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REPLY COMMENT

Methods for measurement of bivalve clearance rate — hope for common understanding

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It is very encouraging that 2 well-known participants (Bayne 2004, Riisgård 2004, both this volume) in the decades-long debate on bivalve suspension-feeder clearance rates (CR) acknowledge our (Petersen et al. 2004) efforts to resolve some of the current controversy and stimulate further discussion. This gives hope for common understanding and further insight into the field of bivalve filtration and what may control and regulate it. Although both are positive, they also have critical comments on our study and conclusions.

The main point of Bayne (2004) is that our conclusion regarding the bio-deposition method is not generally accurate. He further describes how the bio-deposition method, if it is carried out under carefully controlled conditions, will yield results comparable to those obtained with the clearance method. This was our main conclusion, i.e. our results are valid only for the specific methods applied in the study (Petersen et al. 2004). However, our methodology resembles many of the studies previously performed using the bio-deposition method (e.g. Hawkins et al. 1996, Urrutia et al. 1996, Iglesias et al. 1998). Moreover, most of our explanations for the lower CR obtained with the bio-deposition method were controlled for in the experiment described by Bayne (Bayne et al. 1999, Bayne 2004): (1) the risk of faecal material being swept away is minimized by frequent sampling, thus eliminating a potential source of underestimation; (2) the well-defined and constant particle composition and concentration used by Bayne et al. (1999) minimizes potential underestimation of CR, in contrast to the conditions in our experiments. Nevertheless, in 1 out of the 3 experimental groups, Bayne et al. (1999) found a significant difference between methods. This emphasizes a mutual point between our study and that of Bayne et al.(1999), that when using the bio-deposition method, careful attention must be paid to details, and this renders the method less robust e.g. *in situ*, or in situations designed to imitate *in situ* conditions.

Riisgård (2004) has several different comments. We agree that it is regrettable that we did not report the degree of opening of the mussels; the mussels were open during the experiments, as indicated by the acclimation time of *at least* 1 h. Nevertheless, even though the degree of opening is correlated with CR, it is not possible to predict CR merely from the degree of opening (Riisgård et al. 2003). Further, it is crucial to take an exact measurement of shell gape from a picture (photograph or video) and that pictures are taken at identical angles, because both the classification scheme mentioned by Riisgård et al. (2003) and merely visual inspection will involve subjective judgements. Another concern of Riisgård is that differences in feeding history of the mussels may have affected the CR. Starvation prior to the experiment will invoke a lag phase with lower CR upon commencement of feeding (Riisgård et al. 2003). A similar pattern has been found in other benthic suspension feeders (Petersen & Riisgård 1992). But it was clearly stated in Petersen et al. (2004) that the mussels were kept in acclimation tanks with running seawater enriched with *Skeletonema costatum* before they were transferred to the experimental set-ups, and thus the experimental mussels had at no time been starved. We found CR close to, or higher than, the rates reported as maximal (Riisgård 2001), and this further indicates that the mussels were completely open and not impaired by 'starvation stress'.

The remaining concerns of Riisgård (2004) appear to be due to a misunderstanding. He suggested that the systematic difference between the steady-state method and the flow-through method shown in our Fig. 3 (Petersen et al. 2004) and the significantly lower CR obtained with the bio-deposition method could be attributed to inadequate water mixing, differences in shell gape or inadequate chamber geometry. There are no alternative explanations for the different results obtained with both methods, other than inadequacy of the methodology, because both methods were tested in the same experiment, conducted at the same time with the same particle concentrations and the same mussels. As for the difference between the steady-state and the flow-through methods, the only difference

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between the 2 sets of results is the equation used for calculating CR. The equation used to calculate CR is of paramount importance, and the formula should be adapted to the geometry of the chamber. Where the water only passes the mussel inhalent siphon once, the equation for flow-through should be:

$$CR = \{(C_{in} - C_{out})/C_{in}\} \times Q \quad (1)$$

where C_{in} and C_{out} are the concentration of particles >4 µm in inflowing and outflowing water, respectively, and Q is the flow rate. In chambers with fully mixed water, CR should be calculated using the equation for flow-through assuming steady-state:

$$CR = \{(C_{in} - C_{out})/C_s\} \times Q \quad (2)$$

where C_s is the particle concentration surrounding the mussel, which can be considered to be equal to the outflow concentration. With inadequate mixing and/or back-flow, neither equation can be used, as this experimental approach is not valid for CR experiments. With regard to the bio-deposition method, measurements for determination of CR using the flow-through technique and Eq. (2) were taken simultaneously with the collection of bio-deposits. Since we used C_s for determination of total particulate matter and particulate inorganic matter when calculating CR with the bio-deposition method, inadequate geometry or flow rate cannot explain the difference between the CR determined with the 2 methods.

The implication is that Eq. (2) is not valid with a chamber designed for flow-through, and Eq. (1) is not valid for a chamber designed for steady-state. There is a fundamental difference between the 2 equations, which must be reflected in the geometry of the chamber used. Using steady-state geometry and $C_s = C_{out}$ with the bio-deposition method may cause problems. The requirements of fully mixed conditions may conflict with conditions suitable for collecting faecal and pseudofaecal material, which we pointed out as a possible explanation for the difference between CR determined by the bio-deposition as opposed to other methods (Petersen et al. 2004). Depending on particle type and concentration, the use of a steady-state geometry and estimating CR by the bio-deposition method is, however, not necessarily mutually exclusive. The main point is that care should be taken with respect to the possibilities and limitations of the different methods, and to ensure that they are used properly.

With our intercalibration exercise and the helpful comments by Bayne (2004) and Riisgård (2004), it can be hoped that the pitfalls of the different methods will be avoided in future investigations, and that a thorough examination of previous investigations will lead to a more homogeneous view on bivalve clearance capacity. It is further essential that methods that can be applied *in situ* are further developed and tested under these conditions.

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