# Directions in bivalve feeding

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THEME SECTION

# Directions in bivalve feeding

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# Introduction

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ABSTRACT: Manuscripts dealing with bivalve feeding and submitted to the Inter-Research journal Aquatic Biology over the course of 2008 were peer-reviewed in the standard manner, and the successful papers compiled for a Theme Issue entitled 'Directions in bivalve feeding'. The historical progression of research in this field is summarized, and the directions of current research highlighted in view of the compiled papers. Some suggestions for future work are presented.

KEY WORDS: Bivalve biology · Suspension feeding · Bivalve diet · Trophic ecology · Mechanisms · Measurements · Perspectives

Research in suspension feeding has been part of the landscape of bivalve biology since at least the early 20th century (Drew 1906, Dakin 1909, Kellogg 1915, Yonge 1923). There is, undeniably, a certain fascination with animals capable of providing for their metabolic needs by capturing microscopic particles, and which in conse-

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quence have largely given up locomotion somewhere along the evolutionary road. At the same time, investigation of this process presents such formidable obstacles (scale differentials, particle visualization, cryptic capture and processing due to occlusive structures such as valves, gill and palp troughs, or appressed surfaces), that many researchers simply turn to more accessible aspects of the bivalve world. That temptation is all the more acute today, when population biology, physiological ecology, aquaculture, and of course molecular biology, to name a few, offer attractive alternatives.

As a post-doc in the 1980s, I simply assumed, like everyone around me who had even thought about the question, that such a basic thing as feeding must be thoroughly understood by at least some researchers somewhere, in such an intensively-studied group as the bivalves. Wrong, of course. Bits and pieces of the most disparate and often contradictory sort were indeed available, but nothing anywhere close to an intelligible, coherent picture could be found. The pioneering work of the 19th and early 20th centuries was necessarily limited by the observational techniques of those times (although some of that work was remarkable despite these limitations, see especially Atkins 1936, 1937a,b,c, 1938a,b,c, 1943). Studies in the latter half of the 20th century tended to concentrate on aspects which did not require direct observation of the underlying mechanisms — a 'black box' approach — such as clearance and particle retention efficiencies (e.g. Møhlenberg & Riisgård 1978, Wright et al. 1982, Riisgård 1988a, Bacon et al. 1998, Hawkins et al. 1998). Outcome-based observational techniques such as automated particle counting, fluorimetry and flow cytometry were used to establish the basic characteristics of suspension feeding, and provided important clues to underlying mechanisms (e.g. Palmer & Williams 1980, Famme & Kofoed 1983, Cranford & Gordon 1992, Bayne et al. 1993, MacDonald & Ward 1994, Ward & MacDonald 1996, Barillé et al. 1997, Navarro & Widdows 1997, Newell et al. 2001, Filgueira et al. 2006, and see Ward & Shumway 2004 for a review of the voluminous literature on this subject). These studies yielded seminal information which would become at once a foundation and a prism through which we have continued to interpret the characteristics of bivalve feeding, and indeed the techniques are important tools in the panoply we use today. Adaptation of this approach to measurement in the field, either indirectly (via the biodeposition method, Cranford et al. 1998, Iglesias et al. 1998, Cranford & Hill 1999; or pumping from the field site to experimental chambers, MacDonald & Ward 1994) or directly (the InEx method, Yahel et al. 2003, 2005, 2006, 2009 this Theme Section) has allowed us to extend these observations much closer to the natural habitat. Simultaneously, application of the physical principles of fluid mechanics has yielded important insights into the hydrodynamic principles of particle movement underlying suspension feeding in bivalves (Jørgensen 1981, 1982, 1983, Jørgensen et al. 1984, Nielsen et al. 1993, Riisgård & Larsen 2001, 2005, 2007).

The 20th to 21st century interface saw rapid progress in the study of bivalve feeding, with the development or adaptation of new observational techniques, in conjunction with the 'old faithful' methods already in use. Techniques such as cilia and mucocyte mapping (Beninger et al. 1993, 1999, 2003, 2005, Beninger & Dufour 1996, Beninger & Veniot 1999, Beninger & Decottignies 2008), *in vivo* video-endoscopy (Ward et al. 1991, 1994, Chaparro et al. 1993, Tankersley & Dimock 1993, Ward et al. 1994, Beninger et al. 1997a, Beninger & St-Jean 1997), associated sampling in gill particle tracts (Beninger et al. 1992, 2004, 2008, Beninger & Decottignies 2005, Ward et al. 1993a, 1998, Cognie et al. 2003), confocal laser microscopy (Silverman et al. 1996a,c, Beninger et al. 1997b, Silverman et al. 1999), and enhanced micro-structural characterization (Beninger et al. 1994, 2005, Silverman et al. 1996a,b,c, Veniot et al. 2003, Beninger & Cannuel 2006, Cannuel & Beninger 2006, 2007) have either lent strong support to hypotheses arising from the outcome-based techniques, allowed direct testing of these hypotheses, or shown new possibilities in the field.

In addition to the 'hows' of bivalve feeding, recent techniques of diet determination, such as stable isotope and fatty acid signatures, have given us unprecedented insight into the actual diets of bivalves in the field. These are powerful tools for analyzing their place in food webs, potential trophic competition, and position with respect to carrying capacity (Riera & Richard 1996, 1997, Riera et al. 1999, Sauriau & Kang 2000, Page & Lastra 2003, Kasai et al. 2004, Rossi et al. 2004, Decottignies et al. 2007a,b, Dubois et al. 2007a,b, Silina & Zhukova 2007, Compton et al. 2008, Leal et al. 2008, Kang et al. 2009 this Theme Section).

We thus now have in hand many pieces of this puzzle, and while there are still large gaps in the picture, our understanding of feeding processes has moved forward substantially in recent years: an appropriate time to devote a Theme Section to the topic. The standard approach for Theme Sections is to contact the most eminent researchers in the field and request a contribution. While this does ensure good coverage of the theme, it does not necessarily reflect the diversity of researchers and approaches, the actual 'pulse' of the field. We at Aquatic Biology therefore decided to present a Theme Section which drew upon all bivalve feeding papers submitted to Inter-Research journals over the course of a year, to obtain an on-the-ground view of the different approaches and directions in this field today, by researchers of all horizons (worldwide, senior and junior). The papers have undergone thorough quality control through rigorous peer review (3 to 5 reviewers per manuscript), and nearly half of the submitted manuscripts did not receive enough support to allow inclusion. Papers accepted at the beginning of our 'sampling interval' had to wait longer than those at the end of the interval to appear in print, and we consequently transferred to regular issues several for which the authors had very strict time imperatives. Our appreciation goes to the authors who have been able to wait for publication, our apologies to the authors who have been more pressed for time.

The articles accepted for this Theme Section suggest that current directions in bivalve feeding might be mapped out as:

(1) Dynamics of feeding responses, and implications for laboratory measurement of these responses (Robson et al. 2009 this Theme Section, and Pascoe et al. 2009 this Theme Section — in fact, the latter paper was the original impetus for the Theme Section). Both of these papers highlight the importance of methodology in the measurement of feeding responses.

(2) Processing of toxic, or potentially toxic, particles, and underlying mechanisms (Mafra et al. 2009a,b this Theme Section and Persson & Smith 2009 this Theme Section) show that oysters can consume not only dinoflagellates but also their resting cysts, with the obvious implications this has for toxin accumulation and for introduction of harmful algal bloom species through transplant vectors. Mafra et al. reveal why, in contrast to other bivalves, oysters do not accumulate large quantities of domoic acid. These papers tie into several recent studies showing them to be particularly efficient in qualitative selection, both in the laboratory and in the field; this may be related to their very highly-developed and particular gill structure.

(3) Pre-capture selection (Yahel et al. 2009). Qualitative selection in suspension-feeding bivalves has been assumed to be exclusively post-capture, but in the tropical species studied by Yahel et al. 2009, qualitative selection is shown to occur prior to retention. This forces us to re-examine what is meant by 'retention' (certainly different mechanisms for different gill types and sub-types) and how qualitative selection might intervene in some of these scenarios.

(4) The link between food type and digestive enzymes (Navarro et al. 2009 this Theme Section). This is a fascinating, yet little-studied aspect of bivalve feeding. It is obviously one that should be pursued in the future, since it constitutes a potentially important level of regulation of energy and metabolite acquisition.

(5) The effects of suspension-feeding bivalve populations on the plankton community (Maar et al. 2008, Peterson et al. 2008, Lonsdale et al. 2009 this Theme Section). In these papers, the impact of suspension-feeding bivalves on the plankton community are assessed, particularly with respect to culture operations. Such knowledge is obviously critical to both the understanding of benthic-pelagic coupling and the impact on plankton dynamics, and also to the effect of bivalve culture on these processes. Although Maar et al. (2008) and Peterson et al. (2008) have, due to author time constraints, been published in a previous issue of Aquatic Biology, they were originally processed for this Theme Section, and really do belong here.

(6) Particle clearance and retention in larvae (Tezuka et al. 2009 this Theme Section). There is a relative dearth of information concerning the characteristics and mechanisms of larval bivalve suspension feeding (Gerdes 1983, Gallager 1988, MacDonald 1988, Riisgård 1988b, Way 1989, Widdows et al. 1989, Baldwin & Newell 1991, MacIsaac et al. 1992, Baker & Mann 1994, Gallager et al. 1994, Baldwin 1995), compared to the numerous studies on adult bivalves. Information on retention efficiency and clearance in this cultured larval clam species is therefore welcome.

(7) Dietary fluctuations in field populations (Kang et al 2009 this Theme Section). Although sea squirts are a little exotic for this Theme Section, it is interesting to see how field diets vary between co-cultured oysters and sea squirts. The two have very different anatomical equipment for suspension feeding, and oysters here show a capacity to actively modify their diets, probably through the selection mechanisms for which they are becoming increasingly known.

It would be wrong to think that we know a great deal about bivalve feeding at this point in time. We certainly know much more than we did two decades ago, but, to paraphrase Darwin, it is always wise to correctly perceive our own ignorance. Examples of the exciting problems awaiting present and future researchers:

- Direct field study of clearance and retention in turbid or light-limited waters
- The exact mechanism(s) of qualitative particle selection (follow-up to Newell & Jordan 1983 and Ward & Targett 1989), and its corollary, the 'secret' of sorting and processing thousands of particles simultaneously
- Demonstration of the mechanism of particle capture in the vast majority of bivalves (e.g. heterorhabdic filibranchs, eulamellibranchs, pseudolamellibranchs)
- Fine chemical characterization (the equivalent of protein or DNA sequencing) of the different types of mucus which fulfill different processing functions
- An understanding of how precise mucus composition and spatial configuration affect processing
- Capture and ingestion probabilities for individual particles with specific physical and chemical characteristics, under different conditions of satiation.

There is enough in these future directions to keep us happily occupied for some time to come.

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