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The contrasting histories of marine and freshwater meiobenthic research – result of differing life histories and adaptive strategies?

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A B S T R A C T

Although early microscopists first described meiobenthic-sized animals from fresh water, it is widely acknowledged that studies of the ecology of freshwater meiofauna have taken longer to emerge as an independent discipline than those of their marine counterpart. The early literature on this freshwater fauna used terms relating to habitat rather than size. Perhaps this is partly because the term meiofauna originated early in the marine literature that lacked the cognizance of freshwater scientists. However, it is also undoubtedly due to the fact that, in the sea, animals in the meiofaunal and macrofaunal size ranges comprise recognisably separate ecological and evolutionary units with bimodal size spectra, whereas the freshwater size spectrum is more continuous and the division between the two categories is more arbitrary. This is due to the contrasting size-related life-histories of metazoans in the two realms.

1. Introduction

In his comprehensive review of the history of meiobenthic research, Giere (2009) pointed out that studies of the ecology of freshwater meiobenthos have taken longer to emerge as an independent discipline than those of its marine counterpart, a view widely acknowledged in the freshwater literature (e.g. Rundle et al., 2002). Possible reasons for this constitute the subject of this essay.

In the early literature on freshwater benthic faunas, the smaller-sized component was referred to in terms that relate to habitat rather than size, for example *Psammic* (in sand or gravel), *Psammobiotic* (only in sand), *Psammmophilic* (sand loving but also in vegetation), *Psammoxene* (planktonic stragglers found in sand), *Psammolittoral* (in sandy shores), *Phraetic* (in ground water), *Stygobiotic* (in subterranean groundwater aquifers), *Troglobitic* (in caves), *Hyporheic* (beneath the bed of rivers or streams) and *Interstitial* (between sediment grains (Giere, 2009). Indeed, in 1966 the first issue of "Psammonalia", now the official newsletter of the "International Association of Meiobenthologists", was prompted by an informal meeting of mainly marine researchers "to maintain communication among American *psammologists* and to note research items and papers, of *psammic* interest, personal and personnel news and meetings and conferences harbouring papers on the *interstitial fauna* and its milieu". Although this scientific community regarded themselves more generally as *meiobenthologists* by 1968, terms such as *psammic*, *hyporheic* and *stygobiotic* are still more familiar to freshwater scientists than *meiofaunal* and *meiobenthic* (Rundle et al., 2002), despite successful attempts to bridge the nomenclatural and methodological gap and draw parallels between the marine and freshwater fields (e.g. Palmer, 1990a, 1990b; Palmer et al., 1996).

2. The early microscopists

Early observations on benthic metazoans of meiofaunal size were largely made by amateurs, notably religious preachers who must have had plenty of spare time on their hands. They focussed on taxa such as rotifers and tardigrades, which are more abundant in freshwater than marine sediments (Pennak, 1951). Rotifers were first described by the Rev. John Harris, an Anglican priest, in 1696 and tardigrades by the German pastor Johann August Ephraim Goeze in 1773. Perhaps the most significant observations, however, were made by Antony van Leeuwenhoek, 1632–1723, an apprentice to a draper, who constructed a variety of deceptively simple single-lensed microscopes, some of which magnified objects 270 times. He communicated his findings in letters to the Royal Society written in low Dutch, many of which were translated ("English'd") by Henry Oldenberg and published in *Philosophical Transactions*, and employed an artist to illustrate his findings. Ten of these letters concerned rotifers. He did not merely observe, but conducted ingenious experiments on the biology of his tiny "animalcules". For example, in a single letter, number 160 in the catalogue of Cole (1937) dated 14 November 1704, he describes in detail the sequence of ciliary rotation on the velum of two species, evidence of

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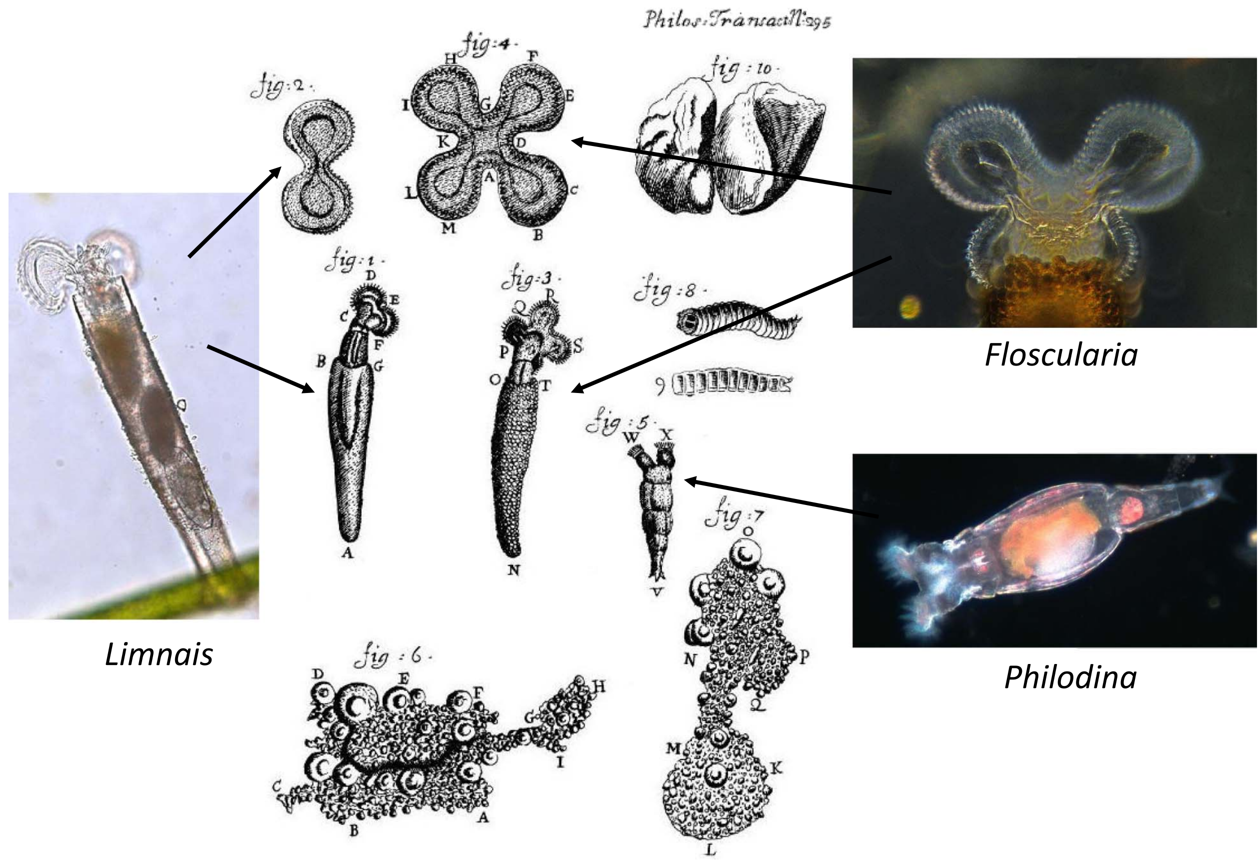

Fig. 1. Illustration accompanying Leeuwenhoek's letter to the Royal Society dated 14 November 1704 (Phil. Trans. XXIV 1705, pp. 1784–1793 plate 295). The three illustrated species are clearly referable to currently recognised taxa.

Table 1
Size related functional traits that switch more or less abruptly at about 45 µg dry weight in temperate shallow water marine benthos. (From Warwick, 1984, with additions).

	Meiobenthos (< 45 µg dw)	Macrobenthos (> 45 µg dw)
Development	Direct benthic	Planktonic
Fertilization	Internal (copulation)	External
Eggs	Few large	Many small
Dispersal	As adults	Planktonic larvae
Generation time	< 1 year	> 1 year
Reproduction	Semelparous	Iteroparous (usually)
Feeding	Discriminate use of particles	Indiscriminate use of particles
Resource partitioning	Particle selection (size, shape, quality)	Spatial segregation
Growth	Reach asymptotic body size	Continue growth throughout life
Mobility	Motile	Sedentary or motile

predation on them by mites, and experiments on their survival of desiccation (Phil. Trans. XXIV 1705, pp. 1784–1793). The three species in his accompanying figure (plate 295) are clearly referable to currently recognised taxa (Fig. 1).

3. Molly Mare's definition of meiobenthos

The pioneering work of Mare (1942) on the benthos of a muddy marine sediment near Plymouth, UK, was perhaps the first to emphasise the importance of studying the whole range of individual size for the understanding of the ecology of the sea bed and indeed the entire marine food web. She recognised that "A new terminology is needed, and these groups are here designated the *macrobenthos*, *meiobenthos* and *microbenthos*". It is a common misconception that *meiobenthos* implied organisms of intermediate size, but in fact was derived from the Greek word *meion* (μείον) meaning smaller or less. She used a 100 µm sieve for extraction, 2.5 times the aperture area of the 63 µm sieve now generally employed for processing the meiobenthos, and consequently this size category comprised taxa "such as small crustaceans (copepods, cumaceans, etc.) small polychaetes and lamellibranchs, nematodes and foraminifera", several of which are much larger than we would now recognise as meiobenthos and would have been the juvenile stages of macrofauna, the so called "temporary meiofauna". The latter are in general larger than the true permanent meiofauna (see section 4) and should, arguably, not be designated as meiofauna, a better definition of which would include not only body size but also the size-related functional traits that characterise them.

4. Marine meiofauna

There are compelling reasons to suppose that the meiobenthos were the first metazoans, appearing in the sea in the Middle Precambrian (Boaden, 1975, 1977, 1989), and since that time subsequently evolving organisms will have acquired adaptations that avoid negative interactions with them. The Platyhelminthes, Gnathostomulids, Nematodes, Gastrotrichs and Kinorhynchs are considered to be the most primitive meiobenthic groups, all motile forms seeking food particles in a highly discriminate manner, some being bactivorous, others herbivorous, others carnivorous and it is probable that this range of feeding specializations was present in the meiobenthos before the major macrobenthic groups (Annelida, Arthropoda, Mollusca, Echinodermata) appeared. The marine meiobenthos, at least in temperate shallow water, is defined on the basis of organisms' size and on a coherent set of