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Variability in particle retention efficiency by the mussel *Mytilus edulis*

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ABSTRACT

Seasonal variation in blue mussel, *Mytilus edulis*, retention efficiency (*RE*) responses to natural seston concentrations were investigated in the Lysefjord, Norway. The smallest particles shown to be effectively retained (100%) were approximately 7 μm and this was observed on only one occasion. The most common response was for *RE* to progressively increase from small to large particles with maximum *RE* at 30 to 35 μm (8 of 12 experiments). Temporal changes in the seston size distribution towards a dominance of smaller particles coincided with a decrease in the *RE* maxima to particles between 7 and 15 μm diameter. The *RE* of 1 μm and 4 μm diameter particles ranged between 14–64% and 12–86%, respectively, showing that small particles occasionally serve as a significant dietary component. The observed temporal variations in particle capture suggest a capacity of *M. edulis* to control particle retention mechanisms based on exogenous dietary cues that are directly or indirectly related to the ambient particle size distribution. Indirect clearance rate (*CR*) measurements require that all particle sizes under study are effectively retained and this has widely been assumed for particles larger than 4 μm. *CR* was calculated for particles ranging in size from 5 to 35 μm and the percentage reduction in *CR*, relative to particle sizes shown to be effectively retained, ranged from 11% to 87%. *CR* calculations that included all particle counts between 5 and 35 μm diameter were underestimated by a mean of 26% (0–48% range). Similar errors in diet characterization may be expected to affect particle selection and absorption efficiency measurements and the compounding of errors may become extreme when a number of physiological rates and efficiencies are integrated (e.g. scope for growth).

1. Introduction

Suspension feeding bivalves molluscs carry out a significant role in the flow of energy and matter in coastal and estuarine ecosystems (Cranford et al., 2007; Gili and Coma, 1998; Newell, 2004). Dense populations, under some conditions, can reduce seston concentration (Dame, 1996; Strohmeier et al., 2005) and change suspended particle composition (Maar et al., 2007; Prins et al., 1998; Strohmeier et al., 2008) and plankton population dynamics (Maar et al., 2007; Prins et al., 1998). The availability of food particles to suspension feeding bivalves is a function of seston concentration and size and the particle retention (capture) efficiency characteristics of feeding structures. Many studies on particle utilization by suspension feeding bivalves have employed algal cell monocultures added to filtered sea water (Møhlenberg and Riisgard, 1978; Palmer and Williams, 1980; Vahl, 1972; Zhang et al., 2010) or have attempted to simulate natural particles by mixing microalgae, bacteria, silt and/or detritus in seawater (Bayne et al., 1984, 1989; Bricelj et al., 1984; Cucci et al., 1985; Kiørboe and Møhlenberg, 1981; Newell and Jordan, 1983; Newell and Langdon, 1986; Shumway et al., 1985; Stuart, 1982). Other studies have promoted the view that ecologically relevant behavior in bivalve suspension feeders can best be observed using natural diets (Cranford et al., 1998, 2005; Newell and Jordan, 1983; Stenton-Dozey and Brown, 1992; Strohmeier et al., 2009; Wright et al., 1982) and this approach has become common in studies of bivalve feeding responses to the natural range of variation in particulate matter availability, chemical composition, size distribution, texture, palatability, etc.

Small particles in natural coastal waters generally dominate particle abundance and can account for a high proportion of total suspended particulate matter mass. It has been reported in numerous studies that bivalves only efficiently retain particles larger than 3 to 7 μm, depending on the species feeding structures (Bayne et al., 1976; Kiørboe and Møhlenberg, 1981; Lucas et al., 1987; Møhlenberg and Riisgard, 1978; Riisgard, 1988; Vahl, 1972, reviewed by Ward and Shumway, 2004). In the mussel *Mytilus edulis*, particles larger than 4 μm are reported to be retained with a nominal efficiency of 100% (Møhlenberg and Riisgard, 1978) and retention efficiency rapidly declines as particle size decreases below this threshold (Møhlenberg and Riisgard, 1978; Riisgard, 1988). These conclusions rely on the common assumption that maximal retention occurred within the narrow particle

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size-range studied (generally between 1 and 10 μm diameter). Dral (1967) provided early evidence of the possible regulation of particle retention by *M. edulis* through the use of non-surgical microscopic techniques and concluded that particles of at least 40 μm must be used to ensure 100% retention. Further evidence supporting the concept of variable retention efficiency comes from field studies on bivalves feeding on natural seston. Lucas et al. (1987), Cranford and Gordon (1992), Stenton-Dozey and Brown (1992) and Barillé et al. (1993) measured 100% retention efficiency for 16, 40, 23 and 12 μm diameter particles, respectively. The results of these studies suggest that effective particle capture is not determined solely by the sieving properties of the gill. The ability of bivalves to alter particle capture efficiency, the factors controlling this response, and the temporal scale over which bivalves control particle capture has been described as a "fertile area for future research" (Ward and Shumway, 2004).

Accurate characterization of particle retention efficiency is fundamental to the calculation of clearance rate (the volume of water cleared of particles of a given size per unit time): a principle physiological function in the modulation of energy acquisition in suspension feeding bivalves (Cranford et al., 2005; Gardner and Thompson, 2001; Hawkins et al., 1999, 2001; Strohmeier et al., 2009). The application of all the indirect methodologies that are currently the primary means for measuring clearance rate requires that particle removal by bivalves from a closed or flow-through suspension is known to be 100% efficient (Coughlan, 1969). The capacity of bivalves to capture available food particles must also be accounted for in absorption efficiency methodologies that require the characterization of absorbed and conservative tracers in food and faeces (Conover, 1966). Accurate information on food retention efficiency is therefore critical to estimating all energy gain parameters within the bivalve energy budget and is also linked to the accuracy of eco-physiological and ecosystem model predictions with dense bivalve communities and aquaculture carrying capacity (Grangere et al., 2010; Grant et al., 2008).

In the present study we revisited the topic of particle retention efficiency in *M. edulis* to investigate the theory of variable particle size capture in nature. Information on the seasonal distribution, abundance and quality of natural food particles was collected in conjunction with mussel retention efficiency and clearance rate measurements to aid in identifying potential factors contributing to variations in food acquisition responses and to examine changes in retention efficiency across spatial and temporal scales.

2. Materials and methods

Retention efficiency (*RE*) measurements for blue mussels exposed to natural seston concentrations were obtained from two experimental sites in Lysefjord from 19 May to 25 August, 2010. *RE* was determined on six dates at each station. Lysefjord is located on the southwest coast of Norway (N 58° 56′, E 6° 8′) and is approximately 40 km long and 0.5–2 km wide with a depth range from 13 meters at the outer sill to a maximum depth of 460 m. The mean tidal range is 0.4 m. The experiments were conducted on the sites; Måkasteinen (MS) near the head of the fjord and Flørli (FL), located 14 km seaward of MS.

Mussels from the 2008 cohort were harvested from suspended aquaculture ropes in Lysefjord, graded to a shell length range of 45–50 mm (mean 47 mm) and transported to the experimental sites at MS and FL on 2 March, 2010. Two groups of 40 mussels were individually marked, and 20 mussels from each group were used to determine *RE*. The mussels were held in lantern nets suspended from a long-line at 7 m depth for the duration of the study.

Temperature and salinity were measured simultaneously at both sites at 30 min intervals during the study using a CTD instrument (SAIV A/S Model 204, Norway) that was moored at the holding depth of the mussels. Water samples for seston analysis were collected from the same depth at biweekly intervals. Suspended particulate matter and particulate organic matter (SPM and POM; mg L^{-1}) were determined in triplicate for seston filtered onto pre-washed (distilled water), ashed, and tared 1.2 μm nominal pore size filters (Whatman GF/C). Salt was expelled from samples by rinsing each filter under vacuum with isotonic ammonium formate. Filters were then dried at 60 °C over night and weighed to ±0.01 mg to calculate SPM. The filters were then burned at 450 °C and reweighed for the calculation of inorganic content and POM concentration. Particle numbers (counts) and size-distribution in water samples were determined using a Pamas GmbH field laser particle counter (Model S4031GO) as described below for determination of *RE*. Particle volume was then calculated under the assumption that particles in all size-ranges were spherical.

Chlorophyll *a* (Chl *a*) concentrations were determined on the same days as SPM samples by filtering seston (0.5 l) onto a 1.2 μm filter (Whatman GF/C). Chl *a* was analysed after extraction with 90% acetone using the fluorescence method with correction for acidified measurements (Strickland and Parson, 1968). The fluorometer (Turner Designs Model 10-AU) was calibrated with known concentrations of Chl *a* (Sigma Chemicals, St. Louis, Mo., USA).

Mussel feeding experiments were conducted using the flow-through method. The feeding chambers were similar in design to those reported by Palmer and Williams (1980), but without the angular baffle in the middle of the chamber. The internal dimensions of the mussel chambers were 3.8 cm wide, 19.5 cm long and 8.1 cm deep. This chamber design constrains recirculation and prevents refiltration of water by the bivalves when an acceptable flow speed is provided (previously determined for similar sized mussels by Strohmeier et al., 2009). On each sampling date, *RE* was measured by temporally transferring 20 individually marked mussels from the holding net to separate flow-through chambers. The bivalves were returned to the net after determination of *RE*. Two additional chambers were left empty to control for any effect the chamber may have on the outflow particle concentration. The bivalves were left undisturbed in chambers with flowing seawater at least 0.5 h to resume feeding before sampling water from the outlet of the chambers. Water samples collected from each chamber outlet were analysed for particle concentration and size-distribution using the Pamas particle analyzer. The analyzer was calibrated before the experiment and set to count particles spanning a total range from 1 to 35 μm (sizes channels: 1, 1.5, 2, 2.5, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 25, 30 and 35 μm). Each water sample comprised three sub-samples, in which particles were counted in 10 ml of seawater. The mean particle count was used to calculate the *RE* per size class for each individual according to the following equation:

$$RE = 1 - (PC_B / PC_C), \quad (1)$$

where PC_C is particle count exiting the control chamber and PC_B is particle count exiting the bivalve chamber. *RE* was calculated for all 27 particle size channels for each bivalve and was replicated for 20 individual bivalves on each sampling date. *RE* data for each individual were then standardized by setting the *RE* in the particle size cleared at the highest efficiency to 100% and then scaling *RE* in the other size-classes proportionately. Standardization was performed for each individual before averaging across the 20 individuals to give the mean cohort RE response for each particle size class. This standardization procedure is widely utilized (e.g. Riisgard, 1988) to constrain the effect of inter-individual feeding rates on *RE*.

Clearance rate (*CR*) was calculated for each individual as;

$$CR = RE * F, \quad (2)$$

where the *RE* measurements are non-standardised and *F* is the flow rate ($l\ h^{-1}$) measured at the outlet of each chamber. The *F* to each chamber was typically 10–15 $l\ h^{-1}$, giving estimated current speeds in chambers at 0.2 cm s^{-1}. *CR* was calculated separately using *RE* calculations for