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COMMENT

Intercalibration of methods for measurement of bivalve filtration rates — a turning point

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The mussel filtration rate (= clearance rate, CR) intercalibration exercise conducted by Petersen et al. (2004) is a laudable initiative and a turning point on the stony road to reliable CR data. It is an expression of true scientific spirit when the participants in the calibration are ready to accept the consequences of the intercalibration, requesting a critical re-evaluation of the literature, including some of their own earlier works. Objective discussions based on scientific facts may hopefully soon replace the barren and polarised discussion climate of recent years (Jørgensen 1996, Bayne 1998, 2001, Riisgård 2001a,b,c,d, Widdows 2001, Cranford 2002).

The intercalibration exercise is an important step in the right direction. Especially the flow-through chamber method used for measurement of CR has caused trouble over the last 25 yr, because the same flaws were repeated over and over again (Riisgård 2001a). It is encouraging to note that the self-appointed Dutch, Danish and French intercalibration teams 'call for a thorough examination of previous investigations' — although it is doubtful whether it is possible to correct erroneous CR for suboptimal chamber flow-through rate and/or poor chamber design (Larsen 2001).

Petersen et al. (2004) correctly state that a prerequisite for obtaining reliable CR data is that the applied experimental methods are technically valid so that — within well-defined conditions — the different methods actually measure the true CR. However, it is regrettable that the participants in the calibration exercise did not report on the degree of opening of the mussels; mussel gape must be determined, to ensure that the CR measured by means of the different methods were actually comparable. Prior to the calibration experiments, mussels were 'acclimated' to the grazing chambers with water flow-through for 'at least 1 h'. This exposure time may not have been sufficiently long to ensure that the mussels attained their clearance capacity, which should be the reference in this type of intercalibration. The degree of valve opening should have been carefully monitored before and during the CR measurements. This well-intentioned comment is further substantiated below in order to draw attention to the importance of the opening degree of bivalves in future CR experiments.

The thick shells of mussels make them robust to handling, but this characteristic does not imply that mussels are insensitive to the experimental conditions. Actually, mussels are very sensitive, not only to mechanical disturbances, but also to the presence of suspended food particles in the ambient water (Jørgensen 1975, 1990, Riisgård & Randløv 1981, Riisgård et al. 2003). This is reflected in the gape of the valves. Thus, valve-opening behaviour ranges from closed valves and retraction of mantle edges, to fully open valves and extended mantle edges (Jørgensen et al. 1988, see Fig. 1 therein, Riisgård et al. 2003, see their Fig. 9). Under optimal conditions, mussels filter the ambient water at a maximum rate; under suboptimal environmental conditions, including low or (very) high concentrations of phytoplankton, the valve gape is reduced and the mantle edges are retracted.

The sensitive opening-closing phenomenon and response times in 3 species of bivalves, *Mytilus edulis*, *Cardium edule* and *Mya arenaria*, have been studied in the presence and absence of algal cells in controlled laboratory experiments by Riisgård et al. (2003). Opening state and the correlated CR at varying or stable algal concentrations was quantified in clearance experiments combined with simultaneous video observation of the opening state: when unfed bivalves were offered algal cells, the animals opened their siphons or valves, and this entailed a simultaneous increase in CR. Further, in feeding–starvation experiments with *M. edulis*, Riisgård et al. (2003) found that when the mussels were fed algal cells for 5 h every day during a week, both the opening and closing response was faster than in mussels starved 3 wk prior to the experiments. Other observations obtained in the field with an underwater video camera indicate that the opening-closing responses may be considerably faster than those found in the laboratory.

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The above observations draw attention to the importance of the previous feeding history of the bivalves and emphasise the importance of shell gape in controlled laboratory experiments on bivalve CR. To further support this statement, some recent examples of clearance rate measurements in the scallop *Aequipecten opercularis* are shown in Fig. 1: CR increases for 2 to 3 h following the first addition of algae. This increase in CR was correlated with increased gape of the shells. The systematic difference between the steady-state method and the flow-through chamber method in Petersen et al. (2004, their Fig. 3) is suggested to indicate 'that the geometry of the grazing chamber was not suitable'. Other explanations may be inadequate water mixing in the steady-state method, or differences in shell gape between the mussels in the 2 experiments.

The suction method (Riisgård 2001a) which allows precise measurements on undisturbed infaunal clams buried in the sediment — representing a promising method for future *in situ* measurements — was regrettably not included in the intercalibration exercise of Petersen et al. (2004). But in a recent study on CR in the soft clam *Mya arenaria*, good agreement was found between the clearance method and the suction method (Riisgård & Seerup 2003).

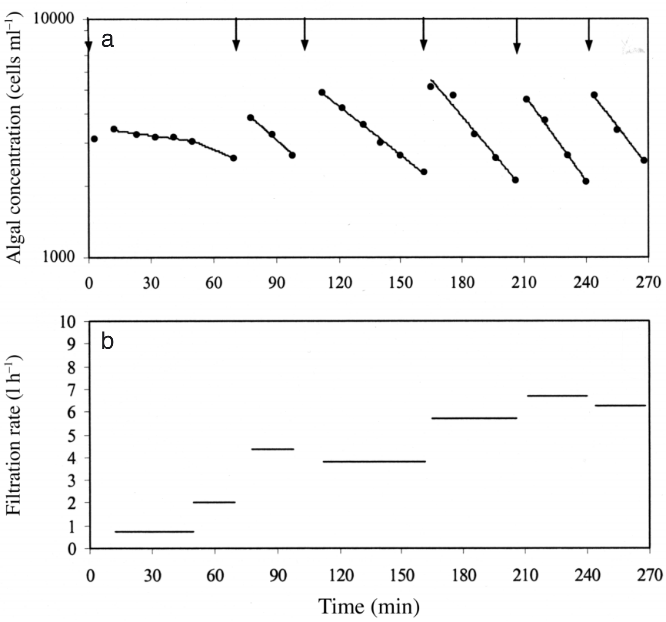

Fig. 1. *Aequipecten opercularis*. Typical example of stimulation of the clearance rate (CR) of a scallop after addition of algal suspension. (a) Exponential reduction in algal concentration due to grazing by a scallop in an aquarium with well-mixed water. Arrows indicate additions of new algal suspension. The estimated regression lines are shown. (b) CR during the experimental period, estimated as clearance = (slope of regression lines) × (volume of water in the aquarium) (Kittner & Riisgård unpubl.)

In particular, the result of the bio-deposition method in the intercalibration exercise was rather predictable, because the prerequisites for correct use of the method were not properly tested, as was done in the case of the flow-through chamber method. In view of the earlier criticism of the bio-deposition method (Riisgård 2001a,b) it is somewhat disappointing to note that apparently no efforts were made to check the importance of flow rate and of the 'geometry' of the trays used in the exercise. Nevertheless, the intercalibartion is a turning point and an important step in the right direction.

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