

## Salinity-dependent sieve pore variability in *Cyprideis torosa*: an experiment

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**Abstract:** Salinity-dependent sieve pore variability in *Cyprideis torosa* (Jones) is tested and confirmed through a culture experiment investigating valves from a salinity range between 0.6 and 14.8. In contrast to results from a previous study, the proportion of sieve pore shapes shows a slight offset at higher values probably caused by relatively lower calcium concentrations in our microcosms. Besides ion concentration, salinity variability and ion composition are assumed to be driving factors for sieve pore shapes, as for the case of nodding in *Cyprideis torosa*. Despite some limitations in using sieve pore shapes as a proxy in quantitative salinity reconstructions in athalassic water bodies, an application for detecting trends and salinity changes in fossil associations and for quantitative reconstructions in marginal marine waters is feasible and adds a valuable salinity proxy, especially for the oligohaline to mesohaline salinity range.

**Keywords:** Ostracoda, microcosms, morphological variation, salinity proxy, brackish water, calcification

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Sieve pores in ostracods are special forms of normal pores, i.e. canals running from the internal side through the outer lamella of the valve and opening on its external surface. They occur in species of the superfamily Cytheroidea Baird (Omatsola 1970). Those canals are externally closed by a sieve plate composed of one small opening bearing a bristle and many other small openings arranged evenly spaced around (Fig. 1). They can be arranged level with the external surface of the valve or depressed; in *Cyprideis torosa* (Jones) they are on the same level as the valve surface (Keyser 1980). The sieve plates have a diameter of about 10 µm, but the tiny openings around the bristle measure <0.5 µm in *C. torosa*. The position of the sieve pores on the valves stays constant but their number increases through ontogeny (Rosenfeld 1982). More details on sieve pore structure can be found in Puri (1974).

The function of sieve pores is still unclear. The bristles coming out of each sieve pore occur in different types (Sandberg & Plusquellec 1969) and have the function of a tactile sensilla (Pokorný 1958; Hartmann 1966; Omatsola 1970; Puri 1974) or may be thermo- or chemotropic (Omatsola 1970). The sieve pore itself, however, was interpreted as an organ of light perception (Müller 1894; Hartmann 1963) and as openings for microvilli secreting substances for protection of the sensilla (Puri 1974). Such microvilli were documented in sieve plates of *Cyprideis torosa* by Keyser (1980), or as supporting oxygen uptake by osmosis (Puri 1974).

In 1976, Rosenfeld & Vesper described for the first time a salinity-dependent variability of sieve pore shapes in the valves of *Cyprideis torosa* (Jones). They observed a logarithmic correlation between salinity of the ambient water and the proportion of round sieve pores on adult valves of this common brackish-water ostracod (Vesper 1972). Those observations have significant implications for its use as a palaeo-salinity indicator because quantitative reconstructions may become possible. Because *Cyprideis torosa* is a euryoecious species which tolerates a broad range of salinities between freshwater and hypersaline conditions (Meisch 2000), it is often dominant or even monospecific in oligohaline or hypersaline waters (Pint *et al.* 2012). In such low diversity associations, mutual range methods or transfer functions based on species assemblages

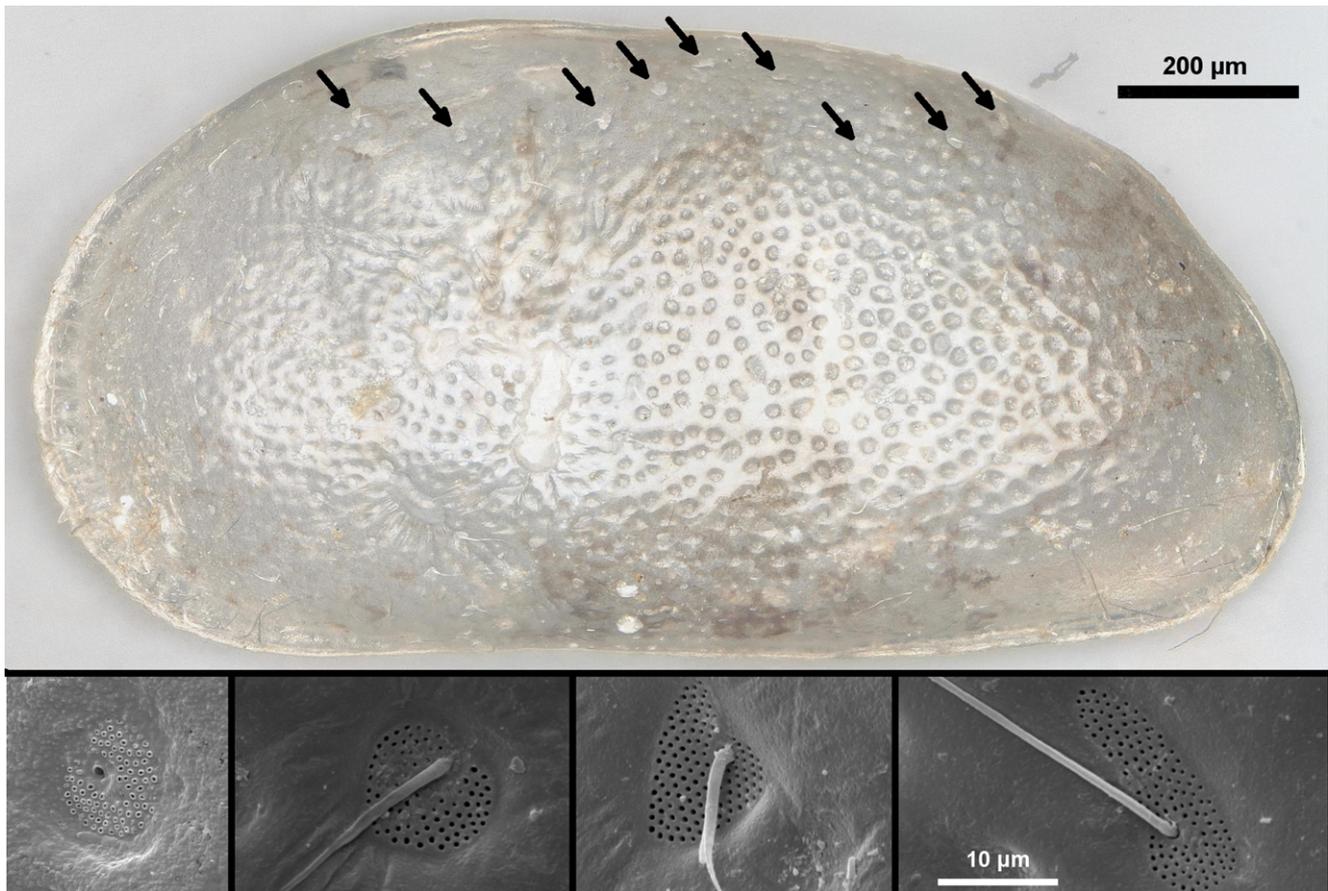
are less useful and could be replaced or complemented by a morphological approach, such as sieve pore variation. Surprisingly, Rosenfeld & Vesper's results were rarely used in palaeoenvironmental analysis and never tested with Recent material. Gliozzi & Mazzini (1998) and Anadón *et al.* (2002) investigated marginal-marine associations with success in central Italy, whereas Keatings *et al.* (2007) and Engel *et al.* (2012) documented over-estimations of palaeo-salinity for athalassic associations in Egypt and Saudi Arabia, respectively. Rosenfeld (1977), Bonaduce & Sgarrella (1999) and Grossi *et al.* (2015) tested sieve-pore variations in another *Cyprideis* species, *Cyprideis agrigentina* Decima. For this species, Grossi *et al.* (2015) did not find correlations between sieve pore shape variation and other palaeo-salinity proxies. Reeves *et al.* (2007), however, found a correlation of sieve pore shapes and palaeo-salinity trends in *Cyprideis australiensis* Hartmann in cores from the palaeolake Carpentaria in Australia. It seems that Rosenfeld & Vesper's (1976) results are only applicable to *Cyprideis torosa* valves and should be used with caution in other species.

In the present study, we test the correlation of salinity and sieve pore shape variation by analysing *Cyprideis torosa* populations grown in microcosms within a known salinity gradient.

### Material and methods

The present study uses material from a *Cyprideis torosa* culture experiment published by Frenzel *et al.* (2012) investigating valve nodding.

Four replicates of microcosms, each in eight salinity levels between initially 0.5 and 13 (psu), were set up in 2002. Each microcosm was kept in glass jars of 4.5–7.5 cm diameter and 3–4 cm height filled with several millimetres of fine to medium sand, which was previously heated at 60°C for 16 h to kill other organisms and their eggs and cysts. After cooling, the sand was covered by water. This water with a salinity of 13 was collected from the Salzhaff, a large lagoon at the southern Baltic Sea coast between the cities of Wismar and Rostock. The intended salinity levels of 0.5, 1, 3, 5, 6, 7, 9, 11 and

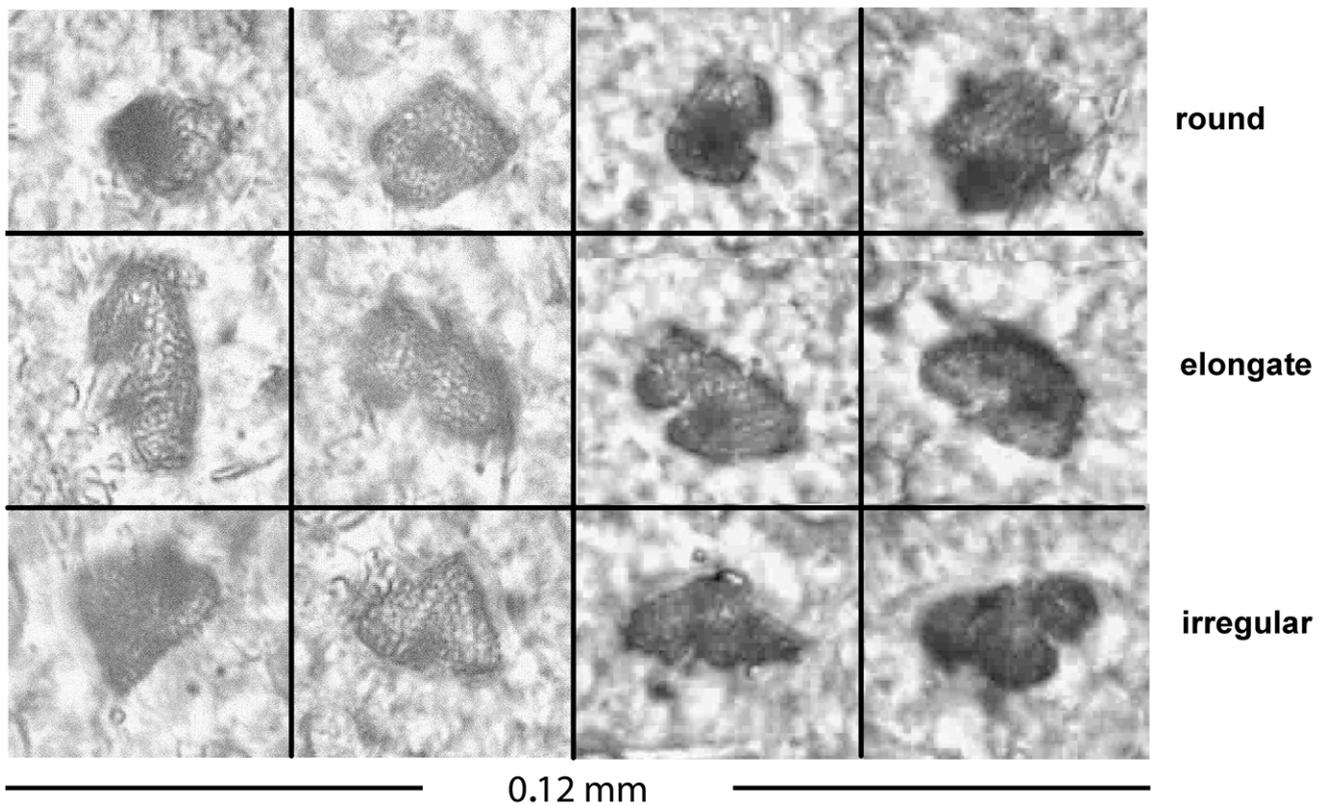


**Fig. 1.** Light microscope photograph of a male left valve of *Cyprideis torosa* (arrows indicate sieve pores of the dorsal area) from a microcosm of lowest salinity and, below (from left to right), scanning electron microphotographs (SEM) of two round sieve pores of a fossil (Holocene) valve and a Recent valve, respectively, as well as an irregular and an elongate Recent sieve pore from the southern Baltic Sea coast. Scale of 10 µm applies to all SEM photographs.

13 were obtained by adding distilled water to the natural brackish water thus diminishing ion concentrations. To keep those salinity levels, glass lids were placed over the microcosms to hamper evaporation and salinity was checked every one to three weeks using a conductivity probe. Each time, distilled water was added until the required salinity was restored. Thus, salinity varied only slightly, reaching a mean standard deviation of only 0.7 (max 1.9).

The ostracods used for the experiment were obtained by sampling surface sediments from shallow water of the Breittling, a lagoon in the Warnow estuary in Rostock, four times between March and April 2002. Ambient salinity ranged between 6.8 and 12.5 and the water temperature ranged between 5.0 and 6.5°C. Adult individuals were picked from the sediment samples using tweezers under a low power stereo-microscope. Every microcosm consisted of ten female and five male individuals, thus reflecting the average sex ratio of the original lagoon population. The culture was kept at room temperature (18.3–26.8°C) under shaded natural light conditions. Diatoms (*Nitzschia* sp.) and a piece of sea grass were added to each microcosm as food source for the ostracods. When checking salinity, bacteria films at the water surface of the microcosms appeared in some of the jars. Those films were removed in order to improve oxygen diffusion. Adult individuals were extracted from the microcosms after juveniles were observed in most of them. This was done between 84 and 113 days after starting the microcosms to ensure that later all adult individuals from the microcosms were individuals that would have moulted for their whole life time within the microcosms under defined conditions. The culture was monitored for 526 days in total and then ostracods were fixed with 70% ethanol.

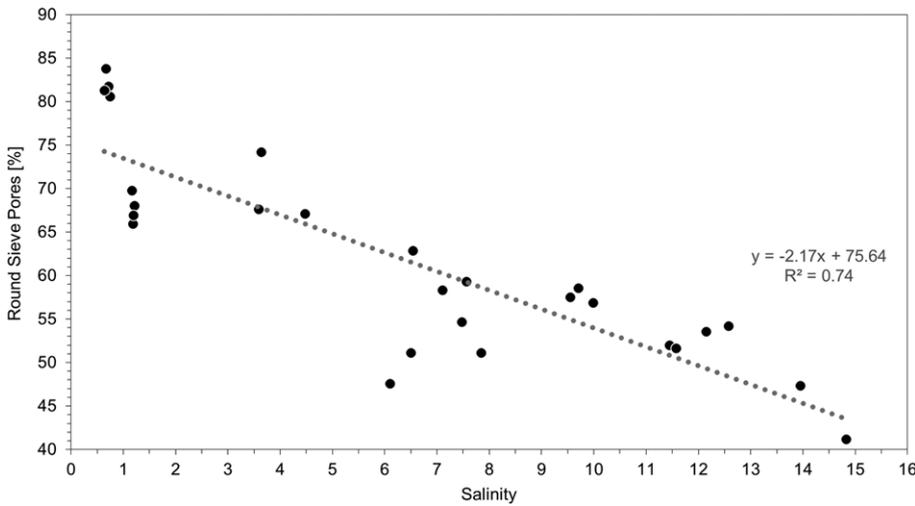
After culturing was completed, all adult individuals were picked from the microcosms. Soft parts were removed with a fine brush after treatment with 10–15% NaOH. The isolated and cleaned valves were examined in water under a microscope in transmitted light using a magnification of  $\times 200$ . We first used stacked light microscope photographs for sieve pore shape analysis, but changed to a classical single focus level thereafter because of identification problems: Irregular sieve pores tend to appear round if stacked photographs are used. This phenomenon causes overestimation of round sieve pore proportions and a much lower change of proportion along the salinity gradient making application for palaeo-salinity reconstruction much less exact. Following the procedure of Rosenfeld & Vesper (1976), we discriminate between round, elongate and irregular sieve pores. Elongate and round sieve pores are distinguished by a largest diameter of more than  $1.5\times$  the shortest diameter for elongate and less difference for round outlines. An irregular shaped pore was identified by a clearly triangular, y-shaped or heart-shaped outline. It is noteworthy that round sieve pores may appear heart-shaped but in a less concise pattern; however, if there was a concave embayment recognizable at the periphery, we classified such a sieve pore as being irregular (Figs 1 and 2). At least 15 valves per microcosm, if available, were investigated by counting 30 sieve pores per valve, and also by avoiding those on the steep ventral, dorsal and posterior parts of the valves. The numbers of sieve pore types were documented for all specimens individually and averages for microcosms were calculated as an average over all individuals and not by comparing sums of all sieve pore types of a given microcosm as applied by Rosenfeld & Vesper (1976) for their samples. This gives us the opportunity to document variance within the populations of microcosms.



**Fig. 2.** Light microscope photographs of several types of round, elongate and irregular sieve pores of *Cyprideis torosa* grown during our experiment. The photographs give the standard counting images.

**Table 1.** Results of sieve pore analysis from the lab culture

Microcosm	Mean salinity	SD of salinity	Number of analysed individuals	Proportion of round sieve pores (mean in %)	SD of sieve pore proportion
A1/2	14.9	1.9	2	40.0	0.0
A1/3	14.8	1.9	14	41.2	4.0
A1/4	14.0	1.1	15	47.3	2.5
A2/1	11.4	0.9	30	52.0	3.6
A2/2	11.6	0.6	15	51.7	3.2
A2/3	12.1	1.2	15	53.6	4.9
A2/4	12.6	1.5	15	54.2	1.5
A3/2	9.5	0.6	15	57.6	3.5
A3/3	10.0	1.0	15	56.9	3.5
A3/4	9.7	0.4	14	58.6	3.3
A4/2	7.6	0.4	15	59.3	1.3
A4/3	7.5	0.4	15	54.7	2.0
A4/4	7.8	0.8	15	51.1	4.1
A5/1	7.1	1.1	15	58.3	3.1
A5/2	7.2	0.7	5	48.0	5.4
A5/3	6.5	0.5	15	62.9	3.4
A6/1	6.5	0.9	12	51.1	3.1
A6/2	6.1	0.6	14	47.6	2.9
A7/1	3.6	0.3	15	74.2	4.6
A7/2	3.6	0.3	15	67.6	5.2
A7/3	4.5	1.6	15	67.1	5.4
A7/4	3.6	0.3	8	64.4	4.1
A8/1	1.2	0.2	12	68.0	2.9
A8/2	1.2	0.1	10	66.0	4.1
A8/3	1.2	0.2	15	67.0	3.3
A8/4	1.2	0.1	15	69.8	3.8
A9/1	0.7	0.2	13	81.8	3.8
A9/2	0.7	0.2	10	80.6	3.6
A9/3	0.6	0.1	15	81.3	3.4
A9/4	0.7	0.1	14	83.8	2.8



**Fig. 3.** Proportion of round sieve pores in adult *Cyprideis torosa* (both sexes) from the culture experiment v. salinity. Every data point represents an average value for all valves analysed within one single microcosm. Microcosms with <10 valves are omitted.

**Results**

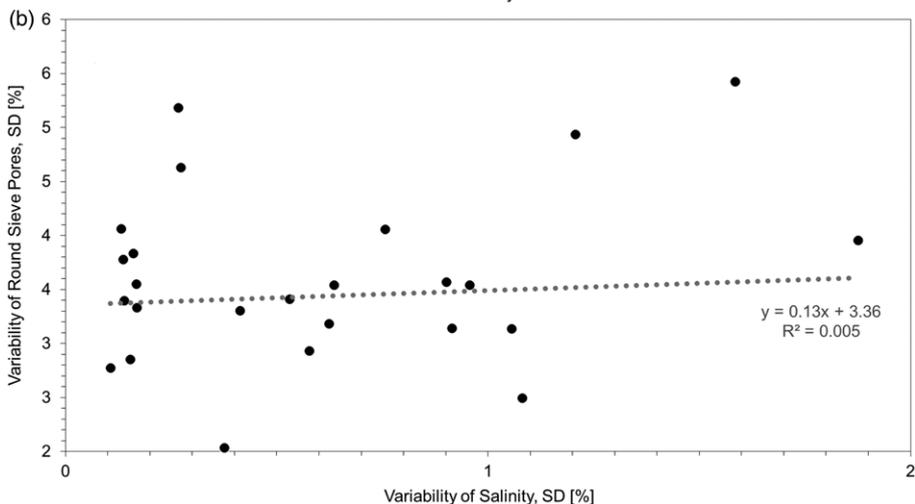
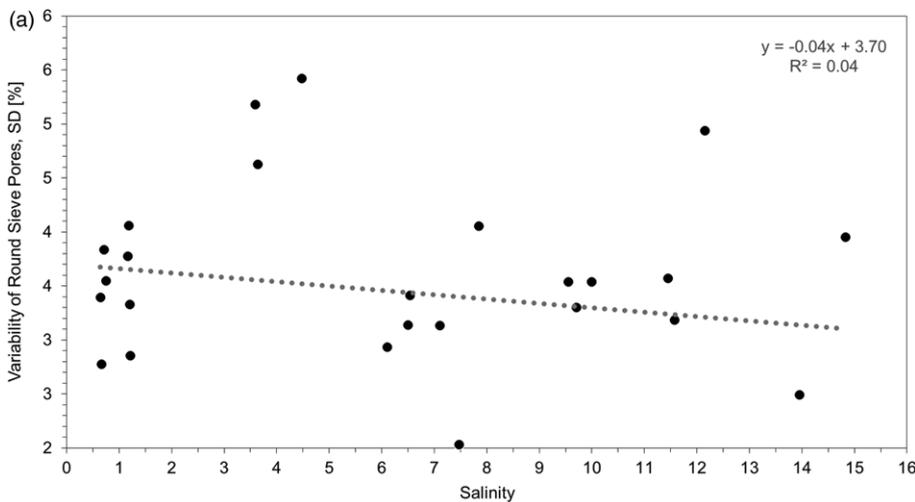
Only one out of 36 microcosms in total failed to produce adult specimens of *Cyprideis torosa*. The number of analysed adult individuals varies between 2 and 30, with an average of 13.8 (Table 1). The abundance of adults shows a decreasing trend with salinity increase except for a step-like offset at a salinity of around 7 where the maximum number of adults hatched and grown up within the microcosms prevailed (Frenzel *et al.* 2012).

Concerning the proportion of round sieve pores along the salinity gradient (0.6 – 14.8) for single microcosms, a decreasing trend in proportion from about 75 to 45% is recognizable (Table 1 and

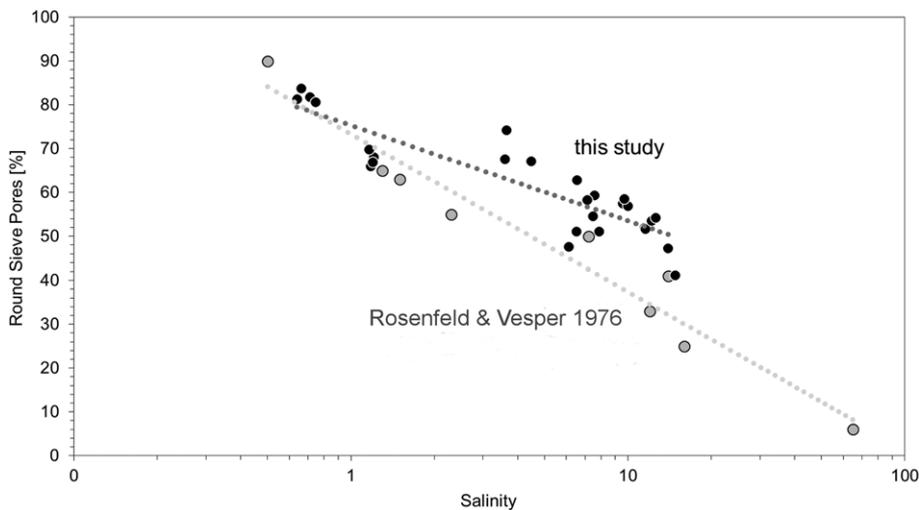
Fig. 3). The correlation between salinity and the proportion of round sieve pores is 0.74 if regarding only microcosms with at least 10 analysed valves. There is, however, no significant correlation between variability of round sieve pore proportion and salinity within any individual microcosm, nor between variability of sieve pore proportion and salinity variability (Fig. 4).

**Discussion**

The correlation between salinity and sieve pore shapes shows a clear ( $R^2 = 0.74$ ) relationship for salinities up to about 15 (Fig. 3). This indicates sieve pore shape distribution to be a physiologically driven



**Fig. 4.** (a) Variability of round sieve pore proportions expressed by standard deviation along the salinity gradient covered within the experiment and (b) variability of round sieve pores compared to salinity variability (SD) within the microcosms.



**Fig. 5.** Plot of salinity on a log scale v. round sieve pore proportion from the present culture experiment (black circles) with those published by Rosenfeld & Vesper (1976) for marginal-marine waters from the southwestern Baltic Sea and Israel coast (grey circles). The lowermost value was obtained from Lake Kinnereth, a very saline athalassic water body in Israel.

reaction of *Cyprideis torosa* to salinity of the ambient water. It is not clear, however, what role sieve pores play in osmoregulation and why they change their outline. A distortion of sieve pores by node formation is rare (Keyser 2005) and not the reason for trends in the proportion of round sieve pores along the salinity gradient. Elongated and irregular shapes increase in frequency with salinity whereas nodding increases in low salinity waters. De Deckker (2002) relates the variation in sieve pore shape to calcification problems under stressed highly saline conditions in estuarine systems of arid regions. This would explain high proportions of irregular shapes in such environments due to poor calcium concentrations. In our experiment, however, irregular shapes did not increase in proportion with lower calcium concentrations, i.e. lower salinity.

There is no recognizable change in sieve pore shapes at the osmoregulation switching point as was documented for reproduction, nodding (Frenzel *et al.* 2012) and length (Boomer *et al.* 2016). This switching point lies between a salinity of about 7 and 9 and was studied physiologically by Aladin (1993). Below this salinity, *Cyprideis torosa* leaves the osmotic equilibrium point and regulates its higher internal osmotic pressure by excreting water. We cannot exclude the possibility, however, that the linear correlation shown in our graph (Fig. 3) may be modified by adding higher salinity data points. A change in the salinity–sieve pore relationship was documented by Frenzel *et al.* (2011) for a salinity series with mixed seawater and lake water at about 7.5 psu where the inclination of the trend line changed from  $-0.51$  below to  $-0.07$  above this point. The use of distilled water for dilution in our experiment could have an influence on sieve pore variability because of different proportion of ionic strengths compared to natural conditions.

Variation of ambient salinity does not seem to affect sieve pore variability within a population, as shown in our experiment. The low and slow salinity variation ( $SD < 2$ ) within the microcosms may be a reason for missing such a correlation. We cannot exclude an influence of highly variable salinity on sieve pore variability. Thanatocoenoses from estuaries or lagoons may well reflect the strong and partly unpredictable salinity variations typical in such environments.

Comparison of our results with those of Rosenfeld & Vesper (1976) reveals very similar proportions of round sieve pores at the lower limit of brackish water, which is 0.5 according to the Venice system of the classification of brackish waters, but slightly higher ones with increasing salinity (Fig. 5). Furthermore, while we can apply a linear trend, Rosenfeld & Vesper (1976) found a logarithmic correlation. The diverging curves may be explained by the same model as proposed by Frenzel *et al.* (2012) for nodding: While noded valves may dominate associations at salinities below 2 in nature, they always make up  $<10\%$  in associations between 2 and *c.* 7 and

disappear above the latter value in the field. This is explained by much higher salinity variability in the field than in the cultures. Individuals in natural conditions may perhaps wait for better osmotic conditions to start moulting. This behaviour would enable them to avoid deformation of their valves through nodding to some degree. The sieve pores are fixed as in the case of nodes during mineralization after moulting and could therefore also represent ecologically ‘better’ salinity values, i.e. closer to the osmotic optimum, as the average situation within the salinity range inhabited. Ostracods living in the microcosms do not have much choice but to accept the given salinity and ionic composition for moulting, thus reflecting it by nodding intensity proportional to average salinity. This effect may explain the two different types of trend lines in Figure 5 but not the offset between both. At lower salinities, using distilled water for the dilution of seawater may create a limitation of ions important for osmoregulation and lowers alkalinity which is important for calcification, as discussed for Ca by Hirschmann (1912), Keyser (2005) and Frenzel *et al.* (2012). The samples studied by Rosenfeld & Vesper (1976) derive mostly from the southwestern coast of the Baltic Sea where tills with reworked chalk provide Ca and bicarbonate via erosion to the coastal waters. An additional factor creating such an offset could be the rising proportion of irregular sieve pores with increasing salinity: While round and elongate sieve pores are quite easy to discriminate using the criteria defined by Rosenfeld & Vesper (1976), irregular sieve pores are hard to separate from round ones because the position of the associated bristle often creates an indentation of the circular shape. We consider it possible that we slightly underestimated the proportion of irregular sieve pores compared to Rosenfeld & Vesper (1976) because of this indentation.

## Conclusions

Our results show the influence of ambient water salinity on sieve pore shapes in *Cyprideis torosa*. Increasing salinity corresponds well to a decreasing proportion of rounded sieve pores. The curve deriving from the culture experiment differs slightly from field observations made by Rosenfeld & Vesper (1976) and may better reflect stable salinity conditions such as might be expected in larger athalassic waterbodies, but not in marginal-marine ones. However, an ionic composition different from this one in marginal-marine environments may produce an offset of sieve pore values as already proposed by Keatings *et al.* (2007). Sieve pore data from marginal-marine waters most likely reflect values closer to the osmotic optimum within the natural salinity variation at the site, not average values. This complex system of influencing factors makes the

quantitative use in palaeoenvironmental reconstructions difficult and needs further investigation. Culture experiments with ionic composition of the water different from the marine one and valves from natural habitats with salinity between 20 and 60 may provide essential information. Past salinity trends in marginal-marine waters, however, may be already successfully reconstructed using sieve pores in *Cyprideis torosa* as a proxy for palaeo-salinity.

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