Review

Comparative ecophysiology of active zoobenthic filter feeding, essence of current knowledge

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Abstract

The present contribution gives an overview of current knowledge of a comprehensive and steadily growing research field. The first section deals with water pumping and particle retention mechanisms in ciliary and muscular filter feeders. The second section examines the biological filter pumps in order to assess adaptation to the environment. Filter-feeding benthic invertebrates have evolved filter pumps to solve common basic problems. This has led to a large degree of similarity between otherwise distant standing species, which makes comparative studies interesting and important. The present review of zoobenthic filter feeding aims at accentuating such recognition. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: water pumping; particle retention mechanisms; ciliary and muscular filter feeders; bioenergetics; minimal scaling; adaptation to the environment

1. Introduction

Active filter-feeding benthic invertebrates are important elements in coastal ecosystems where they sustain life by removing suspended food particles from the water (Jørgensen, 1966, 1975, 1990; Davies et al., 1989; Møhlenberg, 1995; Mann and Lazier, 1996; Wildish and Kristmanson, 1997).

Biological and physical processes are particularly closely coupled in coastal waters. For example, water depth, which affects the importance of wind and tidal mixing, strongly influences the grazing impact of benthic filter-feeder populations, which may be considerable in shallow waters (Officer et al., 1982; Cloern, 1982). Population filtration rates in these areas are typically between 1 and 10 m^3 water per square meter area per day (Riisgård, 1991a, 1994; Petersen and Riisgård, 1992; Riisgård et al., 1995, 1996c,e, 1998; Lemmens et al., 1996; Vedel, 1998), but higher rates may be found for dense mussel beds that can filter more than 100 $m^3\,m^{-2}\,d^{-1}$ (Jørgensen, 1980, 1990).

Quantification of rates of energy transfer between the trophic components in a marine ecosystem is difficult and complex, and the role of zoobenthic filter feeding in the exchange processes is only just coming to light. However, it is clear that energy transfer through filter-feeding invertebrates is often an important route from the pelagic to the benthic components of coastal ecosystems (Baird and Ulanowicz, 1989; Riisgård et al., 1996b; Riisgård, 1998a; Arntz et al., 1999). Recent work has produced evidence of the role of dense benthic filter feeding populations in regulating plankton production in

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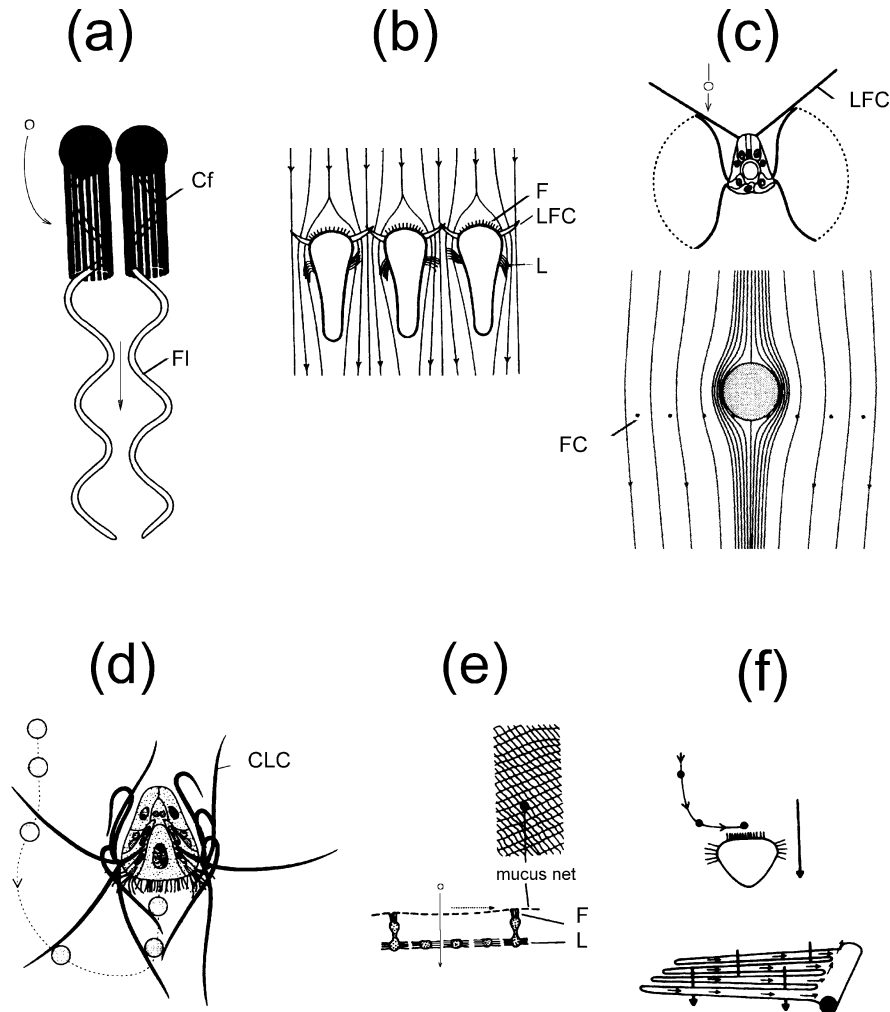*E-mail address:* hur@biology.ou.dk (H.U. Riisgård).

Fig. 1. Types of capture mechanisms in active suspension feeding marine invertebrates. (a) Collar-sieving in sponges; two choanocytes with parallel flagella act as a peristaltic pump; Fl flagellum; Cf, collar of microvilli acting as a filter. (b) Cirri trapping in mussels; three gill filaments are shown; F, frontal cilia; LFC, laterofrontal cirri; L, lateral cilia. (c) Ciliary sieving in bryozoans; upper: cross section of tentacle; LFC, laterofrontal cilia acting as a sieve above the water pumping lateral cilia; lower: filter consisting of stiff laterofrontal cilia has stopped a particle which influences the streamlines for creeping flow through the filter. (d) Cross section of tentacle from a ciliary downstream-collecting animal showing how the compound lateral cilia, CLC catch up a particle and transfer it to the frontal side of the tentacle. (e) Upper: rectangular mucus net of an ascidian; lower: lateral cilia, L in the pharynx slits pump water through the net; frontal cilia, F transport the mucus net with retained food particles. (f) Upstream retention in a brachiopod; upper: cross section of filament, indicating path of particle from through current into surface current; lower: short segment of lophophore with filaments. Figs. modified from: (a) Larsen and Riisgård (1994); (b) Silvester and Sleigh (1984); (c) Nielsen and Riisgård (1998); (d) Riisgård et al. (2000); (e) Riisgård and Larsen (1995); (f) Jørgensen et al. (1984).

littoral systems, including control of phytoplankton blooms and other aspects of relevance for eutrophication problems (Nixon, 1995; Riisgård et al., 1995). But in habitats with a rich and diversified filter-feeder fauna consisting of sponges, cnidarians, bryozoans etc. the role of these species as consumers of pelagic production is still poorly understood (Lemmens et al., 1996; Gili and Coma, 1998).

The filter feeders which have adapted to a life in a nutritionally dilute environment show great variations in the design of feeding mechanisms (Rubenstein and Koehl, 1977; Chapman 1968; Foster-Smith, 1976a,b,

1978; Brown, 1977; LaBarbera, 1984, 1990; Jørgensen, 1990; Shimeta and Jumars, 1991; Vogel, 1994; Riisgård and Larsen, 1995; Nielsen and Riisgård 1998; Grünbaum et al., 1998). During the last decade investigations of filter-pumps and their properties have been intensified, including sponges, polychaetes, bivalves, ascidians, bryozoans and other groups of small ciliary filter feeders. The studies have aimed at giving a more precise description of water pumping systems and particle capture mechanisms, but also at characterising the pumps quantitatively, and assessing energy costs of water pumping as reviewed by Riisgård and Larsen (1995).

The present contribution gives an overview of the essence of current knowledge of a comprehensive and steadily growing research field. The paper consists of two parts. Part 1 deals with water pumping and particle retention mechanisms in ciliary and muscular filter feeders. Part 2 examines the biological filter-pumps in order to assess the adaptation to the environment. The filter-pumps have evolved to solve common basic problems which has also led to a large number of resemblances between otherwise distant standing species. This makes comparative studies interesting and important, and the present review of filter feeding in benthic marine invertebrates aims at accentuating such recognition.

2. Part 1: Water pumping and particle retention

In active suspension feeders, water is pumped through a filter device which separates the food particles from the water so that they can be consumed by the animal. Extraction of suspended particles from the water is based on different capture mechanisms. A review of methods for capturing particles in benthic animals feeding on suspended particles has previously be given by Wotton (1994) and Riisgård and Larsen (1995). The present contribution deals with the six types of mechanisms found in the active filter feeding marine invertebrates depicted in Fig. 1. The paper does not attempt to cover all aspects of filter feeding, such as post-capture transport and sorting of particles although such aspects may at times be of crucial importance, e.g. for certain polychaetes (Nicol, 1931), ascidians (Jørgensen, 1966), and bivalves filter feeding at high seston concentrations (Kiørboe and

Møhlenberg, 1981; Møhlenberg and Kiørboe, 1981; Jørgensen, 1990, 1993, 1996; Ward et al., 1993, 1998a,b). Depending on context, different expressions for water processing by the filter-feeding animals are used: pumping rate = filtration rate (volume flow through the animal's filter per unit time); clearance rate = volume of water cleared of suspended particles per unit of time. For particles that are retained with 100% efficiency by the animal's filter, clearance rate is equivalent to filtration rate.

2.1. Types of particle capture mechanisms

Filter feeders (here used synonymous with suspension feeders) extract their nourishment from suspended micro-organisms and detritus in the surrounding water. The term particle capture mechanism is here used to describe the process of extraction of suspended particles from water which is actively pumped through some kind of filter device which separates the particles from the water so that they can be consumed by the animal. Passive filter feeders, which utilise the natural flow to bring particles in contact with feeding structures (Fauchald and Jumars, 1979; Shimeta and Jumars, 1991; Sponaugle, 1991; Loo et al., 1996; Shimeta and Koehl, 1997), are not treated in the present review. Switching between deposit and suspension feeding in coastal zoobenthos has recently been reviewed by Riisgård and Kamermans (2000).

Six types of food particle capture mechanisms have so far been recognised in marine benthic filter feeders: (1) *collar-sieving* in sponges, where a beating flagellum creates the feeding current through a collar-filter; (2) *cirri trapping* in bivalves with gill filaments possessing laterofrontal cirri that beat against the through current; (3) *ciliary sieving* in bryozoans, where particles are retained by a filter formed by a band of stiff cilia upstream of the water pumping lateral cilia; (4) *ciliary downstream collecting* in a diverse group of filter-feeding invertebrates, where food particles are caught up by compound cilia, which also create the current, and then transferred to the downstream side for collection; (5) *mucus net filter feeding* in some species of polychaete worms, ascidians, gastropods and lancelets, where ciliary or muscular pumps drive water through a mucus net which retains the suspended food particles; and (6) *ciliary upstream collection* in, e.g. brachiopods,

where particles are retained on the upstream side by a water transporting ciliary band. The different types are presented in the following sections, and general principles are at times exemplified by way of specific species.

2.2. Collar sieving

Collar sieving is restricted to sponges, which are simple, multicellular animals whose entire body is specialised for suspension feeding. The basic element for pumping and filtering the surrounding water is the choanocyte, a specialised cell with a flagellum that pumps water through a collar of microvilli acting as a filter (Fig. 1a). The structure of the choanocytes is the same in all sponges, and among the metazoa, sponges are unique in feeding by means of choanocytes. Choanocytes are structurally and functionally identical to the choanoflagellates (Fjerdingstad, 1961a,b; Laval, 1971; Hibberd, 1975; Bergquist, 1978) that filter free-living bacteria from the water. The striking similarity of choanoflagellates to the choanocytes of sponges has given rise to speculations about the evolutionary relationship between the two groups (Barnes, 1987). It has been theorised (Leadbeater, 1983) that sponges have evolved from colonies of choanoflagellates and that the small and simple ascon-type sponge has given rise to the more advanced sycon-type from which the large and more successful complex leucon-type sponge evolved.

The sponge pump was analysed by Larsen and Riisgård (1994) and compared with the choanoflagellate pump in order to identify prerequisite properties of the basic pump units which have enabled the development of large sponges. The pump analysis was based on experimentally measured back-pressure pumping-rate characteristics of the demosponge *Haliclona urceolus* and on mathematical-hydraulic modelling. A curved characteristic was found for *H. urceolus,* and the maximal pressure rise (at zero flow) which could be delivered by the sponge was about 2.4 mm H_2O. To unveil the pumping principle and to propose a pump model for sponges Larsen and Riisgård (1994) considered the free-living choanoflagellate *Monosiga* as representative of a sponge-choanocyte because the two cell types are structurally and functionally identical: a flagellum pumps water through a collar of microvilli acting as a filter. Knowing the flagellum length, beat frequency, wavelength and amplitude the pump head of the choanoflagellate was estimated to be 0.076 mm H_2O. Because this pump head is insufficient to handle the pressure drop in a sponge it was suggested that the closely spaced flagella in the choanocyte chambers of sponges might all together act as a peristaltic pump being able to create the necessary pump pressure to overcome the resistance in the extensive canal system. It was further argued by Larsen and Riisgård (1994) that the basic pump units in a 'standard' demosponge are the choanocyte chambers, constituting 30–50% of

Table 1
Water flow velocity immediately before impact onto mucus-net in various filter feeders. M is the muscular pump; and C the ciliary pump

Species	Flow velocity (mm s^{-1})	Pump type	Reference
Polychaetes			
Chaetopterus variopedatus	1.5	M	Riisgård (1989)
Nereis diversicolor	0.2–0.27	M	Riisgård et al. (1992)
Gastropods			
Crepidula fornicata	0.8	C	Jørgensen et al. 1984)
Ascidians			
Ascidia mentula	0.37	C	Jørgensen et al. (1984)
Styela clava	0.3	C	Riisgård (1988a)
Appendicularians			
Oikopleura vanhoeffeni	0.56	M	Acuña et al. (1996)
Thaliaceans			
Pegea confoederata	1.7	M	Bone et al. (1991)
Salpa maxima	6	M	Madin (1990)
Cephalochordates			
Branchiostoma lanceolatum	0.09–0.34	C	Riisgård and Svane (1999)

the wall structure separating inhalant and exhalant canals, and further, that all pump units operate in parallel and at essentially the same flow and pressure rise.

One crucial difference between sponges and choanoflagellates is the ability of the former to feed on phytoplankton which is retained and digested (phagocytosis) in the extensive inhalant channel system (Kilian, 1952; Simpson, 1984) before the water is finally filtered through the 0.1 μm collar slits of the choanocytes. Few workers have focused on the differences in the physiological performances that may exist between sponges and other filter-feeding invertebrates. Ecophysiological investigations of sponges are few and many questions remain largely unanswered, although Riisgård et al. (1993) and Thomassen and Riisgård (1995) carried out ecophysiological studies in order to uncover the nature of sponges to enable a comparison with other, more advanced filter-feeding invertebrates.

The growth, filtration and respiration of *Halichondria panicea* were measured by Thomassen and Riisgård (1995). The maximum specific growth rate was 4% d^{-1}, and it was stressed that sponges have a low water pumping capacity, expressed as litres of water filtered per cubiccentimeter oxygen consumed (see Table 3, and Section 3.3), compared with other filter-feeding invertebrates, but compensate for this by a high retention efficiency for even very small particles, down to 0.1 μm. It was also found that the energy cost of growth was equivalent to 139% of the actual growth which is comparable with microorganisms, but considerably higher than found for 'true' invertebrates (see Section 3.4).

2.3. Cirri trapping

Bivalves are the best studied filter feeders. The mechanisms of water pumping and particle retention have been reviewed and re-evaluated repeatedly over the years (Dral, 1967; Bayne et al., 1976a,b; Owen and McCrae, 1976; Winter, 1976; Møhlenberg and Riisgård, 1978, 1979; Riisgård and Møhlenberg, 1979; Jørgensen, 1983, 1989, 1990, 1996; Meyhöfer, 1985; Jørgensen et al., 1990; Silvester and Sleigh, 1984; Riisgård 1988a; Ward et al., 1993, 1998a,b; Ward, 1996; Nielsen et al., 1993; Silverman et al., 1996a,b; Riisgård and Larsen, 1995; Riisgård et al.,

1996d; Smaal and Twisk, 1997; Charles et al., 1999; Cranford and Hill, 1999). Especially the particle capture mechanism in mussels has been debated; but considerable progress and also a high degree of agreement in understanding this mechanism seem to have been achieved in recent years (Riisgård et al., 1996d; Beninger, 2000; Silverman et al., 2000; Riisgård and Larsen, 2000).

In the blue mussel, *Mytilus edulis*, bands of lateral cilia produce the main water transport through the interfilamentary canals of the gill (Fig. 1b). Near the entrance to the canals, particles are separated from the main currents and transferred onto the frontal surface by the action of the laterofrontal cirri that have a fixed pattern of alternating beat. Interest in understanding filter feeding by bivalves has led to video recording of water motion inferred from particle motion when particle motion is not restrained by interaction with objects (cilia) or by very small (1 μm) particles. The issue in such studies has been to gain optical access while maintaining undisturbed, natural feeding. Used techniques include isolated gill-filament preparations observed through traditional light-microscopes with lenses immersed in water (Nielsen et al., 1993; Riisgård et al., 1996d), high powered confocal laser scanning microscopy (Silverman et al., 1996a,b, 2000); observations of intact bivalves by means of endoscopy (Beninger et al., 1992; Ward et al., 1993; Ward, 1996), or by using a long working distance dissecting microscope (Riisgård and Larsen, 2000).

The role of laterofrontal cirri in particle capture by *M. edulis* was studied by Riisgård et al. (1996d) using gill filaments mechanically adjusted by 'stretching' to restore the normal interfilament gap of about 40 μm of the intact mussel. When stimulated with serotonin both the beat frequency of the lateral cilia and the laterofrontal cirri were comparable with values measured in intact, small, transparent mussels (Dral, 1967; Jørgensen and Ockelmann, 1991). The video observations showed that suspended algal cells carried with the through current were stopped for a while at the entrance to the interfilament gap. Then the path was reversed 180°, and the particles were transferred to the frontal side of the gill filament to be transported towards the marginal food groove by frontal cilia. Transfer of particles from the through current to the frontal current is made by the laterofrontal cirri or by the water currents they generate as they beat

against the current through an angle of 90°. Riisgård et al. (1996d) concluded that particles larger than 4 μm are stopped and transferred to the frontal side, whereas smaller particles either follow the flow around the cirri or they are stopped by the cirri's branching cilia. Observations of interactions between 1 μm latex particles and laterofrontal cirri described by Silverman et al. (1996a,b) extend at higher resolution the observations of Riisgård et al. (1996d), and the explanation is in agreement with experimentally measured particle retention efficiency in mussels (Møhlenberg and Riisgård, 1978; Riisgård, 1988b; Jørgensen, 1996).

Video observations have recently been made on intact *M. edulis* by Riisgård and Larsen (2000). Using a horizontal dissecting microscope the gills of an actively feeding mussel were seen behind the gaping valves when the animal was fixed on its side in an observation chamber. Video recordings were made through the inhalant opening and the approach speed of particles was measured to be about 1 mm s^{-1}, in agreement with the speed predicted by Riisgård et al. (1996d), and as particles approached the gill their paths curved in the direction normal to the gill frontal surface previous to capture which were to be expected because of the parallel arranged lateral-cilia pumps. This streamline pattern resembles that observed in a channel with porous walls subject to suction, where streamlines curve to become normal to the surface as it is approached. Such paths of particles approaching the gill surface were computed for a model problem simulating the space between two demibranchs by Riisgård and Larsen (2000).

The absence of the laterofrontal cirri in certain bivalve gills, i.e. the Microciliobranchia excluding the Ostreidae (Owen and McCrae, 1976) indicates that the laterofrontal cirri may be a speciality of some bivalves. The basic particle capture mechanism in bivalves without laterofrontal cirri remains largely unknown, see also Owen and McCrae (1976), Beninger and Le Pennec (1988) and Beninger et al. (1992).

2.4. Ciliary sieving

Ciliary sieving in bryozoans (or ectoprocts) seems to be the first documented example of a mechanical ciliary filter in metazoans. Bryozoans are active filter feeders working an energy-consuming lophophore filter pump (Bullivant, 1968a,b; Gordon et al., 1987; Ryland, 1976; Winston, 1978; Gordon et al., 1987; Grünbaum, 1995, 1997; Riisgård and Manríquez, 1997; Riisgård and Goldson, 1997; Eckman and Okamura, 1998; Grünbaum et al., 1998; Larsen et al., 1998; Nielsen and Riisgård, 1998; Lisberg and Petersen, 2000).

The feeding apparatus in the bryozoans consists of a ring of extended ciliated tentacles which form a crown (lophophore), with the mouth at the centre of its base. In all bryozoans (except the cyclostomes, Nielsen and Riisgård, 1998) three types of ciliary rows may be found on the tentacles: lateral, frontal, and laterofrontal. The lateral cilia produce the feeding currents of the lophophore. When the through currents pass between the tentacles outwards this results in the formation of a relatively strong core current directed straight down the lophophore to the mouth (Riisgård and Manríquez, 1997). Particles in the through currents are retained by the stiff laterofrontal ciliary filter (Fig. 1c) and either transported downwards on the tentacles by means of the frontal cilia, or the particles are transferred to the core current by means of inward tentacle flicks triggered by the arrested particles. The mechanism which triggers a tentacle flick is unknown, but particles that are not actually stopped by the filter may not trigger a flick. Thus, a certain extra drag force from the arrested particle, besides the 'background' force exerted on the laterofrontal cilia due to the through current, may be a prerequisite for triggering a tentacle flick.

The same tentacle flick mechanism was observed by Nielsen and Riisgård (1998) in the cyclostome *Crisia eburnea*, which does not have frontal cilia. Here, feeding apparently relies crucially on tentacle flicks and the principle of particle capture is especially easy to observe. Eight tentacles are arranged as a funnel in front of the mouth, the lateral band consists of two rows of very closely spaced cilia, and no frontal cilia are present. The row of 15 μm long, stiff laterofrontal cilia have a spacing of 3–4 μm. When food particles move toward the funnel they get caught by the filter formed by the laterofrontal cilia which, judging from their ultrastructure, are sensory and the tentacle makes a flicking movement towards the centre of the funnel. Again, the relatively strong central current carries the particles downward to the mouth.

The retention efficiency has been measured in two

Table 2
Operating pressure of pump (ΔH), power output (P), total metabolic rate of standard animal (R_t) and overall pump efficiency (P/R_t) in various filter-feeders

Taxonomic group and species	ΔH_0 (mm H$_2$O)	P (μW)	R_t (μW)	P/R_t (%)	References
Sponges					
Haliclona urceolus	0.673	0.677	80	0.85	Riisgård et al. (1993)
Bryozoans					
Crisia eburnea	0.065	–	–	–	Nielsen and Riisgård (1998)
Polychaetes					
Chaetopterus variopedatus	1.43	4.3	107	4.0	Riisgård (1989)
Nereis diversicolor	1.49	2.1	70	3.0	Riisgård et al. (1992)
Sabella penicillus	0.0224	0.451	112	0.403	Riisgård and Ivarsson (1990)
Bivalves					
Mytilus edulis	1.0	10	900	1.1	Jørgensen et al. (1986a), Jørgensen et al. (1988)
Ascidians					
Styela clava	0.3	2.3	891	0.26	Riisgård (1988a)

cheilostomate bryozoans. It was found that particles >5 μm in diameter are retained with near 100% efficiency in both *Celleporella hyalina* (Riisgård and Manríquez, 1997) and *Electra crustulenta* (Riisgård and Goldson, 1997). This shows that the spacing between the 0.2 μm diameter laterofrontal cilia may be about 5 μm in these bryozoans.

The main resistance to water flow in bryozoans is the ciliary sieving system. The pressure drop across the laterofrontal ciliary filter is found to be $\Delta H = 0.065$ mm H$_2$O (see Section 3.2., and Table 2). The operating pressure of the ciliary pump in an isolated bryozoan is therefore predicted to be quite low although it may be considerable in bryozoans in encrusting colonies (Larsen and Riisgård, in preparation), likely of the order of magnitude generally found for filter-feeders (cf. Table 2).

2.5. Ciliary downstream collecting

In ciliary downstream-collecting animals a ciliary band transfers particles from the water current to the downstream side of the band, where the separated particles are taken over by another band of cilia which transports the particles toward the mouth. Ciliary downstream particle collecting is found in different taxonomic groups of invertebrates (Nielsen, 1987, 1995), including meroplanktonic larvae of gastropods (Emlet, 1990; Hansen, 1991), bivalves (Strathmann and Leise, 1979; Gallager, 1988), and polychaetes (Emlet, 1990; Hansen, 1993).

Polychaetes are among the most frequent and important marine invertebrates in benthic environments. The available information on feeding modes was reviewed by Fauchald and Jumars (1979), who noted that filter-feeding has been documented for at least five families (Chaetopteridae, Oweniidae, Sabellariidae, Fabriciinae, Sepulidae-Spirorbidae, Spionidae). Some of the species are partially or wholly filter feeders (Buhr, 1976; Taghon et al., 1980; Miller et al., 1992; Riisgård and Kamermans, 2000). Below are given two examples of ciliary downstream collecting in two polychaetes together with an entoproct and a cycliophore using the same feeding mode. This also underlines the use of ciliary downstream collection as a widespread basic feeding principle, used across taxonomic boundaries and adequately working in spite of often great variation in functional morphology of the feeding organs.

Downstream collecting has been studied in adult specimens of the polychaetes *Sabella penicillus* (Riisgård and Ivarsson, 1990; Mayer, 1994), *Spirorbis tridentatus*, the entoproct *Loxosoma pectinaricola*, and the cycliophore *Symbion pandora* (Riisgård et al., 2000). The ciliary bands show some general structure in all groups as appears from the descriptions given below.

The interpretation of observations of structure and activity of the ciliary bands in *Loxosoma pectinaricola* as summarised by Riisgård et al. (2000) may serve as a general description of ciliary downstream collecting. In *L. pectinaricola* video-observations of

the paths and velocities of particles showed that suspended particles are accelerated with the water that enters the region swept by the compound lateral cilia and then become caught up by one and more likely by more of the compound cilia in their power stroke (Fig. 1d). This element in the process, denoted 'catch-up', accelerates a particle and rapidly moves it in a curved path to the midline at the frontal side of the pinnule. In this phase of the power stroke the particle is pushed out of the main water current which moves past the tentacle, and as the compound lateral cilia come to rest in their angular motion so does the particle and surrounding fluid. The lateral cilia from the two sides of the tentacle may prevent escape of the particle. Finally, the frontal cilia carry the particle along the food groove to the mouth. The basic principle of particle catch-up as adopted for *Loxosoma* (and *Spirorbis*, *Sabella*, and others) applies for the cycliophore *Symbion* although the principle of opposed ciliary bands has instead been obtained by a ciliated mouth ring while the frontal cilia are replaced by a ciliated mouth cavity.

Based on literature data, own video-observations and fluid mechanical considerations it was concluded by Riisgård et al. (2000) that the capture mechanism in all ciliary downstream-collecting suspension feeders is based on the same basic principle described by the catchup hypothesis. According to this hypothesis compound cilia constitute the pump which generates a flow with suspended particles that enters the ciliary region. In this region the same cilia, during their power stroke, catch up with suspended particles and transfer the particles to a food groove, or a mouth cavity. In the particle-size retention spectrum, the lower limit presumably depends on spacing between cilia that beat in phase, while the upper limit depends on cilia length, which may or may not allow particles to enter the ciliary region. The last phase of transfer is likely to involve interactions with other cilia systems which act to prevent intercepted particles from escaping with the main through flow.

2.6. Mucus-net filter feeding

Filter feeding by means of an efficient mucus net which sieves the feeding current has independently evolved in a number of different taxonomic groups of marine animals. Examples of this adaptation to feeding on a dilute suspension of microscopic food particles, including free-living bacteria, are given below:

2.6.1. Chaetopterus variopedatus and other chaetopterids

The mucus-net filter-feeding polychaete *Chaetoptrus variopedatus*, which lives in a parchment-like tube, has been described in several papers, and different aspects of water pumping and particle retention have been treated over the years (MacGinitie, 1939; Wells and Dales, 1951; Brown, 1977; Flood and Fiala-Médioni, 1982; Jørgensen et al., 1984; Riisgård, 1989).

When the worm is feeding, a flow of water is driven through the tube in the antero-posterior direction by three muscular piston-like parapods in the middle region of the body. Two notopodia secrete a mucus net-bag, which filters the water current. The posterior end of the suspended mucus net-bag is rolled up into a food ball within a ciliated cup-like organ, and is ingested at intervals of 15–20 min. The mucus net is built of longitudinal parallel fibre bundles and transverse filaments forming a rectangular mesh (Flood and Fiala-Médioni, 1982) which efficiently retains suspended food particles down to ca. 1 μm (Jørgensen et al., 1984).

The family Chaetopteridae is well known in terms of feeding modes. Besides the above-mentioned 'piston-pump mucus-net' feeding mode of *C. variopedatus*, five additionally species of chaetopterids use filter-nets, similar to the ones produced by *C. variopedatus* (Barnes, 1964, 1965). In some instances a single net is employed (*Telepsavus costarum*, *Ranzanides sagittaria*), but in other cases several nets are formed on successive segments (*Spiochaetoptrus oculatus*, *Phyllochaetopterus socialis*, *Mesochaetopterus taylori*). In *Spiochaetopterus*, *Telepsavus*, and *Phyllochaetopterus* the water current through the tube is generated by ciliary rings of the foliaceous notopodia, whereas *Ranzanides* and *Mesochaetopterus* pump water through the tube by means of peristaltic contractions of a number of segments of the middle body region. These examples illustrate the flexibility by which ciliary pumps, muscular-piston pumps and muscular-peristalltic pumps are being employed more or less indiscriminately even within closely related species that may use either one big or

several smaller mucus nets for straining the tubal water current.

2.6.2. Nereis diversicolor

The common polychaete *Nereis diversicolor* lives in a U-shaped burrow in soft sediment. *N. diversicolor* has been described as a carnivore and/or scavenger, but also as a suspension-feeder and a detritivore, feeding partly by swallowing surface mud around the openings of the burrow (Wells and Dales, 1951; Goerke, 1966; Evans, 1971; Riisgård, 1994). The occurrence of a filter-feeding mechanism in *N. diversicolor* was first described by Harley (1950), and later confirmed by Goerke (1966). Observations of filter-feeding behaviour were made by Riisgård (1991a) on *N. diversicolor* in glass tubes immersed in seawater. When algal cells are added, the worm moves to one end of the glass tube to fix mucus threads to the glass wall, forming the circular opening of a net bag. This funnel-shaped net bag is completed as the worm retreats down the tube. For a period after the bag is completed, the worm pumps water through the net by means of vigorously undulating movements of the body (peristaltic pump). Particles suspended in the inhalant water are retained by the net and after a period of pumping the worm moves forward, swallowing the net bag and its entrapped food particles. The structure of the food-trapping net of *N. diversicolor* was studied by Riisgård et al. (1992). Electron-micrographs of the filter-net structure showed that the net is composed of an irregular mesh made up of long, relatively thick filaments (up to 300 nm) interconnected with a variety of shorter and thinner filaments with diameters ranging from 5 to about 25 nm. The average mesh size was between 0.5 and 1.0 µm (which due to shrinkage during preparation may represent only approximately 75% of the actual dimension of the intact net). Simultaneous clearance measurements of different-sized particles by Riisgård et al. (1992) showed that particles down to 2–3 µm may be efficiently (near 100%) cleared from the water. Thus, the retention efficiency of *N. diversicolor* is as high as found in a most obligate filter feeders (Jørgensen et al., 1984). The main resistance to water flow through a tube holding a filter-feeding *N. diversicolor* is the mucus net. Following Silvester (1983), using the modified Tamada–Fujikawa equation (see Section 3.2.), the pressure drop across the mucus net

was calculated by Riisgård et al. (1992) to be between 0.34 and 0.41 mm H_2O. It is not known whether filter-feeding is of primary importance for any population of this species, but when the phytoplankton concentration is above a certain lower 'trigger level', *N. diversicolor* prefers to filter-feed, while below the trigger level it switches to one of the alternative feeding modes (Vedel and Riisgård, 1993; Vedel et al., 1994; Riisgård, 1994; Riisgård and Kamermans, 2000).

2.6.3. Ascidians

Ascidians pump water through the inhalant siphon into the pharyngeal chamber and through the stigmata into the atrium from which the water leaves the ascidian as a jet through the exhalant siphon. The pharynx is perforated with small slits (stigmata), and ciliary tracts on either side of the stigmata create the feeding current (Fig. 1e). When the water is pumped across the pharynx wall, suspended particles are trapped on the mucus net continuously produced by the endostyle (Holley, 1986). Cilia on the papillae or longitudinal pharyngeal bars transport the endless mucus net, with the retained food particles, to the dorsal side where it is rolled into a cord which is passed downwards into the oesophagus as an unbroken string (MacGinitie, 1939; Millar, 1971; Fiala-Médioni, 1978). Particles down to 2–3 µm are completely retained (Randløv and Riisgård, 1979; Jørgensen et al., 1984), and electron microscopic studies of the mucus net have revealed that in the fixed state, it is composed of 10–40 nm thick fibres arranged in rectangular meshes that vary between 0.2 and 0.5 µm in width and between 0.5 and 2.2 µm in length (Flood and Fiala-Médioni, 1981). The ciliary pump of *Styela clava* was analysed by Riisgård (1988a). Based on direct measurement of the pumping rate, the flow velocity through the mucus filter was found to be 0.3 mm s^{-1} and the pressure drop across the net estimated to be 0.069 mm H_2O. The effects of temperature and algal concentration on pumping of water in *Ciona intestinalis* have recently been studied by Petersen et al. (1999).

2.6.4. Lancelets (amphioxus)

The most common of the transitional species of lancelets, which share characteristics with both vertebrates and invertebrates, is *Branchiostoma*

Table 3

Maximum volumes of water filtered (F_{max}, dm^3) per cubiccentimeter O_2 consumed at starvation (R_m, maintenance metabolism) for various filter-feeding invertebrates, and for comparison the deposit-feeding bivalve *M. balthica* and the deposit-feeding polychaete lugworm *Arenicola marina*

Taxanomic groups and species	F_{max}/R_m ($dm^3\ cm^{-3}\ O_2$)	Reference
Sponges		
Halichondria panicea	2.7	Thomassen and Riisgård (1995)
Mycale sp.	19.6	Reiswig (1974)
Verongia gigantea	4.1	Reiswig (1974)
Verongia fistularis	9.7	Reiswig (1974)
Tethya crypta	22.8	Reiswig (1974)
Bryozoans		
Celleporella hyalina	68	Riisgård and Manríquez (1997)
Copepods		
Acartia tonsa	37	Kiørboe et al. (1985)
Polychaetes		
Sabella penicillus	354	Riisgård and Ivarsson (1990)
Chaetopterus variopedatus	50	Riisgård (1989)
Nereis diversicolor	40	Riisgård (1991a)
Arenicola marina	0.4	Riisgård et al. (1996a)
Bivalves		
Mytilus edulis	15–50	Riisgård et al. (1980)
Mytilus edulis	18	Clausen and Riisgård (1996)
Macoma balthica	0.4–1.6[a]	Kamermans (1994), De Wilde (1975), Hummel (1985)
Ascidians		
Ciona intestinalis	82	Petersen et al. (1995)
Ciona intestinalis	13	Jørgensen (1955)
Lancelets		
Brachiostoma lanceolatum	79	Riisgård and Svane (1999)

[a] Filtration rate (*F*) of *M. balthica* = 5 $cm^3\ h^{-1}$ for a 8 mg body dry wt individual (Kamermans, 1994; Kamermans, pers. comm.), or 6–23 $cm^3\ h^{-1}$ for a 38 mg body dry wt individual (Hummel, 1985). Respiration (*R*) = 0.014 $cm^3\ O_2\ h^{-1}$ for an about 25 mg dry wt *M. balthica* (De Wilde, 1975). *F/R* = 0.4–1.6 dm^3 water filtered per cubic centimeter O_2 consumed.

lanceolatum, generally known as amphioxus. Since the early contributions of Orton (1913) and Van Weel (1937) a number of papers have described lancelets as filter feeders (Barrington, 1958; Olsson 1963; Welsch 1975; Baskin and Detmers, 1976; Rähr, 1982; Riisgård and Svane, 1999; Ruppert et al., 2000). As an obligate filter feeder *B. lanceolatum* obtains its food by straining off phytoplankton in the surrounding water. Amphioxus lies buried in the bottom gravel with the ventral side turned upward and with the mouth opening free of the bottom. A feeding current enters at the anterior end of the animal between the buccal tentacles and flows through the buccal cavity. Then the water flows successively through the mouth, the branchial basket (pharynx) and mucus filter-net, to the atrium chamber, and finally out of the exhalant opening.

The water current is maintained through the animal by the activity of the lateral 'pump' cilia of the branchial bars. As particles pass along the pharynx they are drawn up against the internal wall of the branchial basket and the particles become caught in the mucus filter-net. The endostyle in the ventral part of the pharynx produces the mucus filter which is transported along the branchial bars by means of frontal cilia to the dorsal groove where the filters of two sides with the captured particles are rolled together and transported posteriorly to the oesophagus (Barrington, 1958; Olsson 1963; Welsch, 1975; Baskin and Detmers, 1976; Flood and Fiala-Médioni, 1981; Rähr, 1982).

Little work has been done to describe lancelets as filter feeders. Until recently no data existed on either filtration rates or the efficiency with which food particles

are retained in the mucus filters, but Riisgård and Svane (1999) further described and characterised *B. lanceolatum* as a true filter feeder. Simultaneous measurements of clearance of particles of different sizes showed that particles (at least) down to 4 μm are retained by the mucus filter nets with 100% efficiency (see also Ruppert et al., 2000).

2.6.5. Flow characteristics of mucus-net filter feeding

The lancelet *B. lanceolatum* is a cephalochordate and closely related to the urochordates (or tunicates), including the sessile ascidians, and the planktonic salps and the appendicularians (larvaceans), which all feed with a mucus net secreted by the endostyle (Alldredge and Madin, 1982; Holley, 1986; Madin, 1990; Nielsen, 1995). Table 1 shows a comparison between water flow velocity just upstream of the mucus net in various species of urochordates and the mucus-net filter-feeding polychaetes *N. diversicolor* and *C. variopedatus*, and the mucociliary filter-feeding gastropod *Crepidula fornicata*. As seen from Table 1, there is a tendency for ciliary pumps to occur at relatively low velocities and muscular type pumps at the higher velocities, but type also depends on the pressure drop. Apparently, operating conditions are adjusted to the characteristic of the pump (see Section 3.2). A mucus-net consumer may collect more food particles per unit area of net in a given time by increasing the velocity, but pressure drop increases linearly and pump-work quadratically with increasing pumping rate (Riisgård and Larsen, 1995; Acuña et al., 1996), so depending on predisposition for adaptation there is a natural limit to the increase.

2.6.6. Other taxonomic groups

Another, less studied mucus-net filter-feeder is the echiuroid worm *Urechis caupo* which inhabits a U-shaped burrow and feeds by filtering a current of water set up by peristaltic contractions of the body through a conical mucus net (Lawry, 1966; Chapman, 1968; Pritchard and White, 1981; Jørgensen et al., 1986b). Finally, it can be mentioned that the small polychaete *Pygospio elegans* can filter by building a mucus net within its tube (Hempel, 1957).

2.7. Ciliary upstream collection

In upstream-collecting animals ciliary bands divert the particles from the main water current and concentrate them on the upstream side of the band in a not fully understood way (Nielsen, 1987) (Fig. 1f). Ciliary upstream collecting has been described on the tentacles of adult phoronids, brachiopods, and pterobranchs, and in larvae of phoronids, brachiopods, echinoderms, and enteropneusts (Strathmann et al., 1972; Strathmann, 1973; Strathmann and Bonar, 1976; Strathmann and McEdward, 1986; Nielsen, 1987). In general, the mechanisms involved in separating food particles from the currents set up by the ciliary bands in upstream-collecting organisms are poorly understood. This mechanism is correlated with the presence of only a single band of cilia ('single-band system'), which appears to be responsible for both the water transport and particle retention as suggested by Strathmann et al. (1972).

Upstream-collecting ciliary bands in larvae of phoronids, echinoderms, pterobranchs, enteropneusts, and brachiopods, divert the particles from the main water current and concentrate them on the upstream side of the water pumping ciliary band before the particles are transported toward the mouth (Nielsen, 1987).

In brachiopods the lateral ciliary bands of the tentacles create a water current from which particles become deflected to the frontal side where the frontal cilia transport the particles towards the mouth. Jørgensen et al. (1984) measured the efficiency with which particles of various sizes are retained by the brachiopod *Terebratulina retuso*. It was found that the efficiency of retention increased with particle size in the 1–7 μm range studied, and that the largest 7 μm particles were removed with about 70% efficiency from the water during one passage of the lophophore.

Upstream collection has been studied in planktotrophic echinoderm larvae by Strathmann (1971), Strathmann et al. (1972) and Hart (1991), and in echinoid larvae by Hart and Strathmann (1994). The capture of particles on the upstream side of the ciliated band of the echinoderm larvae was observed to be accompanied by a change in the direction of particle movement toward the circumoral field. This was found to support the hypothesis that echinoderm larvae and other upstream collectors remove particles from suspension by a brief, localised reversal in the direction of beat of cilia on the ciliated band. However, this hypothesis for particle capture by ciliary reversal, suggested also to be in action in
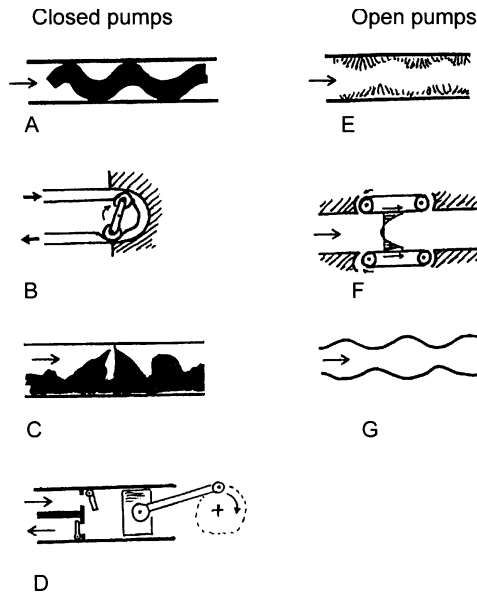
Closed pumps

Open pumps

Fig. 2. Biological pumps and analogous man-made pumps.

bryozoans (Strathmann, 1982; LaBarbera, 1984; Hart, 1996), has recently been rejected by Nielsen and Riisgård (1998), who reviewed the literature on upstream-collecting mechanisms and pointed out that further investigations are needed.

3. Part 2: Filter-pumps and bioenergetics

3.1. Continuous filter pumps and minimal scaling

Filter-feeding marine invertebrates must filter large volumes of water to meet their food requirements. The low concentrations of small suspended food particles in the sea is the key to understanding the characteristics of the filter feeding. Presumably these characteristics evolved according to 'a principle of minimal scaling', whereby dimensions of the filter-pumps are sufficient to enable continuous feeding at low rates, rather than discontinuous feeding at correspondingly high rates (Jørgensen, 1975). This hypothesis appears to exclude physiological regulation of the filtration rate in response to nutritional needs when the algal concentration is above a certain lower 'stimulation level' as in *M. edulis* (Riisgård and Randløv, 1981) and *Ciona intestinalis* (Petersen and Riisgård, 1992), or above the 'trigger level' in *N. diversicolor* (Vedel et

al., 1994). During recent years filter-feeding sponges, polychaetes, bivalves and ascidians have been characterised by analysis of the biological filter-pumps (Riisgård and Larsen, 1995). The studies have shown that low-energy pumps continuously process the surrounding water through filters appropriately dimensioned for coping with the phytoplankton concentrations of the environment. Thus, there is increasing evidence that filter feeding in marine environments is based on the principle of 'minimal scaling'. However, many energetic studies on e.g. filter-feeding mussels are based on the assumption that the filtration rate is physiologically regulated in response to variations in the concentration of phytoplankton (see Section 3.5).

To test the general validity of the above hypothesis for minimal scaling, the influence of algal concentration on feeding and growth in mussels and bryozoans has been studied by Clausen and Riisgård (1996) and Riisgård and Goldson (1997), respectively. It was found that in the presence of algal cells in the concentration interval between a lower 'trigger-level' and an upper 'satiation-level' filter-feeding mussels and ectoprocts are continuously utilising their clearance capacity. Observations of the feeding activity revealed that alterations in clearance rates as a response to either extremely low or very high algal concentrations are caused by valve closure in mussels and shutting down of the number of actively feeding zooids in bryozoans.

Near-bottom vertical profiles of phytoplankton caused by a dense population of *N. diversicolor* have been observed in the field by Riisgård et al. (1996e). Water samples were simultaneously collected at different heights above the bottom where *N. diversicolor* were present, and it appeared that a phytoplankton-reduced near-bottom water layer of 5–10 cm in thickness developed on calm days. That such depletion of phytoplankton in near-bottom waters plays a significant role for this worm was demonstrated in field-growth experiments performed with worms transferred to glass tubes placed at different height above the bottom (Riisgård et al., 1996e). An approximate 10 times reduction in growth rate of bottom-dwelling *N. diversicolor* compared with that of worms elevated just 10 cm above the sediment surface indicates that extremely meagre food conditions are prevalent near the
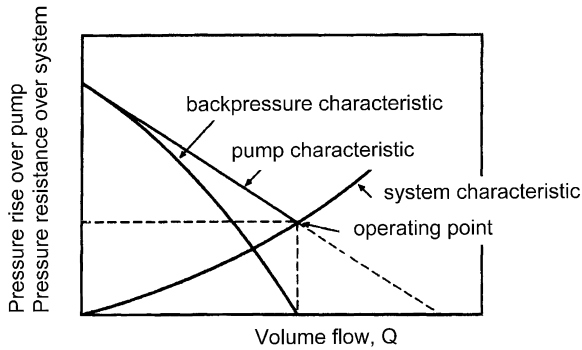
Fig. 3. Pump characteristics and definition of operating point. A pump produces an increasing volume flow when the pressure rise over the pump is being reduced (i.e. the pump characteristic is decreasing). The canal system connected to the pump offers an increasing resistance when the volume flow increases (i.e. the system characteristic is increasing). When plotted on the same graph, the point of intersection of these two characteristics — which simply states that the pressure rise delivered by the pump equals that required to maintain flow through the system — defines the operating point $(Q_o, \Delta H_o)$ of the pump–system arrangement in terms of the resulting operating flow (Q_o) and operating pressure head (ΔH_o) which can be read off the graph.

seafloor. Such situations deserve more attention in future studies on filter-feeding benthos.

3.2. Energetic cost of filter-feeding

A fluid pump delivers a volume flow (Q) and maintains a pressure rise (ΔH) from suction side to pressure side. If the pump is not tight this causes a backward leakage flow. Man-made pumps are usually based on machine constructions with rotary elements that via a crank can be transformed to swinging or backward and forward movements (e.g. displacement and friction pumps). Biological pumps use periodic waving, swinging or pulsating movements and use elastic tissues for sealing and valves.

Pumps may be divided up into closed pumps (ideally without internal leakage flow) and open pumps (always with leakage). Among the closed types of pumps is *N. diversicolor*'s undulating movements in its tube (Fig. 2a) which is analogous to a peristaltic tubing pump (Fig. 2b). *C. variopedatus* uses flexible and moving muscular piston-like parapods (Fig. 2c) which are analogous to a piston pump (Fig. 2d). Open types of pumps are found in ciliary suspension-feeders, e.g. bivalves, ascidians and
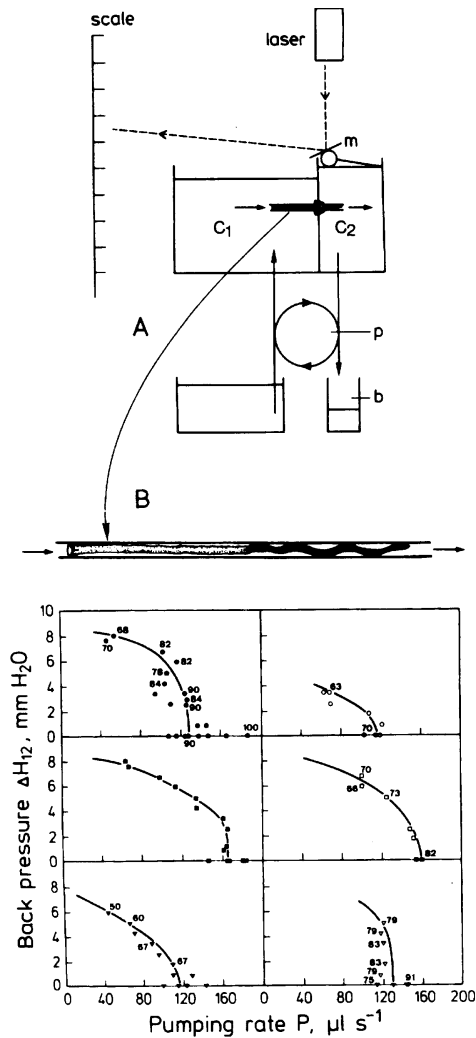

Fig. 4. Upper: direct measurement of pumping rates at different hydrostatic pressures imposed between inlet and outlet end of glass tube with *Nereis diversicolor* inserted in the wall separating the inhalant (C_1) and exhalant chamber (C_2). Water level in C_2 is monitored with a laser beam striking a mirror (m) fixed on a tethered floating ping-pong ball. Pumping rate of the worm is equal to volume of water collected in the beaker (b) when the laser deflection point is maintained in a constant position on the scale. Lower: back pressure-pumping rate characteristic in 6 worms. Frequency of water-pumping undulating body movements (strokes min^{-1}) is indicated.

bryozoans. These pumps consist of ciliary bands (Fig. 2e) and are analogous to belt pumps (Fig. 2f). In sponges the flagella are acting as a peristaltic pump (Fig. 2g).

For any filter-feeding organism it is possible to identify a pump and a system, consisting of canals, filters, siphons etc. Studied separately, the pump and the system can be described by the pump and system characteristics, respectively, which gives the pressure change (ΔH, mm H_2O) as a function of the volume flow (Q), see Fig. 3. A pump will deliver a decreasing flow when the pump is forced to supply an increasing pressure rise (or pump head, ΔH_p). Further, the frictional pressure drop and loss of kinetic energy (or total head loss of the system, ΔH_s), increases with increasing volume flow (see Fig. 3).

The total pressure drop in an animal's pump–system is the sum of frictional resistance, inclusive of pressure drop across the filter (ΔH_f), kinetic pressure loss (ΔH_k) due to creation of an exhalant jet to avoid recirculation of once filtered water at the narrowing outlet of the animal, and hydrostatic back pressure (ΔH_{12}) which under natural circumstances is zero, but may be imposed in an experimental set-up (see Fig. 4), that is:

$$\Delta H_s = \Delta H_f + \Delta H_k + \Delta H_{12}. \tag{1}$$

At the operating point (see Fig. 3) the flow adjusts itself so that the pump pressure (ΔH_p) exactly balances the total resistance of the pump system (ΔH_s), that is:

$$\Delta H_p = \Delta H_s. \tag{2}$$

Insertion of Eq. (1) in Eq. (2) gives:

$$\Delta H_p = \Delta H_{12} + \Delta H_f + \Delta H_k. \tag{3}$$

The pump characteristic cannot be measured directly in the suspension feeders; but the back pressure-pumping rate characteristic can be experimentally determined (Fig. 4) and, according to Eq. (3) used to lay down the pump characteristic when the system characteristic is known.

At the operating point, the useful power received by the water can be calculated as [pump pressure] × [volume flow]:

$$P = \rho g \Delta H_o Q_o, \tag{4}$$

where ρ is the water density and g the acceleration of gravity.

The system characteristic can be calculated by means of an assortment of standard fluid mechanical equations for pressure drop, caused by friction and kinetic energy loss, for water flowing through a pump system with known dimensions (for more thorough explanation and review, see Riisgård and Larsen 1995).

A few examples may illustrate the basic principles. For a flat screen consisting of parallel cylinders with a diameter of d and spacing b forming a filter the pressure drop (ΔH) may be estimated from the equation of Tamada and Fujikawa (1957), see also Riisgård and Larsen (1995, Eq. (16)):

$$\Delta H = K\nu u/gd, \tag{5}$$

where $K = 8\pi/(1 - 2 \ln \tau + \tau^2/6)$, $\tau = \pi(d/b)$, u the velocity of upstream flow, g the acceleration of gravity, and ν is the kinematic viscosity of seawater.

The main resistance to water flow in e.g. bryozoans is the filter consisting of stiff laterofrontal cilia (Fig. 1c). For an approximate estimate of pressure drop (resistance) across this filter, Eq. (5) is a usable model. Assuming $d = 0.2$ μm, $b = 3.5$ μm, and $u = 0.4$ mm s^{-1} the pressure drop across the filter is found to be $\Delta H = 0.065$ mm H_2O (Table 2). Similar equations to describe the pressure drop across for example a rectangular mucus-net has been given by Riisgård and Larsen, 1995, Eqs. (17) and (18) adapted from Silvester (1983) and Munson (1988), respectively.

Another important contribution to the total pump–system resistance may be the exhalant water jet leaving many suspension feeders through a constriction. The pressure drop due to this kinetic energy loss may be calculated as:

$$\Delta H = u^2/2g, \tag{6}$$

where u is the velocity of water leaving through the constriction (e.g. siphon opening) estimated as pumping rate/area of opening. By means of such standard fluid mechanical equations and engineering principles (see also, Vogel, 1994; Garby and Larsen, 1995) a number of suspension-feeding invertebrates have been analysed and characterised in order to determine the operating point and the power output of the pumps. The normal operating pressure head in these pumps has been found to be low, varying between 0.02 and 1.5 mm H_2O in different species, see Table 2.

To illustrate the principles of calculation of useful pumping power output, also shown in Table 2, the blue mussel *M. edulis* may serve as an example (Jørgensen et al., 1986a, 1988, 1990; Jørgensen

1990). Based on detailed information about structures, dimensions and water velocities, and using standard fluid mechanical equations the operating pressure has been estimated to be $\Delta H_o \approx 1$ mm H_2O, and the pumping rate for the 'standard' 35 mm shell length mussel has been measured in the laboratory to be $Q_o \approx 1$ cm^3 s^{-1}. According to Eq. (4) the power output can now be calculated to be: $P = \rho g \Delta H_o Q_o = 10^3 \times 9.81 \times 10^{-3} \times 10^{-6} = 10$ µW.

The energy cost of filter-feeding can be evaluated as the ratio of useful pumping power (P) and total metabolic power expenditure (R_t). This ratio, the overall pump efficiency, P/R_t, has been estimated for representatives of different taxonomic groups and show that the useful pump work constitutes from 0.3 to 4% of the total metabolic expenditure (see Table 2).

Referring to powers estimated for *M. edulis* by Riisgård and Larsen (1995) it may be argued that other measures of efficiency than the overall pump efficiency may be appropriate when characterising the energy cost of filter-feeding. Denoting by R_p the metabolic rate of the part of organism responsible for pumping action (i.e. bands of lateral cilia and the cells carrying the cilia), a minimum efficiency would be: $R_p/R_t = 59.5/900 = 6.6\%$, rather than $P/R_t = 10/900 = 1.1\%$, since mechanical and metabolic energy conversion as well as the metabolism of cells carrying cilia must be included. Moreover, if the ratio gill metabolic rate $R_g/R_t = 175/900 = 19\%$ is used as a measure for energy cost it is seen that the energetic costs of filter feeding by means of large specialised gills are considerable. Obviously, the gill structures are expensive to maintain irrespective of whether the mussel is pumping water or not. This supports the hypothesis of 'minimal scaling' which implies that energy for functions other than pump work can only be justified when the part of the organism responsible for the pumping action is dimensioned for continuous feeding.

From an examination of the literature dealing with possible switching between deposit feeding and suspension feeding in marine invertebrates, Riisgård and Kamermans (2000) found that it was striking that, apart from the occasionally (facultative) suspension feeder *N. diversicolor*, all examples of switching are found among passive suspension feeders that have no pump but passively strain food particles from the near-bottom current without metabolic energetic costs. This attracts the attention to possible prerequisites and limitation to active suspension feeding. From the above considerations and the energetic costs of bivalve suspension feeding by means of large specialised gills it may be realised that the adaptation of *N. diversicolor* to be a facultative suspension feeder is exceptionally cheap in terms of no conspicuous anatomic alterations and accompanying metabolic investments. This has enabled *N. diversicolor* to be flexible so that it only switches from deposit surface feeding to suspension feeding when the ambient phytoplankton concentration is sufficiently high to be profitable.

3.3. Adaptation to environment

To assess the adaptation of a filter-feeding animal to a certain environment it is of interest to know the minimum food energy uptake (ingestion) of the animal needed to cover its maintenance metabolic energy requirement. The maintenance metabolic need may conveniently be expressed as the respiration (R_m) measured as the amount of oxygen consumed by the starving animal. The ingestion may be expressed as the maximum volume of water that the animal can pump through the filter device (F_{max}) times the food particle concentration, and will thus depend on phytoplankton concentration in the environment as well as the particle retention efficiency of the animal's filter. The ratio F_{max}/R_m expresses the dm^3 of water pumped per cubiccentimeter O_2 consumed and may be used as a tool to characterise filter feeding. A typical F_{max}/R_m-value of 10 dm^3 of water pumped per cubiccentimeter of oxygen consumed was stated by Jørgensen (1975) as a minimum to ensure the performance of filter feeders inhabiting inshore waters. This may also be illustrated by the following example. To balance a metabolic energy requirement equivalent to the consumption of 1 cm^3 O_2 (equivalent to 20 J), assuming 100% particle retention efficiency and 80% assimilation efficiency of ingested food, a benthic filter feeder exposed to a realistic near-bottom phytoplankton concentration of 1.5 chl-a dm^{-3} (equivalent to 2.5 J dm^{-3}) must pump $20/(2.5 \times 0.8) = 10$ dm^3 of water.

From the above F_{max}/R_m reference value of 10 dm^3 cm^{-3} O_2, and with a thorough knowledge of particle retention efficiency, it is now possible to evaluate the degree of adaptation of filter feeders to

different environments with different typical phytoplankton levels. As a rule of thumb, without taking retention efficiency into consideration, if: $F_{max}/R_m < 10$ dm^3 cm^{-3} O_2 this suggest that the animal is not a filter feeder grazing on phytoplankton, $F_{max}/R_m \geq 10$ dm^3 cm^{-3} O_2 indicates a true filter feeder, $F_{max}/R_m \gg 10$ dm^3 cm^{-3} O_2 indicates a filter feeder that has adapted to very low phytoplankon levels. Table 3 shows the ratio of independent laboratory measurements of filtration rate (F_{max}) and respiration rate (R_m) in a number of filter-feeding invertebrates. It is notable that sponges with their extremely efficient collar filters that capture free-living bacteria and other small particles down to about 0.1 μm have the lowest F_{max}/R_m-values, whereas the much less efficient polychaete *Sabella penicillus* has a remarkably high F_{max}/R_m-value suggesting an adaptation to very low phytoplankton concentrations.

Unfortunately, relevant field measurements of phytoplankton concentrations in the inhalant water, or very near benthic filter feeders, are still missing though of great importance for understanding the adaptation of animals to their environment. But both the pump-characteristics and the F_{max}/R_m-value of an animal may be used to settle uncertainty about a possible filter-feeding mode of life, as appears from the low value shown by the deposit-feeding bivalve *Macoma balthica*, and by the example given below.

It has been proposed by Krüger (1959, 1962, 1964, 1971) that the lugworm *Arenicola marina* can make a living as a filter feeder, using the sand immediately in front of the head as a filter to retain suspended food particles in the ventilatory water. This assumption has been investigated by Riisgård et al. (1996a) and Riisgård and Banta (1998). The maximal pressure head that can be delivered by the *A. marina* pump is 200 mm H_2O (Riisgård et al., 1996a). This is 30–150 times higher than found in true filter feeders (Riisgård and Larsen, 1995) which are also characterised by pumping more than 10 dm^3 of water per cubiccentimeter of oxygen consumed (cf. Table 3). Thus, the three filter-feeding polychaetes *Sabella penicillus*, *C. variopedatus* and *N. diversicolor* pump 354, 50 and 40 dm^3 of water per cubiccentimeter of oxygen consumed, respectively. These values may be compared with 0.4 dm^3 cm^{-3} O_2 in *A. marina*. This very low value excludes the lugworm from making a living as a true filter feeder, although it is possible that some fraction of its nutrition may

come from suspended material drawn down into the sediment during irrigation. Especially resuspended material from the sediment surface may represent a potential food source (Riisgård and Banta, 1998).

3.4. Respiration and energetic cost of growth

Respiration rate (R) as a function of body weight (W) is usually expressed as $R = aW^b$. West et al. (1997) have recently proposed a '3/4 power law' for the allometric scaling for respiration rates, i.e. the exponent $b = 3/4$. Empirically, the b-value is often close to 3/4 (Wieser, 1994; Garby and Larsen, 1995), but a b-exponent of 3/4 is not always the case, particularly not during stages of significant growth as pointed out by Riisgård (1998b). Thus, respiration rate as a function of size throughout the ontogeny of *M. edulis*, from early larval to the adult stage, during which the mussel increases its weight by a factor of 10^8, has revealed that the b-exponent is about 0.9 throughout the early pelagic larval stage (Riisgård et al., 1981) as well as during the juvenile stage up to a size of 1–10 mg tissue dry weight (Riisgård et al., 1980; Hamburger et al., 1983), above which the b-value decreases to about 0.7 in the adult stage (Hamburger et al., 1983). The reason for such a change in the b-exponent was not immediately obvious, but research on the energetic cost of growth in various marine invertebrates has demonstrated that, as growth decreases with age, the respiration decreases because respiration and growth are connected through the energetic costs of growth.

M. edulis may serve as an example of how growth influences respiration (Clausen and Riisgård, 1996). The specific growth rate (μ, d^{-1}) of *M. edulis*, fed algal cells at different maintained concentrations, was calculated according to the equation: $\mu = \ln(W_t/W_0)t^{-1}$ where W_0 and $W_t = mean$ body mass of the mussels on Day 0 and Day t, respectively. By simultaneous measurements of respiration and growth in mussels with body mass W the relationship between total respiration rate (R_t) measured on Day t and growth rate (μW) was described as: $R_t = R_m + n\mu W$ or $R_t/W^b = a + n\mu W^{1-b}$, where $R_m = aW^b$ is the maintenance (starvation) respiration rate, and n is the energy cost per unit of growth. In the mentioned work the energy cost of growth was estimated by using $b = 0.66$ (Hamburger et al., 1983) and
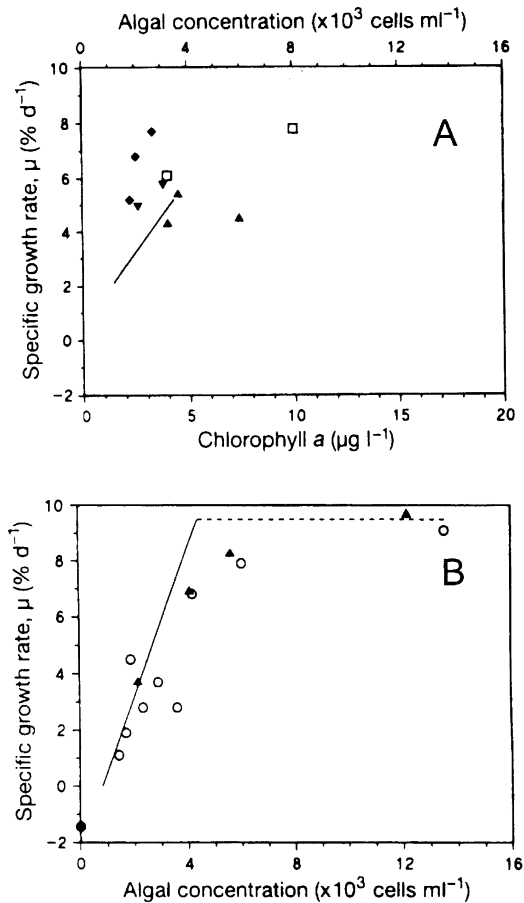
Fig. 5. *M. edulis.* (A) Specific growth rate (μ) in field experiments as a function of food concentration expressed as μg chl-a dm^{-3} (lower axis) and algal equivalents (*Rhodomonas* sp.) concentration (upper axis). Open symbols: maximum growth rates found for net-bag-transplanted mussels in the Limfjord (Denmark) by Riisgård and Poulsen (1981); closed symbols and regression line ($n = 35$, $r^2 = 0.55$): growth data obtained for net-bag-transplanted mussels in Kerteminde Fjord/Kertinge Nor (Denmark) by Clausen and Riisgård (1996), and by Riisgård et al. (1994), respectively. (B) Specific growth rate as a function of algal concentration in laboratory growth experiments without silt (open symbol) and with 5 mg dm^{-3} silt (closed symbol). The actual specific growth rates may be compared with the estimated growth rates shown by the inserted unbroken line based on the growth model expressed by Eq. (7) assuming 80% assimilation efficiency and exploitation of the filtration capacity. It is seen that only at algal concentrations above roughly 5 μg chl-a dm^{-3}, where the growth potential of 9.5% d^{-1} is utilised, the growth model may need to accept reduced filtration rates to fit the experimental growth data. Figs. from Clausen and Riisgård (1996).

experimentally determined values of R_t and μ which enabled the identification of n (i.e. slope of regression line for R_t/W^b as a function of μW^{1-b}). Thus, it was experimentally found that the energy cost of growth (n) was equivalent to 12% of the actual growth. This value may be compared with those found in a similar way for other marine invertebrates: 20–26% of the growth in the polychaetes *N. diversicolor* and *N. virens* (Nielsen et al., 1995), 21–23% in the ascidian *Ciona intestinalis* (Petersen et al., 1995), 19% in the copepod *Acartia tonsa* (Kiørboe et al., 1985), and 139% of the biomass production in the sponge *H. panicea* (Thomassen and Riisgård, 1995). However, dependent on feeding conditions and thus growth rate, the respiration rate of the individual organism may vary considerably (Nielsen et al., 1995). This explains why the *b*-exponents may assume many different values which may sometimes be larger than 3/4: e.g. $b = 1.2$ in *N. diversicolor* (Nielsen et al., 1995), $b = 0.93$ in *H. panicea* (Thomassen and Riisgård, 1995), and $b = 0.86$ in jellyfish *Aurelia aurita* (Frandsen and Riisgård, 1997). From the above examples it is clear that the '3/4 power scaling law' suggested by West et al. (1997) is not a biological law because respiration cannot be separated from growth (Riisgård, 1998b). The relation between water pumping and respiration in filter feeders has been reviewed by Jørgensen et al. (1986b) and Jørgensen (1990).

3.5. Mytilus edulis — a case model of general validity?

A comprehensive literature deals with bivalves, especially the blue mussel *M. edulis.* The following section may serve as a short introduction to relevant bioenergetic considerations and further reflects on possible physiological regulation of filtration rates in zoobenthic filter feeders.

The energy balance of a filter feeder can be expressed as: $I = G + R_t + E$, where $I =$ ingestion; $G =$ growth (production), R_t is the total respiration (sum of maintenance respiration, R_m, and respiratory cost of growth, R_g), and E is excretion. The growth may also be expressed as $G = I \times AE - (R_m + R_g)$ or $G = (F \times C \times AE) - (R_m + R_g)$, where $AE = (IBE)/I$ is the assimilation efficiency, F the filtration rate, and C is the algal concentration.

The growth of *M. edulis* was estimated according to

the latter equation by Clausen and Riisgård (1996). The maximum specific growth rate of a 100 mg dry weight (W_t) 'standard' mussel was approximately $\mu_{max} = 9.5\%\ d^{-1}$ corresponding to a maximum growth rate $G_{max} = W_t\mu_{max} = 2255\ \mu W$. The maintenance metabolism (R_m) was estimated at $0.1\ cm^3$ $O_2\ h^{-1} = 570\ \mu W$, and the maximum filtration rate measured to $F_{max} = 1.8\ dm^3\ h^{-1}$. The energetic cost of growth was found to be 12% of the growth (see Section 3.4), i.e. $R_g = 0.12G$. Thus, the growth rate may be expressed as: $G = A - R_m - 0.12G$ or $G = (A - R_m)/1.12$. Assuming $AE = 80\%$ (Kiørboe et al., 1981; Riisgård and Randløv, 1981; Poulsen et al., 1982), the estimated actual growth rate as a function of algal concentration (C) may now be expressed by the equation (Clausen and Riisgård (1996):

$$G = [(F_{max} \times AE \times C) - R_m]/1.12 \qquad (7)$$

or $G = bC - a$. The concentration of algal cells (*Rhodomonas*) needed to cover the energy cost of maintenance ($G = 0$) was found to be: $C = a/b = 810\ cells\ cm^{-3} = 1.0\ \mu g\ chl\text{-}a\ dm^{-3}$, and the concentration of algal cells necessary for maximum growth was: $C = (G_{max} + a)/b = 4420\ cells\ cm^{-3} = 5.5\ \mu g\ chl\text{-}a\ dm^{-3}$. On the assumption that the maximum filtration rate (F_{max}) is continuously being exploited, lower and upper chlorophyll a concentrations define the interval within which there is a direct correlation between phytoplankton concentration and growth.

Fig. 5 shows the actual specific growth rate (μ) of *M. edulis* in both field and laboratory experiments as a function of food concentration. The actual specific growth rates may be compared with the estimated growth rates represented by the inserted line in Fig. 5b based on the above growth model expressed by Eq. (7). It is seen that the estimated growth describes the actual growth fairly well up to about $5\ \mu g\ chl\text{-}a\ dm^{-3}$ (both with and without silt). But at algal concentrations above roughly $5\ \mu g\ chl\text{-}a\ dm^{-3}$, where the growth potential of $9.5\%\ d^{-1}$ is utilised, the estimated growth needs to be based on reduced filtration rates (i.e. lower than the maximum filtration rate) and/or assimilation efficiencies $<80\%$. In nature, however, the growth potential seems generally not to be exploited and for that reason it can be argued that in most waters there may not be a conspicuous need for physiological regulation of the filtration rate.

Likewise, it may be argued that the prevailing algal concentration in the actual, inhalant water of mussels may often be $<5\ \mu g\ chl\text{-}a\ dm^{-3}$. On this background it is relevant to make a note of measured phytoplankton concentrations in the sea.

The median concentration between March and December varies between 1.7 and $7.7\ \mu g\ chl\text{-}a\ dm^{-3}$ in the open coastal areas around Funen (Denmark), and a median value of $5.1\ \mu g\ chl\text{-}a\ dm^{-3}$ based on about 1400 data series collected in the period 1985–1991 has been found for Danish fjords and coastal waters (Sand-Jensen et al., 1994). In the South San Francisco bay the phytoplankton levels remain at 2–$5\ \mu g\ chl\text{-}a\ dm^{-3}$ year around except for a few days during early spring (Officer et al., 1982). In the Menai Strait (Wales, UK) Blight et al. (1995) found that the chl-a concentration in 1993 remained low during the summer, near $1\ \mu g\ dm^{-3}$. In the lower intertidal zone in Port Erin Bay (Isle of Man, northern Irish Sea) Sanderson et al. (1996) found that the chl-a concentration varied over the course of the tidal cycle from about $16\ \mu g\ chl\text{-}a\ dm^{-3}$ at low tide to approximately $3\ \mu g\ chl\text{-}a\ dm^{-3}$ at high tide (mean $8 \pm 5\ \mu g\ chl\text{-}a\ dm^{-3}$). In the Marsdiep tidal inlet (Dutch Wadden Sea) the annual average is about $8\ \mu g\ chl\text{-}a\ dm^{-3}$, while the monthly averages vary from $1\ \mu g\ chl\text{-}a$ in winter to $30\ \mu g\ chl\text{-}a$ during the spring peak period (Cadée and Hegeman, 1993; see also Beukema and Cadée, 1997). Meeuwig et al. (1998) recorded a mean chl-a concentration of $2.4\ \mu g\ chl\text{-}a\ dm^{-3}$ in fifteen Canadian estuaries. Dame and Prins (1998) compared 11 coastal ecosystems where the chl-a concentration ranged from 3 to $22\ \mu g\ chl\text{-}a\ dm^{-3}$ with a mean concentration of $7.7\ \mu g\ chl\text{-}a\ dm^{-3}$. From this it is obvious that the phytoplankton biomass varies considerably between different localities and no unequivocal statement about adaptation of the mussel filter-pump to the environment can be made without reservations. But it seems likely that in many marine areas the *M. edulis* filter pump may be operating more or less continuously at the prevailing natural algal concentrations, which may be especially low in the near-bottom water over mussel beds (Wildish and Kristmanson, 1984; Fréchette and Bourget, 1985a;b; Loo and Rosenberg, 1989; Jørgensen, 1990; Butman et al., 1994; Petersen et al., 1997; Dolmer, 2000a,b).

The amount of available food for mussels may also

be dependent on vertical wind mixing of the water column. Thus, Møhlenberg (1995) measured that the phytoplankton biomass in the water column decreased during windy periods because the benthic mussels were brought into contact with the entire phytoplankton biomass during such events (see also Small and Haas, 1997). In other situations benthic filtration may deplete the near-bed water layers and cause a vertical gradient in the phytoplankton biomass (Dolmer, 2000a). The available phytoplankton for the mussels is then likely to drop to $<5\ \mu g$ chl-a dm^{-3} where physiological regulation of the filtration rate seems to be irrelevant. Therefore, a physiological regulation mechanism for filter-feeding mussels may be an appropriate requisite in only few situations (see also Dolmer, 2000b).

It is well known that very low algal concentrations may cause reduction of water pumping due to closure of the valves, and likewise, high algal concentrations may cause closure of the valves (Riisgård and Randløv, 1981; Riisgård, 1991b; Clausen and Riisgård, 1996). In a recent study by Dolmer (2000b) the feeding activity of *M. edulis* in Limfjorden (Denmark) was related to near-bottom current velocities and phytoplankton biomass in the near-bottom water. The content of chl-a in the mussels and shell gap size were used as indices of filtration activity. At low current velocities (about $1-2\ cm\ s^{-1}$) the near-bed algal biomass was low; 40–70% of the mussels had closed shells and they accumulated only a small amount of chl-a in the body. But on days with higher near-bottom current velocities ($4-7\ cm\ s^{-1}$) only 17–25% of the mussels had closed valves, and the mussels accumulated a larger amount of chl-a. This confirms that mussels in nature react by closing the valves if phytoplankton concentrations are below a certain lower threshold. The valve closing phenomenon seems to represent a real physiological adaptation to suspension feeding in extremely meagre situations: by reducing the water transport through the mantle cavity the bivalve reduces the oxygen uptake which leads to reduced metabolism (Jørgensen et al., 1986b). So far, no studies have attempted to quantify how much time bivalves in nature experience algal concentrations below the threshold level (presumably $<1\ \mu g$ chl-a dm^{-3} to judge from the above estimation of minimal algal concentration needed to cover the maintenance metabolism; see

also Dolmer (2000b), who suggests the threshold concentration is about 0.4–0.5 μg chl-a dm^{-3}).

In long-term laboratory feeding and growth experiments Clausen and Riisgård (1996) observed that high algal concentrations, equivalent to about 17–31 μg chl-a dm^{-3}, caused closure of the valves and for that reason reduced filtration rate (see also Riisgård, 1991b). The valve closure phenomenon may be a response to overloading and interpreted as a protective mechanism with the same strength of argumentation as used for assuming physiological regulation of the bivalve filter-pump to nutritional needs (Winter, 1973; Widdows, 1976; Navarro and Winter, 1982; Bayne et al., 1976a,b, 1977, 1987, 1988, 1989, 1993; Widdows and Johnson, 1988; Hawkins and Bayne, 1992; Willows 1992; Stenton-Dozey and Brown, 1992; Navarro et al., 1994; Kreeger et al., 1995; Sprung 1995; Cranford and Hill, 1999). Riisgård and Randløv (1981) and Riisgård (1991b) pointed out that low growth rates obtained on bivalves in laboratory studies, as compared to maximal growth rates in nature (see Jørgensen, 1990, Table 8) may be due to the use of very high algal concentrations (Winter, 1973, 1976; Winter and Langton, 1976; Tenore et al., 1973) which lead to overloading of the feeding system, reduced filtration rate, and eventually reduced growth. The view of physiological control or regulation of filtration rate has in particular been contradicted by Jørgensen (1990, 1996), who advocates that, when phytoplankton is available, as a rule filter-feeding bivalves always utilise their filtration capacity for food uptake.

Meticulous laboratory measurements are a necessity for dealing with the physiology and bioenergetics of suspension feeding bivalves. Here the filtration rate is an important bioenergetic parameter and different techniques may be employed for obtaining filtration rates (see review by Riisgård, 2001).

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