes of dissected specimen. FW—follicle wall; O—oocyte. Scale bars at A–E = 100 μm, at f 5 mm.

along the Israeli, Turkish and Cyprus coasts (Mienis *et al*. 1993; Çeviker and Albayrak 2006; Zenetos *et al*. 2009; Shabtay *et al*. 2013).

The current study revealed that, along the Mediterranean coast of Israel, *S. spinosus* features an annual reproductive cycle, with an inferred summer spawning (June–August; Fig. 3). It is gonochoric (Figs 1, 2), with a sex ratio of 1:1, similar to other bivalves (e.g., *Chlamys islandica* Müller, 1776, Greenland [Pedersen 1994]; *Adamussium colbecki* Smith, 1902, Antarctica [Heilmayer *et al*. 2003]; *Placopecten magellanicus* Gmelin, 1791, Canada [Wang and Croll 2004]). In addition, in this study, for the first time histological sectioning was successfully applied to a *Spondylus* species in order to examine its gametogenic cycle and the timing of its inferred spawning period (Figs 1, 2). Previous studies have only used macroscopic examination of gonads (e.g., Cudney-Bueno and Rowell 2008; Soria *et al*. 2010). However, we consider that histological examination is more precise and informative. The average oocyte diameter of *S. spinosus* increased in size, albeit not significantly, from the early gametogenesis stage (40 ± 8 μm) to the ripe stage (97 ± 41 μm), and then decreased to 67 ± 12 μm at the spawning stage (see Results). Although the increase in oocyte size from early gametogenesis to the ripe stage was not statistically significant, the small increase was clear in sections. We suggest that in future studies a larger sample size be used and it is likely that this will confirm the observed pattern of increasing oocyte size during gametogenesis. The observed decrease in average oocyte diameter from the ripe stage to spawning, together with the observed large deviation from average, resembles the

Table 1. Number of *Spondylus spinosus* males, females or unidentified sex, according to the reproductive stage index during the study period.

		Reproductive stage										
		0	1		2		3		4		5	
Year	Month	U	M	F	M	F	M	F	M	F	M	F
2010	April	5	–	–	4	1	–	–	–	–	–	–
	May	–	–	–	–	6	2	2	–	–	–	–
	June	–	–	–	–	–	–	–	8	2	–	4
	July	–	–	–	–	–	–	–	1	1	6	3
	August	–	4	1	–	–	–	–	–	–	4	1
2011	April	4	–	–	3	3	–	–	–	–	–	–
	May	–	–	–	5	2	3	3	–	–	–	–
	June	–	–	–	–	–	3	–	5	1	–	1
	July	–	–	–	–	–	–	–	–	–	5	5
	August	2	2	3	–	–	–	–	–	–	–	2

0—sexual rest; 1—spent gonads; 2—early gametogenesis; 3—late gametogenesis; 4—ripe; 5—spawning gonads; F—female; M—male; U—unidentified. $n = 9$–14 individuals per month. No data indicated by –.

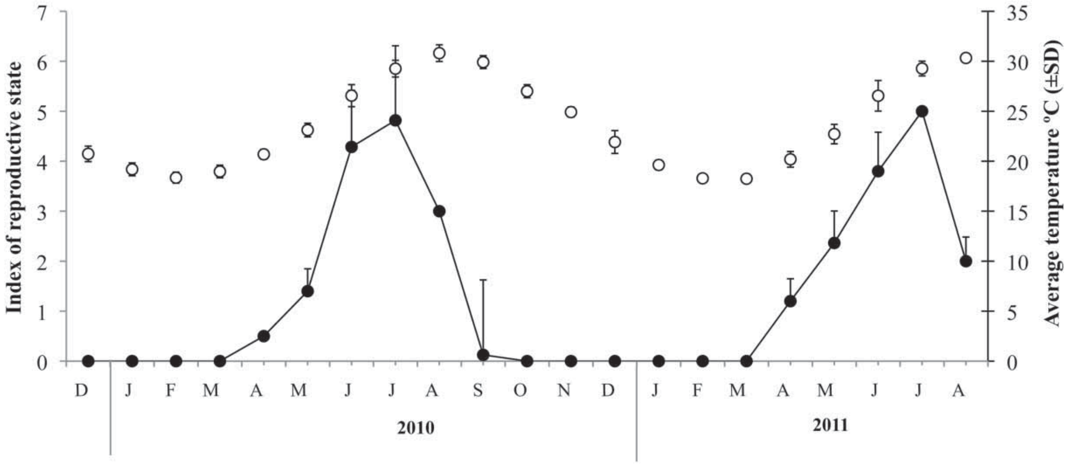

Figure 3. Average monthly reproductive index (IR ± SD) of *Spondylus spinosus* (•, $n = 8$–14 per month) and respective seawater temperature curve (○).

pattern that has been found among bivalves with a continuous reproductive cycle and no resting period a (e.g., *Argopecten purpuratus* Lamarck, 1819 [Cantillanez *et al.* 2005]; *Pecten maximus* Linnaeus, 1758 [Devauchelle and Mingant 1991]). Therefore, we suggest that *S. spinosus* spawned during a relatively long period of several months in 2010 and 2011 (June–August; Table 1). Similarly, an extended spawning period of several months was found in the congeners *S. princeps* and *Spondylus calcifer* Carpenter,1857 in the Gulf of California (Cudney-Bueno and Rowell 2008), thus implying that it is shared by *Spondylus* species from various zoogeographic regions, including the Eastern Mediterranean.

A sex ratio of 1:1 among gonochoric species is thought to be a result of natural selection that acts to favour it (Fisher 1930; Alexander and Borgia 1978; Uyenoyama and Bengtsson 1979). Among bivalves, sex ratio is related to reproductive success as it may affect gamete dispersal and fertilisation success (e.g., Claereboudt 1999; Arnaud-Haond *et al.* 2003). Thus, the 1:1 sex ratio of the invasive *S. spinosus* along the Mediterranean coast of Israel may contribute to fertilisation success of the spawned eggs. At this stage it is unknown whether size at first spawning is also related to age, as the relationship between size and age of *S. spinosus* is still not known.

The onset of gametogenesis in both sexes of *S. spinosus*, and the timing of its inferred spawning, coincided with an increase in seawater temperature towards the height of summer (Fig. 3), and it thus resembles many other bivalves in this respect (e.g., *C. islandica*, Greenland [Blicher *et al.* 2010]; *S. calcifer*, Gulf of California [Cudney-Bueno and Rowell 2008]; *P. magellanicus* [Wahle and Jumars 2014]). Coinciding with the onset of rising temperatures, phytoplankton blooms occur in the Mediterranean (Bosc *et al*. 2004), supplying the food required for gamete development, as shown for example in *S. calcifer* (Fabara 2003) and *Spondylus leucacanthus* Broderip, 1833 (Villalejo-Fuerte *et al*. 2002). Undoubtedly, future studies on the energy budget of *S. spinosus*, including its reproduction costs, will further illuminate the adaptation of the population to the new environment.

The current study revealed a synchronised occurrence of the reproductive stages in *S. spinosus*, both within each sex and between sexes, which was also reflected in the inferred spawning period of males and females (Table 1), which may enhance fertilisation success (Lotterhos and Levitan 2010). Moreover, studies have shown that, among other bivalves, spawning by part of the population induces further spawning in the rest of the population (e.g., *Pecten fumatus* Reeve, 1852 [Mendo *et al*. 2014]; *P. magellanicus* [Wahle and Jumars 2014]). Although the phenomenon was not previously demonstrated in Spondylidae, we suggest that *S. spinosus* spawning may induce nearby conspecific spawning, leading to the high synchronisation observed. The high density of sexually-reproductive *S. spinosus* along the Israeli Mediterranean coast may therefore lead to successful reproduction and high fecundity.

The initial presence of a non-indigenous species in a new environment does not necessarily reflect its successful establishment. However, if the environmental conditions are suitable for sexual reproduction, the population might rapidly establish due to an increasing number of reproductive individuals and subsequent recruitment (e.g., Spencer *et al*. 1994; Maggs *et al*. 2010). The reproductive features of *S. spinosus* in the Eastern Mediterranean are characterised by a 1:1 sex ratio, synchronised gonad development of both sexes, and an extended inferred annual spawning period—all indicative of a population with a potential for high fecundity. It is therefore highly probable that this invasive species will continue to maintain flourishing populations over time in its new environment (see also Sakai *et al*. 2001).

We were only able to compare the reproduction features of *S. spinosus* in the Mediterranean Sea to those of the population in the region of origin to a very limited extent, by examining the reproduction of *S. spinosus* at Eilat (northern Gulf of Aqaba), its northernmost native distributional range, under the constraints of an extremely low population size and the strict conservation policy there (Shabtay 2011; Shabtay *et al*. 2013). Following thorough surveys, we located and examined only 15 individuals, and found that in Eilat they were generally much smaller and started reproducing at a smaller size (but not necessarily age) than the Mediterranean population. This finding is interesting, but in order to determine whether these populations have truly different reproductive features a comprehensive sampling of indigenous populations in regions where *S. spinosus* sustains substantial densities is needed.

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