

Population ecology, reproduction, and locomotion of the sand dollar *Sculpsitechinus auritus* (Echinodermata: Echinoidea) in the Gulf of Suez, northern Red Sea

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Abstract The population ecology of the sand dollar *Sculpsitechinus auritus* was studied in shallow coastal habitats of the Gulf of Suez, Egypt, from January 2013 to October 2014. Bimonthly sampling revealed that 95 % of the individuals had a width of 100–145 mm and that juveniles were absent throughout the sampling period. The mean gonadosomatic index (GSI) reached peaks of >2 % in September 2013 and August 2014, which concurred with seasonal highs of water temperature. Declining GSI values indicated that spawning took place between October and January. Histological examination of the gonads confirmed that spawning started in October. Locomotion rate was 88.7 mm h⁻¹ in September, which was significantly higher than 56.3 mm h⁻¹ in December. Similarly, water temperature was significantly higher in September (26 °C) than in December (17 °C), most probably explaining locomotion differences. Organic matter and grain size fractions of the sediment were not significantly different. Maximum density of 0.68 individuals m⁻² was found at 4 m depth, whereas at other depths densities were significantly lower (≤0.05 individuals m⁻²). The epibiotic brittle star *Ophiodaphne scripta* was found on >67 % of the sand dollars and its frequency was significantly higher (>1.5 per host) between September and November coinciding with the onset of *S. auritus*'s spawning period.

Keywords Clypeasteroidea · *Echinodiscus* · Indo-Pacific · Sea urchin · Sediment

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Introduction

The sand dollar *Sculpsitechinus auritus* (Leske 1778) is an echinoid (Echinodermata: Echinoidea: Clypeasteroidea) belonging to the infauna of coastal areas in the Red Sea, the Indian Ocean, and the western Indo-Pacific (Schultz 2010), where it plays an important ecological role by permanently mixing the upper layer of the sediment. *Sculpsitechinus auritus* is one of the largest sand dollar species reaching a maximum diameter of 183 mm (Schultz 2010). It inhabits relatively shallow habitats at 1–5 m depth (Schultz 2010), but has been recorded up to 50 m (Rowe and Gates 1995). Individuals of *S. auritus* are generally found at densities less than 1 individual m⁻², but a maximum density of up to 3 individuals m⁻² has been reported (Nebelsick 1999). Individuals bury themselves 1–2 cm into the sediment in habitats dominated by poorly sorted, fine sands (Piller and Mansour 1990). Locomotion forms an important component of this species' ecology, because, being deposit feeder, it must continuously move to separate organic matter from the sediment. The locomotive ability has been studied for several echinoderms (Mueller et al. 2011), including sand dollars (Yeo et al. 2013). Locomotion of *S. auritus*, however, has never been studied and it is unknown to what extend environmental parameters, such as organic matter content of the sediment and water temperature, affect this ability. Furthermore, density dependent effects on food availability may play a role in locomotion and distribution.

Reproduction of the closely related sand dollar *Echinodiscus bisperforatus* Leske 1778 was studied in coastal habitats of South Africa revealing that this species has an annual reproductive cycle with a single spawning season in December and January, which coincides with increasing water temperatures (Bentley 1998). Other sand dollars have been reported to reproduce biannually (e.g. Olivares-Bañuelos et al. 2012), whereas some

echinoids may even follow the lunar cycle (e.g. Pearse 1968; Pearse et al. 1988; Coppard and Campbell 2005). The reproductive cycle of *S. auritus* has never been studied, and it is unknown what cycle it follows.

Symbiotic relationships in which echinoderm representatives are host are numerous, but these mostly involve epibionts of other phyla (e.g. Seilacher 1979). The brittle star *Ophiodaphne scripta* Koehler (1904) is a small epibiont with a maximum disk diameter of 4 mm known to be hosted by individuals of the sand dollars *S. auritus* and *E. bisperforatus* (Parameswaram et al. 2013). Little is known about the ecological interactions between the echinoid hosts and the brittle star.

The present study aimed at determining the reproductive season of the sand dollar *S. auritus* by analyzing population characteristics and gonad development over time. Moreover, its locomotive ability in relation to sediment quality, food availability, and water temperature, and its role as host for the epibiont *O. scripta* were studied.

Materials and methods

The present study was conducted in the coastal waters of Ain Sokhna, Gulf of Suez, Red Sea, Egypt (approximately 29.72°N and 32.40°E) between January 2013 and October 2014. During each field visit, water temperature was measured at 1 m depth at 1 °C accuracy.

Individuals of *Scalpsitechinus auritus* were studied at approximately bimonthly intervals between January 2013 and October 2014 to determine population size frequencies and growth. This infaunal sand dollar is rarely seen uncovered, but leaves conspicuous tracks in the sediment, like other infaunal echinoids (Lohrer et al. 2004), making them easily located. During each field visit, at least 40 sand dollars were collected during low tide at 0–3 m depth while snorkeling. The width of each individual (maximum length perpendicular to axis between mouth and anus) was measured with calipers at 1-mm accuracy. While measuring, sand dollars were carefully searched for individuals of the brittle star *Ophiodaphne scripta*. The total number of brittle stars per sand dollar host was counted during all field visits except in January 2013.

Densities of *S. auritus* were studied in shallow coastal habitats along a depth gradient (0.5, 2, 4, 6, and 8 m) perpendicular to the shore on 21 March 2014. As the coast of Ain Sokhna is characterized by an extremely gentle slope, subsequent depth localities were separated by about 300 m. At all selected depths, five transects of 20 m², each separated by 5 m, were conducted parallel to the shore using SCUBA. Sand dollars were searched for by following their tracks (see above) and by carefully pulling a plastic shovel through the sediment to possibly detect smaller individuals. Once detected, organisms were uncovered, identified, and the width of the sand

dollars was measured in situ. The density of other echinoid species was additionally recorded.

Fifteen sand dollars with a width ranging from 100 to 140 mm were collected during each field visit for studying seasonal gonad development. After collection, specimens were stored in a freezer at −4 °C until further analysis. In the laboratory, width of each specimen was measured (as explained above) and mass determined at 0.01 g accuracy. Subsequently, gonads were removed under a dissecting microscope and separately weighed at an analytical balance with an accuracy of 0.0001 g. The gonadosomatic index was calculated using the following equation: Gonadosomatic Index (GSI) = wet gonadal mass ÷ wet body mass × 100 (Lane and Lawrence 1979).

Histological examination of gonads was conducted to confirm seasonal changes of gonadal mass by verifying gonadal development at a cellular level in May, August, and October 2014. During field visits in those months, fresh gonads of 10 individuals were immediately fixed in 4 % formaldehyde. In the lab, each gonad was dehydrated through a series of graded ethanol prior to being embedded in paraffin wax. Serial sections (10 μm thick) obtained from the paraffin blocks were mounted on glass slides. From each tissue block, two sections (always sections 7 and 15) were stained with hematoxylin and eosin (Byrne 1990). Stained gonadal sections were used to assess gametogenesis under a microscope at 100× and 400× magnification. Photographs were taken with a digital camera (Leica EC3) mounted on a microscope (Leica DM100).

The locomotion of *S. auritus* individuals was studied in a shallow (2–4 m) sandy bay on 27 September and 21 December 2013 to determine the potential mobility in relation to size of the individuals, sediment quality, food availability, and water temperature. Locomotion was measured by putting a thin labeled stick into the sediment just posterior to the rear of the sand dollar without disturbing the organism. After a time period of about 60 min, a second stick was put into the sediment posterior to the organism's rear. The elapsed time was measured with a stopwatch in seconds and the distance between the two sticks was measured with a ruler (1 mm accuracy). Two extremely curved tracks with a deflection of >90° were removed from the dataset, because the actual travelled distances could not be accurately measured.

A volume of 1350 mm³ of sediment was collected from the upper 2 cm layer alongside each sand dollar track between the labeled sticks used for locomotion measurements. After collecting sediment, sand dollars were carefully removed and their widths measured (as explained above). Water temperature was measured at the bottom of each locality at 1 °C accuracy. Sediment samples were stored in a freezer at −4 °C before further analysis. Dry weight of the sediment was determined by drying the samples in an oven at 105 °C. Organic matter was determined after combusting the sediment in a muffle furnace at 450 °C. Grain size fractions were determined by

putting the samples through four sieves with decreasing mesh sizes (2, 0.2, 0.02, 0.002 mm). Each fraction was weighed on an analytical balance at 0.0001 g accuracy.

Sand dollar width frequencies were presented in a 12-month graph, because new cohorts were not observed during the 22-month sampling period. A slight shift in timing of the bimonthly sampling occurred, causing January and May to be sampled in both years and no data to be collected in February, April, and July.

One-way ANOVA was used to test for differences between sand dollar width at varying depths, monthly GSI, and brittle star frequency hosted by *S. auritus*. Homogeneity of variances of the GSI (Levene's Test: $L_{9,142} = 1.977$; $p = 0.046$) was significantly different between months. Therefore, square root transformation was applied to meet the test assumptions (Levene's Test: $L_{9,142} = 1.324$; $p = 0.229$). Data of brittle star frequencies and sand dollar density were transformed by the square root of $X + 0.5$ to correct for uninhabited sand dollars and transects without sand dollars (zeros in the database). The Tukey HSD test was used for post hoc analyses ($\alpha = 0.05$).

The non-parametric Mann–Whitney-U test was used for testing differences between data representing sand dollar locomotion rate, organic matter and grain size fractions of the sediment, and water temperature, because these were not normally distributed and data transformations did not result in homogeneity of variances. The relationship between sand dollar width and wet body mass varied between months with a mean GSI $>1.5\%$ (reproductive period) and $<1.5\%$ and width and mass data were pooled into two groups. The corresponding exponential relationships $M = a \times W^b$, with M = wet body mass (g), W = width (cm), and a and b two constants, were corroborated by curve fitting with SigmaPlot (Version 11). One-way ANCOVA was used to test for a difference in slope.

Results

A total of 642 individuals of *Sculpsitechinus auritus* were measured between January 2013 and October 2014 (Fig. 1). The vast majority (95.0 %: $n = 610$) had a width larger than 100 mm. The few individuals with a width smaller than 100 mm were neither found in a particular month nor in a particular season. The smallest and largest individuals, with a width of 78 and 145 mm, respectively, were both found in May (Fig. 1). Population growth could not be determined due to the absence of small individuals (<78 mm) and lack of monthly size increments between successive observations.

Mean density of *S. auritus* was 0.68 individuals m^{-2} at 4 m depth. Maximum density was 0.90 individuals m^{-2} in one transect at 4 m. At 0.5, 2, 6, and 8 m depth, *S. auritus* was found at significantly lower densities (ANOVA: $F_{4,20} = 65.066$, $p = 0.000$) with a maximum of 0.05 individuals m^{-2} at 6 m. *Sculpsitechinus auritus* was completely absent at 0.5 m. The

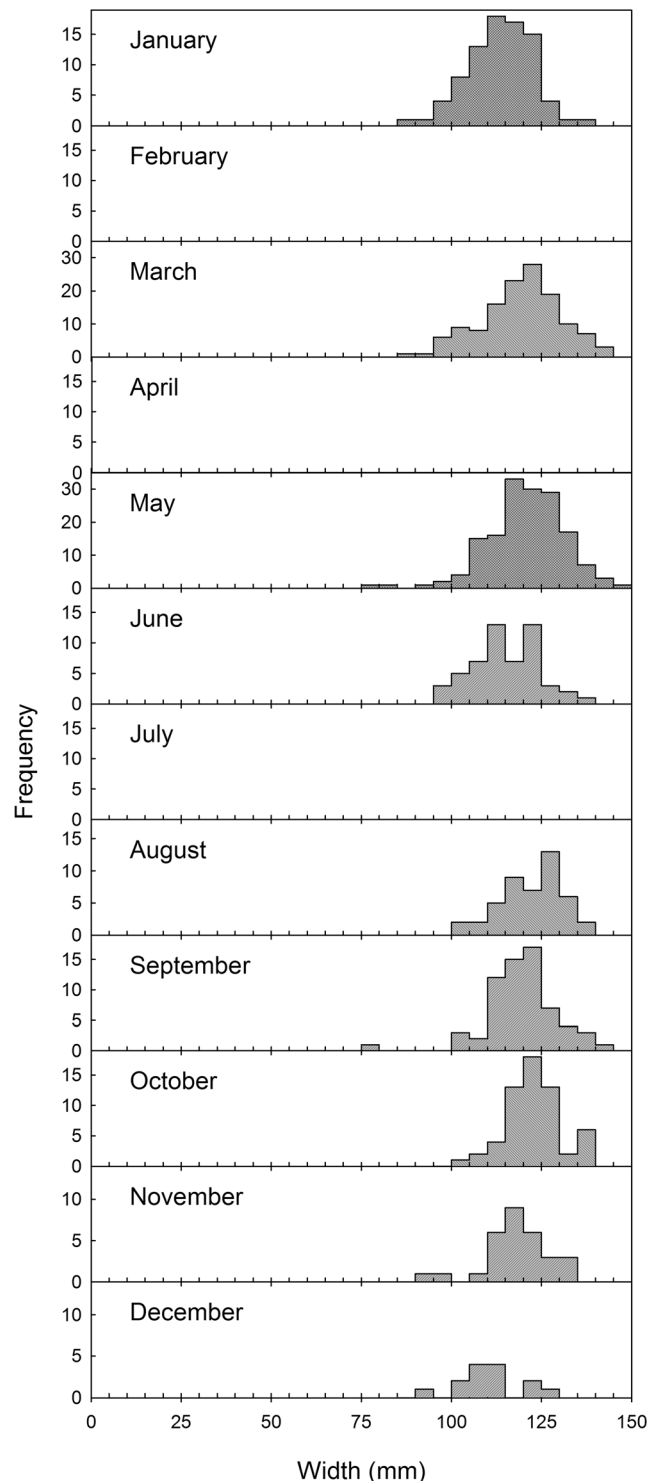


Fig. 1 *Sculpsitechinus auritus*. Bimonthly width frequency distributions from January 2013 to October 2014. Data from 2013 and 2014 are represented by a forward and backward diagonal patterns respectively. No data available for February, April, and July

width of *S. auritus* individuals was not significantly different between depths (ANOVA: $F_{3,74} = 1.153$, $p = 0.334$) with a mean width of 122.6 mm. Individuals of the sand dollars *Echinodiscus bisperforatus* and *Clypeaster humilis* were observed in transects,

but their densities were only high at depths where *S. auritus* was uncommon. The echinoid *Lovenia elongata* was found in high densities (as high as 220 individuals 100 m⁻²) at 4 m depth.

Mean GSI ranged from 0.8 to 2.6 % (Fig. 2) and was significantly different between months (ANOVA: $F_{9,142} = 13.009$; $p = 0.000$). Post hoc analysis revealed that the mean GSI was always significantly higher when exceeding 1.5 % (Table 1) compared to months when a lower mean GSI was found (Fig. 2). The highest mean GSIs of 2.6 and 2.4 % were found in September 2013 and August 2014, respectively, both occurring when water temperature was high. The highest GSI value for an individual sand dollar was 4.5 % observed in August 2014. Mean GSI declined in November 2013 and October 2014, indicating that spawning had started. In the first year, mean GSI was relatively high until January 2014 suggesting that spawning was still ongoing. Water temperature reached its peak at 26 °C in September 2013 and 27 °C in August 2014 (Fig. 2). Lowest water temperatures of 17–18 °C were found in December and January in both years.

The relationship between sand dollar width and wet body mass was significantly higher during months when mean GSI was >1.5 % (ANCOVA: $F_{1,149} = 42.951$; $p = 0.000$) than during months when the mean GSI was lower (Fig. 3). The exponential function $M = 0.0323 \times W^{2.993}$ ($r^2 = 0.391$, $n = 94$) described the width mass relationship for the reproductive period (mean GSI > 1.5 %), whereas $M = 0.0393 \times W^{2.8203}$ ($r^2 = 0.622$, $n = 58$) described the width mass relationship for other months (Fig. 3).

Histological examination of gonads confirmed that gametogenesis in *S. auritus* was in a terminal stage in October 2014 (Fig. 4). Spermatogenesis, based on the maturity of spermatozoa, their abundance and location, suggested that males were ready for spawning in October (Fig. 4a–d). Primary spermatoocytes and nutritive material filled the recovering testes in May (Fig. 4a). Maturing spermatozoa populated the lumen of premature testes, while nutritive material was less abundant in August (Fig. 4b). Maturing spermatozoa were produced and released into the lumen by the spermatoocyte columns (Fig. 4b) that lined the germinal epithelium of the pre-mature testes.

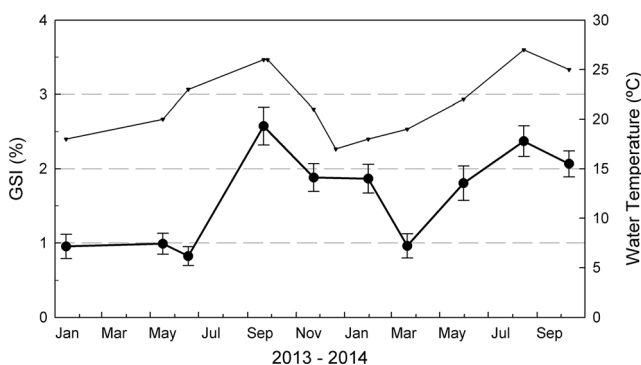


Fig. 2 *Sculpisitechinus auritus*. Mean Gonadosomatic Index (black dots) with standard error and water temperature (°C) from January 2013 to October 2014

Mature spermatozoa were present in the lumen in October (Fig. 4c and d).

Oogenesis, based on the amount of nutritive material and the size of oocytes, indicated that the females gonads were also ripe in October 2014 (Fig. 4e–h), occurring synchronically with spermatogenesis. The nutritive material was abundant in the recovering ovary in May (Fig. 4e) and dispersed throughout the premature ovary in August (Fig. 4f). The majority of gametes in the premature ovary were vitellogenic oocytes while only few were previtellogenic. Mature oocytes were mostly abundant in October (Fig. 4g and h) and nutritive material was rarely observed in partially spawned ovaries.

Individual locomotion rates varied between 22.3 and 165.0 mm h⁻¹. The mean locomotion rate of 88.7 mm h⁻¹ in September was significantly higher than 56.3 mm h⁻¹ in December 2013 (Table 2). Locomotion rate was not significantly correlated to the width of the individuals (Linear regression: $r^2 = 0.14$, $n = 25$, $p > 0.05$). However, the water temperature of 26 °C in September was significantly higher than 17 °C in December (Table 2). The organic matter content of the sediment of 1.38 % in September and 1.31 % in December were not significantly different (Table 2). Ninety-three percent of the sediment was dominated by grain sizes smaller than 0.02 mm, while half of that fraction was smaller than 0.002 mm (Table 2). The various grain size fractions were not significantly different between September and December 2013 (Table 2).

The number of *S. auritus* individuals hosting the brittle star *Ophiodaphne scripta* varied between 31.5 and 76.7 % (Table 3). However, only in September, October, and November, at least 67 % of the sand dollars hosted brittle stars. During other months the hosting percentage was lower (Table 3). The mean number of brittle stars ranged from 0.38 to 2.63 individuals per sand dollar (Table 3). The mean number of brittle stars per host was significantly higher in October (Tukey HSD, $p < 0.05$) compared to all other months but September and November. Furthermore, the mean number of brittle stars per host was significantly higher in September (Tukey HSD, $p < 0.05$) than in January, March, May, and June. The high percentage of hosting sand dollars and the high number of brittle stars per host coincided with the onset of the spawning period of *S. auritus*.

Discussion

Reproduction of *S. auritus* was confirmed to follow an annual cycle, as observed in many other sand dollars (e.g. Bentley 1998) and echinoids (e.g. Gonor 1973). The GSI showed a peak in gonad mass in August and September during two consecutive years (Fig. 2). Furthermore, histological examination confirmed that both male and female gonads were ripe in October (Fig. 4). Generally speaking, water temperature is an important parameter regulating the reproductive cycle of

Table 1 *P*-values resulting from Tukey HSD post hoc comparison of the monthly Gonadosomatic Indexes of *Sculpisitechinus auritus* from January 2013 to October 2014

	2013					2014			
	Jan	May	Jun	Sep	Nov	Jan	Mar	May	Aug
May 2013	1.000	–	–	–	–	–	–	–	–
Jun	1.000	0.995	–	–	–	–	–	–	–
Sep	<u>0.000</u>	<u>0.000</u>	<u>0.000</u>	–	–	–	–	–	–
Nov	<u>0.028</u>	<u>0.014</u>	<u>0.000</u>	0.481	–	–	–	–	–
Jan 2014	<u>0.033</u>	<u>0.017</u>	<u>0.000</u>	0.390	1.000	–	–	–	–
Mar	1.000	1.000	1.000	<u>0.000</u>	<u>0.002</u>	<u>0.002</u>	–	–	–
May	0.077	<u>0.047</u>	<u>0.001</u>	0.178	1.000	1.000	<u>0.007</u>	–	–
Aug	<u>0.000</u>	<u>0.000</u>	<u>0.000</u>	1.000	0.814	0.733	<u>0.000</u>	0.445	–
Oct	<u>0.003</u>	<u>0.001</u>	<u>0.000</u>	0.854	1.000	0.998	<u>0.000</u>	0.969	0.990

Underlined *p*-values are ≤ 0.05

echinoderms (e.g. Bos et al. 2008; Pearse 1968). Moreover, the closely related sand dollar *Echinodiscus bisperforatus* has an annual spawning season in December and January coinciding with high water temperatures (Bentley 1998). In the present study, gonads of *S. auritus* developed with increasing water temperatures (Fig. 2). Therefore, it seems plausible that gametogenesis of *S. auritus* is mainly affected by seawater temperature. Similarly, the gonad development of the sea urchin *Echinometra mathaei* was triggered by increasing water temperature and spawning occurred during late summer and fall in the Gulf of Suez (Pearse 1969). Also, Bronstein and Loya (2015) confirmed the water temperature to be the determining factor of the annual reproductive season of *E. mathaei* in the northern Bay of Aqaba, northern Red Sea, with peak spawning occurring in September and October. Moreover, Pearse (1969) found that *E. mathaei* in southern waters of the Gulf of Suez, where the water temperature difference between summer and winter was much smaller, did not reproduce during a well-defined season. Although other environmental factors may play a role in the timing of reproduction of echinoids, water temperature seems to be the major determining parameter.

Mean GSI of *S. auritus* was 2.6 % at its peak in September 2013 and a similar value was found in August 2014 (Fig. 2). In other echinoderms much higher GSI values have been observed at the onset of the spawning season (e.g. Bos et al. 2013), but those of sand dollars are generally lower. For example, mean GSI of the sand dollar *Dendraster excentricus* ranged from 2.0 to 6.5 % (Olivares-Bañuelos et al. 2012). Bentley (1998) reported GSI values of 1.5 to 6.0 % for *Echinodiscus bisperforatus*. Even lower values were found for the sand dollar *Mellita quinquesperforata* with a mean GSI of 0.3 to 1.6 % (Tavares and Borzone 2006). Despite low values, Tavares and Borzone (2006) were able to detect a peak season for females, but seasonality was unclear for males. During the present study however, reproductive

seasonality of *S. auritus* was confirmed based on combined data of male and female gonads.

The population of *Sculpisitechinus auritus* consisted exclusively of adults, because the vast majority of individuals had tests wider than 100 mm (Fig. 1). The absence of juveniles throughout the study period of 22 months could be explained by juveniles occupying a different habitat than adults. Habitat changes during ontogenetic development have been observed in other echinoderms, including sand dollars. For example, Yeo et al. (2015) reported juveniles of the sand dollar *Peronella lesueuri* to be very rare in a population in western Australia. Although this sand dollar grows to a similar size as *S. auritus*, the smallest individual found had a diameter of 5 cm (Yeo et al. 2015). Bos et al. (2011) found a clear ontogenetic separation of sea stars in shallow coastal waters in the western Pacific with juveniles inhabiting relatively protected habitats, such as mangrove prop roots and seagrasses, whereas large adults were exclusively found on wave-exposed sand

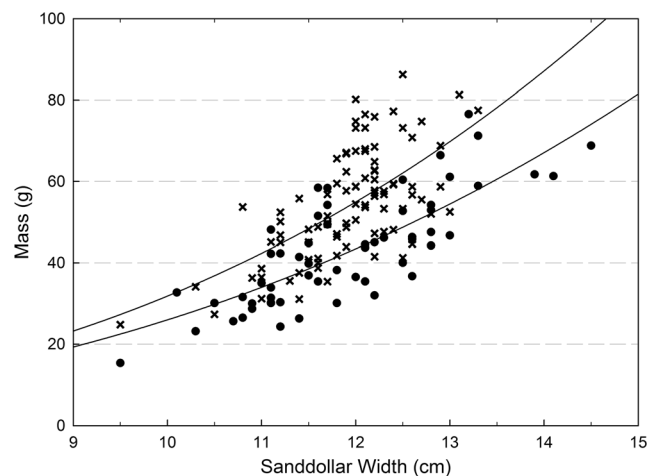


Fig. 3 *Sculpisitechinus auritus*. Sand dollar width (cm) and wet body mass (g) relationships for months during the reproductive period with mean GSI > 1.5 % (cross) and during the rest of the year (black dot)

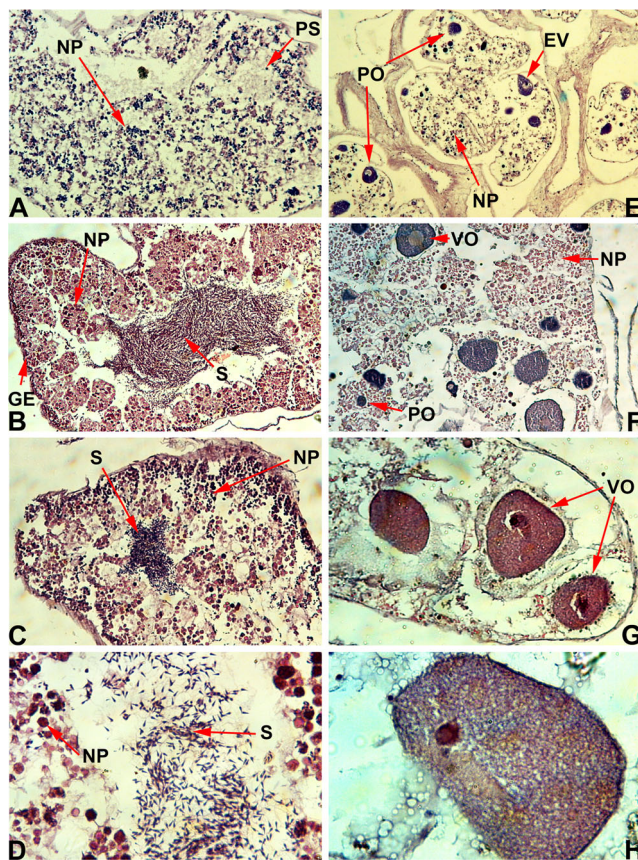


Fig. 4 Gametogenesis of *Sculpisitechinus auritus*. **a** May 2014. Recovering testis mainly filled with nutritive phagocyte (NP) meshwork and primary spermatocytes (PS = darkly stained cells at 100× magnification). **b** August 2014. Premature testis with darkly stained germinal epithelium (GE) wall lined with NP and many spermatozoa (S) accumulating in lumen at 100×. **c** October 2014. Partially spawned testis characterized by mature sperm in lumen. Few NP at 100×. **d** October 2014. Mature sperm occupied lumen of partially spawned testis at 400×. **e** May 2014. Recovering ovary filled with NP meshwork and few oocytes. Oocytes at previtellogenic stage (PO) and very few at early vitellogenic stage (EV) at 100×. **f** August 2014. Premature ovary mainly filled with vitellogenic oocytes (VO) and very few PO at 100×. **g** October 2014. Partially spawned ovary with VO and ripe ova at 100×. Void of NP. **h** October 2014. Mature oocyte at 400×

banks. In the Gulf of Suez, mangroves are absent, but there are some sparse seagrass meadows (pers. observation) where juvenile sand dollars could settle. Also, juveniles may settle in deeper locations after their pelagic larval phase. However, the option of juveniles migrating from deeper sediments to shallow shore habitats seems not plausible for the following reasons: First, the study area has an extremely gentle slope separating habitats by long distances; second, densities of *S. auritus* were significantly lower at 6 and 8 m than at 4 m depth; third, sand dollars size did not vary significantly between different depths. The latter two observations, however, were done in March 2014 and could be different in other seasons. Alternatively, the studied population of *S. auritus* may consist of very long lived adults while replenishment

Table 2 Locomotion rate (mm h^{-1}) of *Sculpisitechinus auritus*, water temperature ($^{\circ}\text{C}$), and organic matter (%) and four grain size fractions (%) of the sediment in September and December 2013 presented with standard errors between brackets

	September	December	<i>p</i> -value
Locomotion rate	88.7 (8.6)	56.3 (5.2)	0.011
Water temperature	26 (0.0)	17 (0.0)	0.000
Sediment			
Organic matter	1.38 (0.05)	1.31 (0.01)	0.291
GF 0.2–2 mm	2.90 (0.30)	3.12 (0.30)	0.645
GF 0.02–0.2 mm	3.42 (0.18)	3.76 (0.30)	0.505
GF 0.002–0.02 mm	47.14 (6.80)	43.59 (5.64)	0.878
GF <0.002 mm	46.57 (6.55)	49.56 (5.64)	1.000

p-values result from Mann–Whitney–U comparison

may be at a very low annual rate or by rare events of unusually high recruitment (Ebert 2008). However, we did not observe small individuals nor test dead juveniles. Ecological knowledge of juvenile echinoderms in general and of juveniles of *S. auritus* in particular is needed to support profound decisions in coastal management and should have a high priority in future research.

Mean locomotion rate of *S. auritus* was significantly higher in September (88.7 mm h^{-1}) than in December (56.3 mm h^{-1}). Also, water temperature was significantly different between those months, whereas organic matter and grain fractions of the sediment did not vary significantly. This suggests that the water temperature is the factor that determines locomotion rate of *S. auritus*. Similarly, the sand dollar *Peronella lesueurii* had a mean movement rate of 53 mm h^{-1} in summer, which was significantly higher than the mean rate of 27 mm h^{-1} in winter (Yeo et al. 2013). The authors concluded that seasonal change in water temperature and physiological requirements were the most likely reason for the seasonal difference in locomotion. The latter species has a similar size (maximum width of 150 mm) as *S. auritus*, but is suspension feeder and not deposit feeder. The difference in feeding strategy may explain the higher locomotion rates found for *S. auritus* during the present study.

Grain size and organic matter content of the sediment is extremely important for a deposit feeder such as *S. auritus*, because they determine the efficiency of feeding. During the present study, these two parameters did not vary between summer and winter. Moreover, individuals were found at the exact same depth in the shallow habitats throughout the year, suggesting that the composition of the sediment determines the presence of this species. The sediment was relatively fine with grain sizes of 45 % between 2 and 20 μm and 50 % smaller than 2 μm . Preferred sediment grain size was determined for the sand dollar *Mellita tenuis* being relatively coarse sediment particles of 250–499 μm (Pomoroy et al. 1995).

Table 3 Percentage of *Sculpisitechinus auritus* individuals hosting the brittle star *Ophiodaphne scripta* (%) and mean number of brittle stars per host (\pm standard error) between May 2013 and October 2014

	2013				2014			
	May	Jun	Sep	Nov	Mar	May	Aug	Oct
Hosting sand dollars	59.6	31.5	76.7	67.7	50.9	43.8	52.2	74.6
Brittle stars per host	1.32 (0.15)	0.59 (0.14)	1.74 (0.27)	1.52 (0.28)	0.64 (0.11)	0.67 (0.14)	1.17 (0.22)	2.63 (0.36)

Also, Borzone et al. (1998) found a narrow depth distribution of the sand dollar *Mellita quinquesperforata* most probably based on the portion of fine material in sandy sediments. Varying grain size of sediments may thus be a determining factor for niche segregation between sympatric sand dollar species.

The sand dollars *E. bisperforatus* and *S. auritus* live in sympatry throughout the Red Sea and Indian Ocean (Schultz 2010). They are both found in shallow coastal habitats with the same depth distributions, but *E. bisperforatus* has a smaller size and reaches its maximum width at 80 mm (Bentley and Cockcroft 1995; Schultz 2010). Researchers have mostly reported observing only one of the two species during their studies in coastal habitats (Price 1981; Ong and Krishnan 1995; Raut et al. 2005). However, Nebelsick (1999) reported the presence of both species at the same locality. During the present study, two sand dollar species were found at varying depths with finer (*E. bisperforatus*) and courser (*Clypeaster humilis*) sediment compositions (pers. observation AR Bos). Congregations of these sand dollars were found at other depths than where *S. auritus* was abundant. An interesting follow-up would be a comparative study to the preferred sediment compositions of the deposit feeding sand dollars, in particular the morphologically similar species *S. auritus* and *E. bisperforatus*.

Sand dollar densities vary dramatically with species partly depending on their feeding strategies. Density dependent effects may mainly occur in deposit feeders competing for the same sediment, whereas filter feeders continuously receive new organic material by the prevailing currents supporting higher densities. Suspension feeders such as *Dendroaster excentricus* may reach extreme densities of 1300 individuals m^{-2} (Merrill and Hobson 1970), whereas deposit feeders such as *Mellita quinquesperforata* may reach a maximum density of 500 individuals m^{-2} (Tavares and Borzone 1998) probably consisting of mostly juveniles after successful recruitment. The deposit feeder *E. bisperforatus* was reported to occur at 44 individuals m^{-2} (Ong and Krishnan 1995) and has a width range of 60–80 mm, which is similar to that of the earlier two species (Schultz 2010). This relatively high density may be supported by the smaller size of *E. bisperforatus* than that of *S. auritus*, which reached a maximum density of 0.9 individuals m^{-2} in the present study.

At 4 m depth, the density of the deposit-feeding heart urchin *Lovenia elongata* was almost 2 individual m^{-2} being about three times higher than that of *S. auritus*. A cumulative density for the two species resulted in a density of 2.5 individuals m^{-2} , still being much lower than the reported densities of 200 individual m^{-2} for *L. elongata* (Ferber and Lawrence 1976). With a similar depth distribution, *S. auritus* and *L. elongata* may compete for the same food source. However, the different shapes of their tests suggest that *L. elongata* feeds slightly deeper in the sediment than *S. auritus* (Schultz 2010) allowing for niche segregation.

Echinoids have tests of fused calcium carbonate plates which fossilize well (Schultz 2010). Therefore, echinoids are, among echinoderms, the most abundant representatives in the fossil record. High density assemblages of fossil sand dollars in Egypt were considered to be the result of accumulations induced by storms and winnowing (Kroh and Nebelsick 2003). As a result of reproductive strategies, many echinoderm populations have the ability to fluctuate highly and appear in very high or low densities depending on predominant environmental conditions (Uthicke et al. 2009). It is, therefore, important to understand density fluctuations of echinoderms in shallow coastal habitats and how these affect the population ecology of other coastal inhabitants.

Conclusion

This study is a contribution to the knowledge on the reproduction and growth of sand dollars that are highly understudied compared to other representatives of the Echinoidea. We provide new ecological information of *S. auritus* through observations on a population in the Bay of Suez, northern Red Sea, Egypt. This sand dollar reproduces annually with its spawning period from October to January, while the annual water temperature regime determines the timing of gametogenesis. During the spawning period, *S. auritus* is an attractive host for the symbiotic brittlestar *O. scripta*. Highest densities of *S. auritus* were found at 4 m depth suggesting that it is most successful at this depth, possibly avoiding competition with other echinoids. Water temperature also affects the locomotive ability of *S. auritus* as individuals move faster during summer than during winter. The relatively low locomotion rates (56–

89 mm h⁻¹) allow efficient filter feeding, but do not support long migrations. Therefore, the absence of juveniles in the studied population forms an interesting topic for future research on this species and other echinoids. Furthermore, continued research may focus on individual growth and age and how recruitment takes place.

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