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Review

BIVALVE FEEDING — HOW AND WHAT THEY EAT?

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Summary

Based on the mechanism of food collection, bivalves can be suspension–feeders or deposit–feeders, or even utilize both feeding methods. Although some authors describe bivalve feeding as "automatized" process, recent studies show that some bivalves species have ability to regulate filtration and select particles based on their size, shape, nutritive value or chemical component on the surface of the particle. Several recent studies also showed that phytoplankton is not necessary primary food source for bivalves and pointed out the importance of other food sources such as bacteria, detritus and even zooplankton, including bivalve larvae. Ingestion of bivalve larvae indicates that adult bivalve grazing influence different life stages of these organisms and could have impact on bivalve stocks. Due to these process bivalves have great influence in energy and nutrient flux between benthic and pelagic communities, what makes them important part of marine food webs. This paper gives us the overview of current literature and understanding of bivalve feeding mechanisms, particle selection and food sources.

Key words: bivalves feeding, bivalves diet, particle selection, bivalva aquaculture

INTRODUCTION

Bivalves are highly abundant group of organisms in majority of costal marine environments. Today, 7500 bivalves species are identified and can be found from intertidal zone to the abyssal. They inhabit different marine ecosystems including temperate, tropical and polar seas, brackish estuary, hydrothermal vent etc. Some species live buried in soft bottoms, while others are attached on hard substrate or even drilled in hard substrate (Gosling, 2003).

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In the eastern part of the Adriatic Sea 224 bivalves species were recorded out of which 66 species are used for human consumption, but only 16 species can be found in the market (Zavodnik, 1997, 1999). Further on, in the Croatian part of the Adriatic Sea only two species are commercially cultured, black mussel *Mytilus galloprovincialis* and Europea flat oyster *Ostrea edulis*. In 2007 production of these two species were 3000 tons and 1 000 000 pieces, respectively (Mišura et al., 2008). Along the east Adriatic coast three main bivalves aquaculture areas exist: Lim channel, river Krka estuary and the larger one, Mali Ston Bay. In these areas production relies only on seeds collected from nature what makes this aquaculture highly dependant on environmental conditions. Recently, several projects started to investigate possibilities for aquaculture production of other bivalve species including small scallop (*Chlamys varia),* Mediterranean scallop (*Pecten jacobaeus*), warty venus (*Venus verrucosa*), grooved carpet clam (*Ruditapes decussates*), Noah's ark shell (*Arca noae*) and horse bearded mussel (*Modiolus barbatus*) (Peharda et al., 2006, 2007; Mladineo et al., 2007; Marguš, 2009;).

One of the factors that influent bivalve growth both in natural populations and aquaculture conditions is availability and quality of food. Traditionally phytoplankton was considered as primary food source for bivalves (Dame, 1996; Gosling, 2003). However, number of studies pointed out that energy is also derived from other food sources such as bacteria, detritus and even zooplankton (Stuard et al., 1982; Cranfort and Grant, 1990; Langdon and Newell, 1990; Davenport et al., 2000; Lehane and Davenport, 2002, 2006). Through filter feeding process bivalves play important role in marine ecosystems by controlling abundances of primary producers, zooplankton and larval stages of other marine species including bivalves. Due to this process bivalves have great influence in energy and nutrient flux between benthic and pelagic communities (Dame, 1996).

Planning of bivalve aquaculture that includes calculations of carrying capacity of specific region, such as Mali Ston Bay where all production is based on seed collected from nature, require data on feeding ecology of bivalves and interactions between different species. Recently a study was initiated in the Mali Ston Bay that comparatively investigates feeding ecology of two aquacultured bivalve species (*Mytilus galloprovincialis* and *Ostrea edulis*) as well as two commercially important species from natural populations (*Arca noae* and *Modiolus barbatus*). This study will provide valuable data for development of bivalve aquaculture in the region (Peharda pers. comm.) and this paper provides the overview of current literature and understanding of bivalve feeding mechanisms, particle selection and food sources necessary for successful implementation of the above mentioned project.

BIVALVE FEEDING MECHANISMS

Based on the mechanism of food collection, bivalves can be suspension–feeders or deposit–feeders, or even utilize both feeding methods. Although there are some differences in particles processing, basic mechanism remains the same. Once particles entered the mantle cavity they are transferred along the ctenidium to the labial palps which are considered as a main site of particle selection. After selection on the palial organs, some particles are rejected as pseudofeces while other are ingested. When particles through esophagus enter the stomach, mechanical and enzymatic decomposition of ingested food begins. Rotating crystalline style mechanically breaks large particles while enzymes released from the style start to decompose organic particles. Stomach is a place of post–ingestive particle selection, where lighter organic particles enter the duct of the digestive diverticule and continue with the intracellular digestion. Remaining ingested particles go through the interstine to the mid–gut where they mix with other undigested material and incorporate into fecal pellets which are eject through anus and exhalant opening (Gosling, 2003; Ward and Shumway, 2004).

Two opposite theories exist today on regulation of filtration and feeding in bivalves. The first one, led by Jørgensen, considers feeding processes automated and dependant only on characteristics of certain species. Further on, this theory assumed that particles selection depend only on gill structure and particle concentration in the surrounding water (Jørgensen, 1996). Opposite theory, led by Bayne, assumes that filtration is physiologically controlled process which depends on nutritional needs of bivalve and qualitative and quantitative composition of seston. This theory presents suspension feeding as a complex interaction between physiological, morphological and behavioural characteristics which are sensitive on variation of available food in the environment (Bayne, 1998). Although many studies support this theory, its author is aware of the lack of information about mechanisms underlying these responses. One of the proofs of Bayne's theory is that bivalves under the condition of low food levels in the environment are able to increase absorption of ingested particles during the digestion process. *Mussel Mytilus edulis* and scallop *Placopecten magellanicus* showed higher absorption of organic matter during the period of low food concentration in seston, while during the period with high food concentration in seston absorption was lower (Bayne et al., 1993; Cranford and Hill, 1999). This adaptation is one of the proofs that bivalve feeding processes are not "automatized" is in fact regulated by physiology.

PARTICLE SELECTION

Existence of particle selection has been described in numerous studies but question why some particles bivalve ingest and other reject is still not well understood. In those studies authors usually assume that selection is based on particle size (Defossez and Hawkins, 1997; Lehane and Davenport, 2006), shape (Bougrier et al., 1997), nutritive value (Prins et al., 1991; MacDonald and Ward, 1994; Hawkins et al., 1996, 1998) or chemical component on the surface of the particle (Yahel et al., 2009). Shumway et al. (1985) performed experiment with six bivalves species including *Ensis directus, Mya arenaria, Placopecten magellanicus, Arctica islandica, Ostrea edulis* and *Crassostrea virginica* and fed them mixed cell suspensions of the dinoflagellate *Prorocentrum minimum,* diatom *Phaeodactylum tricornutum* and the cryptomonad flagellate *Chroomonas salina.* Their study showed that different species use different mechanisms of particle selection, for example *O. edulis* is selecting on the ctenidia where it mainly rejects dinoflagellates while particle selection in bivalves *E. directus, P. magellanicus* and *A. islandica* occurs on the labial palps were diatoms are rejected as pseudofecal material. Lack of cryptomonad flagellate in fecal material suggests that post — ingestive particle selection occurres in the majority of bivalve species. Scallop *P. magellanicus* also showed capability of selecting chlorophyll a containing particles and rejecting significant proportion of non–chlorophyll a containing particles as pseudofeces (MacDonald and Ward, 1994). Process of low nutritious particles rejection is important in situations when seston has high concentration of inorganic matter since rejection of non nutritional particles increases quality of ingested food (Prins et al., 1991; Hawkins et al., 1996, 1998). Evidence of size selection of zooplankton by mussel *M. edulis* is well described in Lehane and Davenport (2006). This study showed that mussels can ingest zooplankton organisms up to 3 mm in length but such organisms are not highly abundant in bivalve's stomach, what indicates that there is a size selection. Same author noted that there were differences in clearance rate of *Artemia* with respect to its size. Clearance rate of mussels fed with small *Artemia* (~600μm) was higher than those fed with larger ones (~900μm) (Davenport, personal observation in Lehane and Davenport, 2006). Research conducted on a tropical bivalve *Lithopaga simplex* pointed out that this species does not select particles only on the basis of their size but that it also selects according to the external cell characteristic and higher pigment content. This finding suggests that some bivalve could use chemosensory detection as selection mechanism (Yahel et al., 2009). All the above mentioned suggests that bivalves are able to make food selection but the mode how they do it is still unknown and needs to be further investigated.

BIVALVE FOOD SOURCES

Phytoplankton was considered as a main food source for bivalves and many studies looked at the influence of bivalves on phytoplankton community. Results of previous studies demonstrated that in shallow areas phytoplankton abundance could be strongly controlled by bivalve grazing (Cloern, 1982;

Dolmer, 2000a; Ogilvie et al., 2000). Dolmer (2000b) showed that in shallow water with low flow rates, mussel could reduce the phytoplankton densities above the mussel bed to the less than 1000 cells/cm^3. Asmus and Asmus (1991), Kimmerer et al. (1994) and Noren et al. (1999) have found a decline in phytoplankton abundance and biomass as consequence of bivalve grazing. Despite this effect it was considered that with recycling inorganic nutrients, primarily dissolved nitrogen and silica from suspended particulate organic matte bivalves could promote phytoplankton productivity (Asmus and Asmus, 1991; Ogilvie et al., 2000, 2003). This positive effect was considerably evident in periods and areas where primary production is limited with nutrients. Asmus and Asmus (1991) had developed hypothesis that positive contribution of bivalve grazing could be more significant than its negative contribution on decreasing of phytoplankton biomass. Importance of phytoplankton in bivalve diet was evident from comparison of bivalve growth rate and concentration of chlorophyll *a*. Page and Hubbard (1987) and Jasprica et al. (1997) have showed that bivalve growth rate was highest in the periods with maximum chlorophyll *a* concentration, i.e. the period of development of dense phytoplankton population.

Bivalves can also significantly reduce consequences of eutrophication with grazing of the phytoplankton (Officer et al., 1982). This is important for shallow areas with low water exchange rate and high density of mussels on the seabed, which are capable of filtering entire volume of water faster than the natural processes of water mass exchange. Good example of this situation is southern part of San Francisco Bay, where in spite of sufficient light and nutrients during the entire year only one spring phytoplankton bloom occurred while concentration of chlorophyll *a* remained low during the rest of the year (Cloern, 1982).

Research of Xu and Yang (2007) confirmed that phytoplankton is the most important food source for intertidal oyster *Crassostrea gigas* and mussel *Mytilus galloprovincialis*, as well as for the subtidal cultured scallop *Chlamys farreri*. However, depending on their size and habitat, bivalves utilize different fractions of phytoplankton. By analyzing fatty acid markers, Xu and Yang (2007) found that primary food sources of cultured scallop *C. farreri* were diatoms, while in a diet of oyster *C. gigas* and mussel *M. galloprovincialis* dinoflagellates prevailed. Stomach content analysis of mussel *M. galloprovincialis* collected during the dinoflagellate bloom showed expected dinoflagellate predominance (Sidari et al., 1998). Other studies on *M. galloprovincails* diet suggested that contribution of diatoms and dinoflagellates was lower than that of other phytoplankton groups (Prato et al., 2010). Shumway et al. (1987) analyzed stomach contents of scallop *Placopecten magellanicus* and found 27 phytoplankton species, mainly diatoms. Benthic and pelagic diatoms were evenly represented in stomach of *P. magellanicus* from the shallow area, while benthic diatoms were predominated in stomach of *P. magellanicus* collected from the deep sea. Compton et al. (2008) conducted a research on a deposit feeding species *Tellina capsoides*, *Tellina piratical* and *Tellina* sp. and found out that benthic diatoms are their most important food sources. Presented data show that contribution of different groups of phytoplankton in bivalve diet depends on the position of bivalves in a water column and also on structure of phytoplankton community in the surrounding water.

Although phytoplankton presents primary food sources for majority of bivalve species, several studies pointed out the importance of additional food sources such as bacteria, detritus and even zooplankton (Stuard et al., 1982; Cranfort and Grant, 1990; Langdon and Newell, 1990; Davenport et al., 2000; Lehane and Davenport, 2002, 2006; Prato et al., 2010). Kiørboe et al. (1981) noted that growth of *Mytilus edulis,* apart from abundance of diatom *Phaeodactylum tricornutum,* was also dependant on concentration of mud. The highest growth rate was recorded only with particular concentration of diatom and mud, which pointed out the importance of suspended particles of mud as additional food source for bivalves. Further on, bivalve can use additional food sources such as dissolved organic matter, especially dissolved free amino acids. Mussel *M. edulis* was capable of removing 94% of amino acids present in a surrounding water (Manahan et al., 1982), and normal amino acid concentration from seawater can satisfy up to 34% of metabolic needs of *M. edulis* (Manahan et al., 1983). Rice and Stephens (1987) analyzed incorporation of 10 amino acids in oyster *Crassostrea gigas* and showed that all of them were ingested and incorporated in different tissue like gills, mantle, adductor muscle and hemolimph.

Detritus contribution in bivalve diet is important during the periods when abundance of phytoplankton is too low to satisfy bivalve energy needs (Stuart et al., 1982; Cranford and Grant, 1990; Langdon and Newell, 1990). Fatty acid analysis of subtidal cultured scallop *C. farreri* showed small but still significant contribution of terrestrial organic matter derived from decomposed leaves and branches (Xu and Yang, 2007). Same study showed that macroalgae *Ulva pertusa,* during its bloom, contributed from 8.7% to 11.0% to the carbon budget of intertidal oyster and mussel. Fatty acid analysis of mud clam *Geloina coaxans* from mangrove forest showed that the main component of its diet were mangrove detritus particles while phytoplankton had the minor contribution (Bachok et al., 2003). Bacterial nutritive value for bivalve could be significant in stagnate water, marsh and eutrophic estuaries, where their abundance is high enough to contribute to the bivalve diet. Due to a small size of bacterial cells (1μm) bivalve utilization of bacteria varies between different bivalve species. Langdon and Newell (1990) showed that during the spring period when metabolic activity was high, bacteria satisfied between 5.5% and 31% of metabolic demand for carbon and between 26.7% and 70.6% metabolic demand for nitrogen in species *Crassostrea gigas* and *Geukensia demissa*, respectively. According to Prato et al. (2010), contribution of bacterial cells in mussel *M. galloprovincialis* diet was moderate during all seasons. Even though all bivalve species were not able to consume bacterial cells directly, they indirectly participated in bivalve diet. Above mentioned *G. coaxans* showed high concentration of bacterial fatty acid markers what suggest that this clams assimilated bacteria attached to mangrove detritus (Bachok et al., 2003).

For a long time it was considered that bivalves only indirectly influence zooplankton community trough competition for phytoplankton, but recently some studies pointed out that bivalve actually consume zooplankton (Davenport et al., 2000; Lehane and Davenport, 2002, 2004, 2006; Prato et al., 2010). Stomach content analysis of *Myilus edulis, Cerastoderma edule* and *Aequipecten opercularis* showed that bivalve could ingest variety of zooplankton organisms including calanoid copepods, harpacticoid copepods, crustacean nauplii, barnacle cyprids, bivalve larvae, amphipods, ostracods, unidentified eggs, cladocearans, hydromedusae, euphausiacea and foraminifera (Lehane and Davenport, 2002, 2004, 2006). One of the reasons why the role of zooplankton in bivalve nutrition was overlooked could be found in the short time of digestion, that is estimated to last 40 min at 15–20°C for *Mytilus edulis* (Davenport et al., 2000). Significant impact of bivalves on zooplankton community was demonstrated for the first time in San Francisco Bay after introduction of allochthon bivalve species *Potamocorbula amurensis* which caused significant decrease of copepods (Kimmerer et al., 1994). Heterotrophic flagelats and ciliats with rotifers also have important role in bivalve nutrition (Kreeger and Newell, 1996; Dupuy et al., 2000). Further on, it was shown that bivalves are capable of assimilating up to 73% of organic matter from rotifers, depending on bivalve species and concentration of rotifers (Horsted et al., 1988; Wong et al., 2003a, 2003b). Kršinić and Mušin (1981) suggested possible contribution of tinitinids in a diet of oyster *Ostrea edulis* in Mali Ston Bay, and few years later that hypotheses was confirmed with the analysis of oyster feces (Kršinić, 1987). Horsted et al. (1988) and Le Gall et al. (1997) pointed out high ciliate contribution in bivalve's diet. Additional food sources for bivalves are also bivalve larvae, and larval stages of other marine invertebrates (Cowden et al., 1984; Davenport et al., 2000; Lehane and Davenport, 2006). Bivalve larvae, up to 446μm in size, were recorded in stomachs of *Mytilus edulis* what indicates that adult bivalve grazing influence different life stages of these organisms (Lehane and Davenport, 2004). Larviphagy was also reported in pacific oyster *Crassostrea gigas* and cockle *Cerastoderma edulis* (Troost et al., 2008). Bivalve grazing on different bivalve larval stage could be strongly expressed and could cause decrease of bivalve stock. Above mentioned studies demonstrate that bivalves could use a wide range of organisms and particles suspended in the water column, what makes them important part of marine food webs.

CONCLUSION

Due to their high abundance in many marine ecosystems and their role in nutrient flux bivalves present significant trophic link in the marine environment. Feeding with wide range of food sources bivalves directly influence not only phytoplankton community but also bacterioplankton and zooplankton communities. Bivalve growth depends on quality of their diet, so from aquaculture point of view it is important to know under what condition bivalves have optimum energy available to maximize their growth. Further on, knowledge of bivalves feeding processes is important for aquaculture planning, because through filter feeding process bivalves can remove significant amount of bivalve larvae present in the water column, and thereby have direct impact on the bivalve production. This is important for areas where production still depends only on seed collected from the nature, what is the case for aquaculture areas along the eastern Adriatic coast including Mali Ston bay.

Sažetak

PREHRANA ŠKOLJKAŠA — KAKO I ŠTO JEDU?

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Školjkaše, prema načinu prikupljanja hrane, možemo svrstati u tri kategorije: one koji se hrane česticama suspendiranim u vodenome stupcu (suspension–feeders), zatim one koji se hrane depozitom (deposit–feeders), te one koji pri prehrani kombiniraju oba načina. Iako neki autori hranjenje školjkaša opisuju kao »automatizirani« proces, novija istraživanja pokazala su da neke vrste školjkaša mogu regulirati filtraciju te vršiti selekciju čestica na osnovi njihove veličine, oblika, nutritivne vrijednosti ili kemijskih komponenti na površini čestica. Novija su istraživanja također pokazala kako fitoplankton nužno nije primarni izvor hrane za školjkaše te su istaknula važnost drugih izvora hrane kao što su bakterije, detritus pa čak i zooplankton, koji uključuje i ličinke školjkaša. Hranjenje adultnih školjkaša ličinačkim stadijima može imati značajan utjecaj na prirodne stokove. Zbog gore navedenih procesa školjkaši imaju veliki utjecaj na protok energije i tvari između bentosnih i pelagičkih zajednica, što ih čini važnim dijelom morskih hranidbenih mreža. Ovaj rad izlaže pregled postojeće literature radi razumijevanja procesa prehrane, selekcije čestice te izvora hrane za školjkaše.

Ključne riječi: prehrana školjkaša, selekcija čestica, akvakultura školjkaša

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