

Table 4.1. Stages in the physiology of feeding, assimilation, growth, and elimination in suspension feeding benthic animals.

Stage	Stage number	Description
Feeding	1	- Transport of seawater past the filtration surface
	2	- Capture of seston at the filtration surface
	3	- Transport of particles to the mouth involving sorting and rejection, e.g. as pseudofaeces in bivalves
	4	- Ingestion
Assimilation	5	- Transport through the gut
	6	- Uptake across specific gut surfaces
Growth	7	- Anabolic metabolism
	8	- Catabolic metabolism
Elimination	9	- Waste solids voided as true faeces
	10	- Metabolic wastes voided as urine

In this chapter, our concern is primarily with the first filtration stage of feeding as defined later. In the next chapter, we deal with the second stage of suspension feeding, which involves the mechanisms of particle capture on the appropriate surface. Because these two stages of feeding are the only ones directly affected by flow, they are the only ones considered in physiological detail in this book.

### Background

In suspension-feeding animals, feeding and growth involves a series of coordinated steps. Each of these steps is dependent on the preceding one (Table 4.1). We will refer to suspension feeding as inclusive of the first four steps shown and reserve the term *filtration* for the first two only. Filtration or clearance rates (see Chap. 2, the section, Initial feeding responses) need not, therefore, equal feeding rates if particle sorting leads to rejection as pseudofaeces. Growth encompasses the remaining catabolic and anabolic steps. Growth rates need not be directly related to the feeding rate because of differential digestion of sestonic particles. For example, in the giant scallop, some microalgae pass through the gut undigested (Shumway et al. 1985b). Residence times of food in the gut may be increased or decreased (Bricejij, Bass, and Lopez 1984) and thus change the contact time between ingested food, and digestive and absorptive surfaces. Thus, filtration rate is not necessarily equal to feeding rate and feeding rate need not always be directly proportional to the growth rate.

Two major categories of suspension feeding benthic animals can be recognized by the extent to which the filtration process is dependent on external flow (Vogel 1981; LaBarbera 1984):

- *Passive suspension feeders*—the individual is solely dependent on the external ambient flow to bring seston close enough to the filtration surface for its capture
- *Active suspension feeders*—the individual must supply its own energy in the form of ciliary or muscular pump power to transport seawater with its load of seston across the filtration surface where particle capture is effected

In addition, there are *facultative active suspension feeders*, where individuals are able to switch from passive to active feeding and back again, depending on the ambient flow conditions. These individuals behave as passive suspension feeders at high velocities and as active suspension feeders at low velocities. In another category, the *combined passive-active suspension feeders*, the individual has two parallel mechanisms, one passive and one active, for creating a flow through the body for feeding purposes. The latter group differs from the facultative active suspension feeder in that there is no switching at critical velocities and both active and passive filtration may occur simultaneously. The passive mechanism involves ambient velocity induced flow, and the active mechanism involves a ciliary or flagellar pump. This is a new category, not explicitly considered by Vogel and LaBarbera, and tentatively includes some ascidians, sponges, and, possibly, brachiopods. Finally, there are the *deposit-suspension feeders*, individuals that ingest already deposited sedimentary particles at low velocities, but switch to suspension

feeding at a higher threshold velocity. Examples include spionid polychaetes and some infaunal bivalve molluscs.

We view these generalizations as helpful in analyzing the wide diversity of methods of suspension feeding to be found among benthic animals. As further detailed knowledge of suspension-feeding mechanisms accumulates from a wider range of benthic animals, we can expect further modification of the categories presented. We feel that creating too many categories is counter-productive because, eventually, the process will be competing with taxonomy. It is not the artificial categories that developed new suspension-feeding mechanisms, but populations from individual species (Chap. 9).

Expected filtration responses of suspension feeders to increases in unidirectional flows are shown in Fig. 4.1. In this representation, it is assumed that the suspension feeder is optimally positioned with respect to flow direction. The filtration responses appear to be some form of unimodal function of velocity. In earlier studies this response was described as a "reverse ramp" for part of b and c (Wildish and Saulnier 1993). Since this engineering term is unfamiliar to biologists, we have replaced it with the more general term *continuous unimodal function*. Its use does not imply a precise mathematical relationship between filtration and velocity. For filtration responses and velocity, parabolic, orthogonal, sharp peaked, or ramp functions may be obtained, depending on the species and environmental conditions considered. Given constant seston concentrations, increments in velocity enhance filtration (Fig. 4.1a) at very low velocities up to a maximum (Fig. 4.1b) beyond which velocity increase has no further effect on filtration because other processes (e.g. stage 3 or 4; see Table 4.1) limit it. An example of suspension feeding in Protozoa is given by Fenchel (1980); in it particle transport after capture and the rate of ingestion may be the rate-limiting factors. Bivalves have a pseudofaecal rejection mechanism that avoids overloading ingestion (stage 4) and assimilation (stages 5 and 6). At higher velocities (Fig. 4.1c), flow conditions begin to have a negative effect on the filtration process and finally filtration (Fig. 4.1d) is completely suppressed, e.g. by mantle edge closure or withdrawal of siphons in infaunal bivalve molluscs. The precise mechanisms by which the filtration responses are governed depend on the species of suspension feeder, as will be discussed in some examples in later sections of this chapter. Thus, in active suspension feeders such as siphonate bivalves, in which the inhalant is normal to the flow, flow-induced inhibition may be absent, while in non-siphonate bivalves, ambient flow inhibits seston capture (Fig. 4.1). In

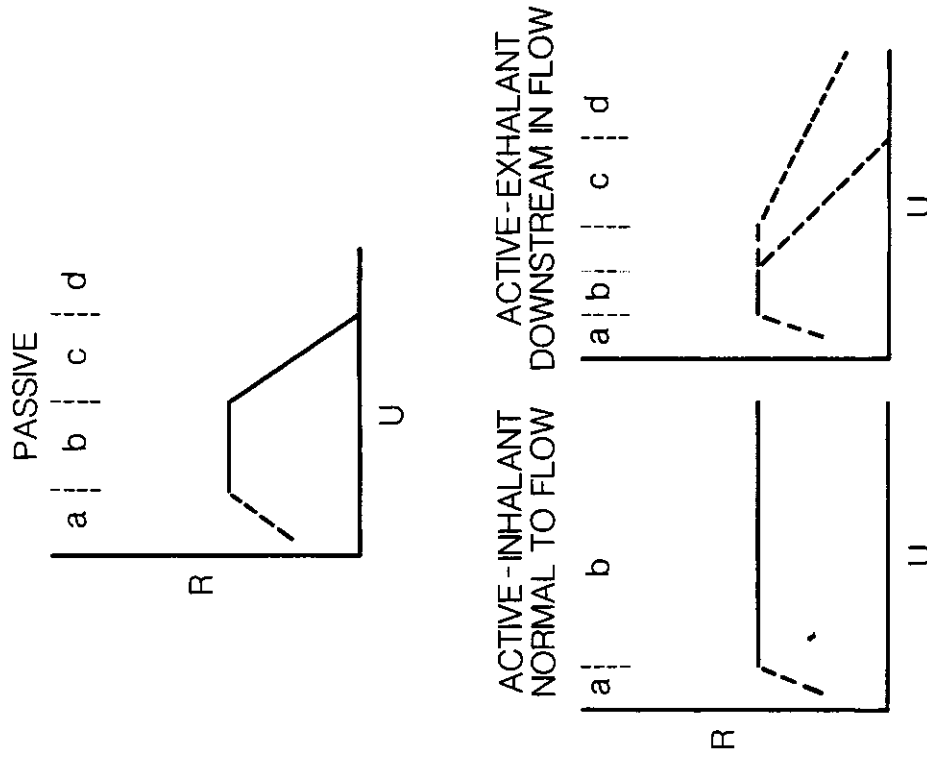


Figure 4.1 Effects of velocity,  $U$ , on filtration rate,  $R$ : a, increasing velocity enhances filtration; b, optimum filtration rates; c, velocity inhibition of filtration; d, filtration suppressed by velocity.

general, in stage a, filtration is limited by seston supply as a result of seston dilution and limited transport; in b, filtration is not limited by seston dilution and transport; and in c, filtration is inhibited by excessive ambient flow forces that interfere with seston capture processes.

Seston concentration and quality may also have an influence on the filtration rate, which may be either independent of or interactively linked to velocity; this is the case, for example, for bivalve molluscs (Wildish, Kristmanson, and Saulnier 1992). These responses permit active suspen-

Table 4.2. Representative list of macrobenthic passive suspension feeders.

Common name	Scientific name	Major taxa	Reference
Sea pen	<i>Ptilosarcus gurneyi</i>	Cnidaria: Pennatulacea	Best (1988)
Hydroid	<i>Plumilaria setacea</i>	Cnidaria: Hydrozoa	Warner (1977)
Sea whip	<i>Leptogorgia virgulata</i>	Cnidaria: Anthozoa	Leversee (1976)
Black coral	<i>Cirripathes lutekeni</i>	Cnidaria: Antipatharia	Warner (1977)
Feather star	<i>Oligometra serripinnia</i>	Echinodermata: Crinoidea	Leonard et al. (1988)
Brittle star	<i>Ophiothrix fragilis</i>	Echinodermata: Ophiuroidea	Warner and Woodley (1975)
Sea cucumber	<i>Cucumaria curata</i>	Echinodermata: Holothuroidea	Jørgensen (1966)

sion feeders rapidly to increase both the time spent filtering and the volumetric throughput for filtration to take advantage of temporally discrete pulses of good quality sestonic food.

For active suspension feeders, the filtration response also depends critically on whether the exhalant siphon flow follows or is opposed to the principal direction of ambient flow. Where the exhalant flow opposes the ambient flow, the adverse pressure field causes a reduction in filtered flow, as extraciliary pump work cannot be done to overcome the applied external flow force.

#### Passive suspension feeders

Passive suspension feeders are found in many of the phyla which have benthic representatives. Table 4.2 gives an idea of the diversity of the taxonomic forms represented. A detailed hydrodynamic study of filtration responses to velocity and the mechanism of seston capture is available for only a few passive suspension feeders.

#### Cnidarians

The sea pen *Ptilosarcus gurneyi* is a common cnidarian of soft, sandy-mud sediments in Puget Sound and the San Juan Archipelago of the U.S. West Coast (Best 1988). Its body consists of a central supporting pedun-

cle inserted in the sediment, a joint, and a rachis. The sea pen is oriented so that its flat surface faces the major prevailing flow. A parallel series of semi-circular leaves carries the filtering elements. These filtering elements are polyps with radiating tentacles bearing pinnules which are located on the downstream part of each leaf. The rachis is flexible and bends downstream as ambient velocities increase.

Volume flow rates through *P. gurneyi* have been determined by estimating the rate of dye movement to determine velocity and a measure of the rachis area from the dye-stained part of the sea pen (Best 1988). Volumetric flow rates were related to the square of the height since the filter area increased linearly with size. The maximum volumetric flow through the rachis occurred at an ambient velocity which was a function of sea pen size: thus  $6.5\text{--}8.5\text{ cm}\cdot\text{s}^{-1}$  for small,  $12\text{--}14\text{ cm}\cdot\text{s}^{-1}$  for medium, and  $14\text{--}18\text{ cm}\cdot\text{s}^{-1}$  for large sea pens.

Velocity measurements between the leaves and near the polyps made with a thermistor flow probe showed that near the polyps velocities were much reduced at the highest free-stream flows tested ( $25\text{ cm}\cdot\text{s}^{-1}$ ) as a result of drag near the filtration surfaces.

Filtration efficiency (RE; see Chap. 2) was examined in flume experiments by taking seawater samples upstream and downstream of the sea pen (with a suction sampler so that sampling was possibly not isokinetic). The sample was examined in a particle counter and the efficiency of capture of each particle size determined. Smaller sea pens were significantly less efficient than medium or large individuals. Free stream velocities ranging from  $1.5$  to  $6.0\text{ cm}\cdot\text{s}^{-1}$  significantly reduced RE.

Filtration and seston uptake rates, determined from independent estimates of volume flow rate and filtering efficiency as outlined, were equal in *P. gurneyi* and unimodal functions of velocity (Fig. 4.2). For the sea pen, increasing velocity in low flow conditions enhances the filtration seston uptake rate because of the increase in volumetric flow through the filter. The plateau reached around  $7\text{ cm}\cdot\text{s}^{-1}$  (Fig. 4.2) occurs as ambient velocity just begins to deform the sea pen. This process eventually causes both volume flows and filtering efficiency to decline in the c stage because pinnules and tentacles are swept back as the flow increases and, consequently, less filtering surface is presented to the flow. For small sea pens, the c stage begins at  $13\text{--}16\text{ cm}\cdot\text{s}^{-1}$  and, in medium and larger ones, at  $18\text{--}21\text{ cm}\cdot\text{s}^{-1}$ . Filtration/seston uptake rate inhibition in *P. gurneyi* can be seen to begin in Fig. 4.2 but, because the highest velocities tested were only  $25\text{ cm}\cdot\text{s}^{-1}$ , the full unimodal function responses were not obtained.

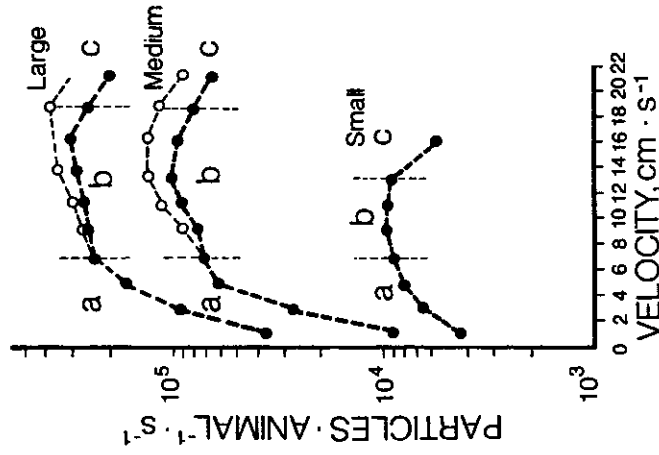


Figure 4.2 Seston uptake rate in *Ptilosarcus gurneyi* as a function of ambient velocity: open circles, retention efficiency at 30%; closed circles, at 20%. The unimodal response limits are suggested (modified from Best 1988).

No test was made of the effect of seston concentration on capture rates during this study (Best 1988).

The gorgonian corals exhibit whole colony flexibility where water movement forces reach moderate to high levels. Two species, *Pseudopterogorgia acerosa* and *P. americana*, found off Jamaica, were studied by Sponaugle and LaBarbera (1991). Coral feeding was studied in a recirculating flume in unidirectional flows measured within 2 mm of the polyp using a thermistor flow probe with a sensing head of 0.5 mm. *Artemia* nauplii were used as food at concentrations of 2.5–4 nauplii · L<sup>-1</sup>. Captured rhodamine-stained nauplii were easily observed in the individual polyp gastrovascular cavity. Results showed that the capture rate of *Artemia* was a unimodal function of velocity with a peak at intermediate velocities (~15 cm · s<sup>-1</sup>).

Model studies of the individual polyp of the tropical gorgonian *Pseudopterogorgia acerosa* were made by Sponaugle (1991). She noticed that, in addition to colony flexion, which keeps flow velocities near the

polyps low, individual polyps are deformed by increased velocities. Two effects were noticed: the first that polyp flexion helped maintain reduced and constant velocities near the polyp with the effect most marked at intermediate flows; the second that flow patterns downstream of the polyp at intermediate ambient flows suggested an upward circulation, similar to that in tube-living suspension feeders discussed in Chapter 6 (see the section, Tube-living epifauna) which enhanced particle capture. Both mechanisms contribute to the unimodal feeding response of this gorgonian to flow described by Sponaugle and LaBarbera (1991).

Studies of particle capture by individual polyps of the octocoral *Alcyonium siderium* collected from either the Massachusetts or the California coast were made in a cooled, recirculating flume at three flows: 2.7, 12.2, or 19.8 cm · s<sup>-1</sup> (Patterson 1991). These flows were measured with a thermistor flowmeter probe positioned 1 cm above the coral polyp. It was shown at the lowest flow tested that *Artemia* cysts were captured on the upstream tentacles of the *Alcyonium* polyp, but that at flows of 12.2 cm · s<sup>-1</sup> or greater, capture was transferred to the downstream tentacles. At the highest flow tested, the number of cysts captured per polyp per unit time was significantly less than at the lower flows. These observations are consistent with the unimodal feeding response of other suspension feeders to flow, although there are insufficient data for *A. siderium* to determine the precise velocity limits. At the 19.8 cm · s<sup>-1</sup> flow the polyps are bent downstream and eddies form over the tentacular surfaces. At these higher flows, the cysts are captured all over the tentacles in a radially symmetrical pattern and move towards the tentacle tip, although capture efficiency decreases with increasing Reynolds number.

Filtration efficiency of three species of gorgonian corals were shown by Dai and Lin (1993) in recirculating flume experiments to be a unimodal response to velocity with a maximum efficiency near 8 cm · s<sup>-1</sup> (Fig. 4.3). A wide range of velocities was tested during these experiments with *Subergorgia suberosa* feeding limited to the range 7–9 cm · s<sup>-1</sup>, *Melithaea ochracea* to 4–40 cm · s<sup>-1</sup>, and *Acanthogorgia vegae* to 2–22 cm · s<sup>-1</sup>. Dai and Lin (1993) found that the typical feeding range for a species was related to the polyp size and its deformability in flow.

### Echinoderms

The stalkless crinoid *Oligometra serripinnia* from the Great Barrier Reef was used in experimental flume tests by Leonard, Strickler, and Holland (1988). This crinoid lives at 10–15 cm above the sediment–water interface

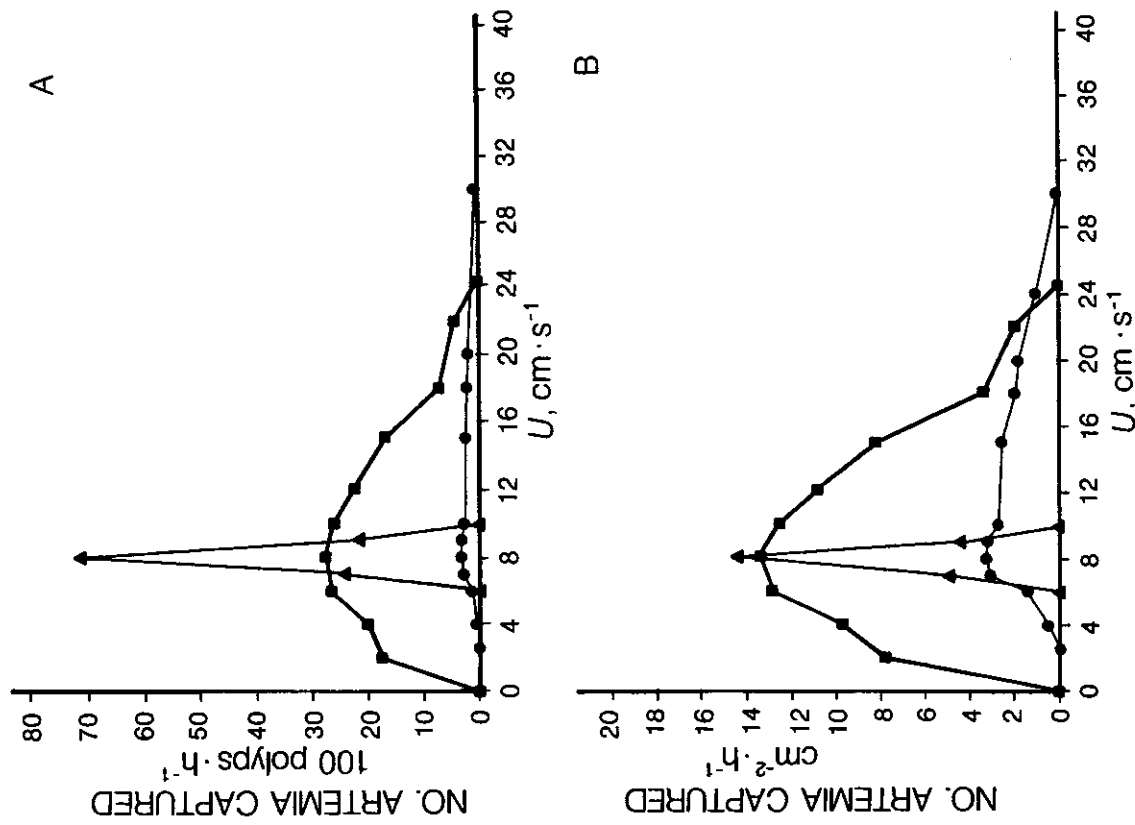


Figure 4.3 Normalized feeding effectiveness with respect to ambient velocity: ■, *Acanthogorgia vegae*; ●, *Melithaea ochracea*; and ▲, *Subergorgia suberosa*; A, polyp feeding rates; B, feeding rate per unit surface area (Dai and Lin 1993).

as an ectocommensal on sea fans, where it occupies the downstream side of its host. The adult animals used in the experiments described here were star-shaped with 10 radiating arms, each ~3 cm in length. Each arm had 55–80 pinnules with 40–60 tube feet per pinnule for feeding. There was a relatively wide gap between arms but smaller distance (up to 0.69 mm) between pinnules. At higher flows, the distance between pinnules was a function of velocity due to flow deformation.

Velocity was determined by Leonard et al. (1988) to affect filtration in the following ways:

- By changing the rate of encounters with seston particles
- By affecting the size and quality of available seston
- By changing the fine-scale flow regime near the filter
- By changing the shape of the filter
- By changing the efficiency of capture by tube feet and pinnules

Capture efficiency rates were determined independently in this study by tracking individual particles by dark field photography so that seston approach, capture, and escape rates as a function of velocity (Fig. 4.4) could be determined. The results suggest that for the adult size crinoids used ( $n = 4$ ), the following unimodal responses occur:

- 0.9–4.8 cm·s<sup>-1</sup>: rate of encounter with seston low but capture efficiency high
- 4.8–6.4 cm·s<sup>-1</sup>: optimum flow rate with rate of encounter with seston higher and capture efficiencies still high
- >6.4 cm·s<sup>-1</sup>: highest rate of encounter with seston but high flows causing deformation of the filter and the capture efficiency lower

The maximum velocity tested by Leonard et al. (1988) was 13.3 cm·s<sup>-1</sup>, at which the absolute approach rate of seston particles for a whole crinoid had reached an asymptotic level.

Studies by Leonard (1989) on another stalkless crinoid, *Antedon mediterranea*, found in the Mediterranean Sea off Monaco, included measurement of both velocity and seston concentration to determine the effect on feeding responses. Feeding activity was recorded by the dark field illumination technique (see Chap. 2), focused on the pinnules bearing approximately 70 tube feet. The feeding rate was assumed to be directly proportional to the number of single or multiple tube foot flicks made when a sestonic particle was captured by the filter. The crinoids in a small capacity Vogel–LaBarbera recirculating flume were subjected to a cycle of increasing step changes of velocity (0.4–3.7 cm·s<sup>-1</sup>) followed by decreasing step changes of velocity (3.7–0.4 cm·s<sup>-1</sup>) for a wide range of seston concentrations (25–10,000 cells of *Hymenomonas elongata*/ml). This microalga is a spherical cocolithophore of ~11 μm diameter. The

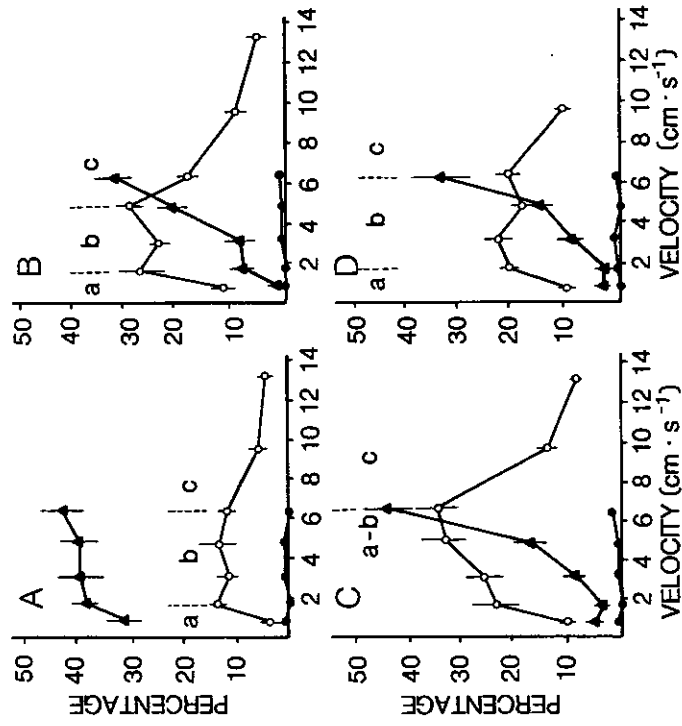


Figure 4.4 *Oligometra serripinnia* capturing pollen grains at different ambient velocities in four individuals (A–D): ▲, passes; ○, captures; ●, escapes as a percentage of those possible. The unimodal function limits are suggested (modified from Leonard et al. 1988).

optimum concentration for filtration was  $2000 \text{ cells} \cdot \text{ml}^{-1}$ , beyond which further increases caused a progressive decrease in feeding activity (flick responses). For each concentration tested, there was a maximum flick activity at  $2.3 \text{ cm} \cdot \text{s}^{-1}$  (a). Beyond  $2.3 \text{ cm} \cdot \text{s}^{-1}$ , feeding rate declined (c), suggesting a limited b region. Statistical analysis of the data by analysis of variance suggested that flick activity depends on velocity and particle concentration, but not on the rate at which particles approach the filter. Thus, one cannot assume that filtration rate is the product of velocity and seston concentration.

#### Active suspension feeders

Bivalve molluscs are perhaps best described as active suspension feeders, although some are deposit feeders and others are facultative suspension-

Table 4.3. Representative macrobenthic active suspension feeders.

Common name	Scientific name	Major taxa	Reference
Scallop	<i>Placopecten magellanicus</i>	Bivalvia	Wildish et al. (1987)
Mussel	<i>Mytilus edulis</i>	Bivalvia	Walne (1972)
Winkle	<i>Serpulorbis natalensis</i>	Gastropoda	Hughes (1978)
Bryozoan	<i>Fiustrellidra hispida</i>	Bryozoa	Best and Thorpe (1983)
Sea squirt	<i>Ciona intestinalis</i>	Ascidiacea	Flood and Fialo-Médioni (1981)
Worm	<i>Chaetopterus variopeatus</i>	Polychaeta	Flood and Fialo-Médioni (1982)
Sand dollar	<i>Dendrastrus excentricus</i>	Echinodermata	Timko (1976)

deposit feeders. Examples of taxa which are thought to be active suspension feeders are listed in Table 4.3. Besides bivalves, they include Bryozoa and sea squirts, plus a few species of echinoderms, polychaetes, and gastropods.

In most cases, the pump which moves seawater in the trophic fluid transport system is a ciliary one. Only in a few polychaete species, such as *Chaetopterus variopeatus*, is a muscular piston pump employed.

#### Bivalves

Although many early bivalve biologists (e.g. Kerswill 1949) recognized the importance of flow in bivalve production, the precise mechanisms by which this was achieved were not addressed until relatively recently. Kirby-Smith (1972) was the first to study the effect of flow on bay scallops (*Argopecten irradians*) in a growth tube apparatus (Chap. 2). Flow was measured as the bulk velocity flow rate. Kirby-Smith (1972) was also the first to demonstrate that higher velocities could inhibit bay scallop growth. Wildish et al. (1987) have reinterpreted his growth results as a unimodal function of velocity, in general agreement with later studies made in a flume with this bay scallop (Cahalan, Siddall, and Luckenbach 1989; Eckman, Peterson, and Cahalan 1989). Growth results with the giant scallop (*Placopecten magellanicus*) in flume experiments also show that the growth of this species has a unimodal function response to velocity. Flume studies (Wildish and Saulnier 1993) where a wide range of velocities were tested confirm that filtration by the giant

scallop is a unimodal function of velocity, suggesting that it is the relationship underlying the growth responses.

Considering the possible mechanisms involved in the giant scallop filtration response to velocity and using the labelling of Fig. 4.1, the following observations can be made:

- At zero velocity, the filtration rate is time dependent and, because of mixing limitations, usually affected by the geometry of the experimental apparatus. The exhalant jet itself, consisting as it does of seawater cleared of seston, and in otherwise static conditions will cause some mixing and result in seston dilution near the inhalant. As the seston concentration declines, inhibition of filtration may result. The effect of small increments in velocity is to help remove the localized buildup of seston-diluted seawater around the scallop.
- Beyond the point where the ambient flow is sufficient to remove completely any localized seston dilution around the scallop, flow has no further influence on filtration. The flat-topped unimodal response seen and lack of a continuing increase in filtration rate with increasing velocity argue against the latter being used for enhancement of filtration rates, as is suggested by LaBarbera (1977) in brachiopods.
- As ambient velocity further increases, the pressure field around the animal will be altered. The difference between ambient pressure at the inhalant ( $P_A$ ) and the exhalant ( $P_B$ ) may become significant with respect to the pressure difference generated by the ciliary pump. If  $P_A \gg P_B$ , seawater will tend to be forced through the system at a rate greater than can be handled by the ciliary pump filter, as described by Jørgensen et al. (1986a). This causes a behavioral response involving valve and mantle wall partial closure, thereby reducing the volume that can be processed. The internal homeorheostat (Wildish and Saulnier 1993) can to some extent overcome the closing response when seston concentration is sufficiently high (Fig. 4.5).
- At high ambient velocities, the siphons retract and close because they cannot filter. This velocity is not fixed but variable for the scallop because seston concentration and other environmental variables, such as temperature, can influence the endpoint.

Behavioral responses of a bivalve to external pressure fields which oppose the internal pressure field created by the ciliary pump can be expected in phases c and d. The ciliary pump in some bivalve molluscs can generate pressure differences of the order of 0.1–2.0 mm of water (Foster-Smith 1976). If the external pressure differences are of the same order of magnitude, it can be predicted that the flow through the pump, in the absence of behavioral response, will be either much reduced or considerably enhanced, depending on the sign of the pressure differential.

If the scallop is oriented with the inhalant pointing upstream, the pressure difference between the inhalant and the exhalant is given approximately by the stagnation pressure. The streamlined shape of the

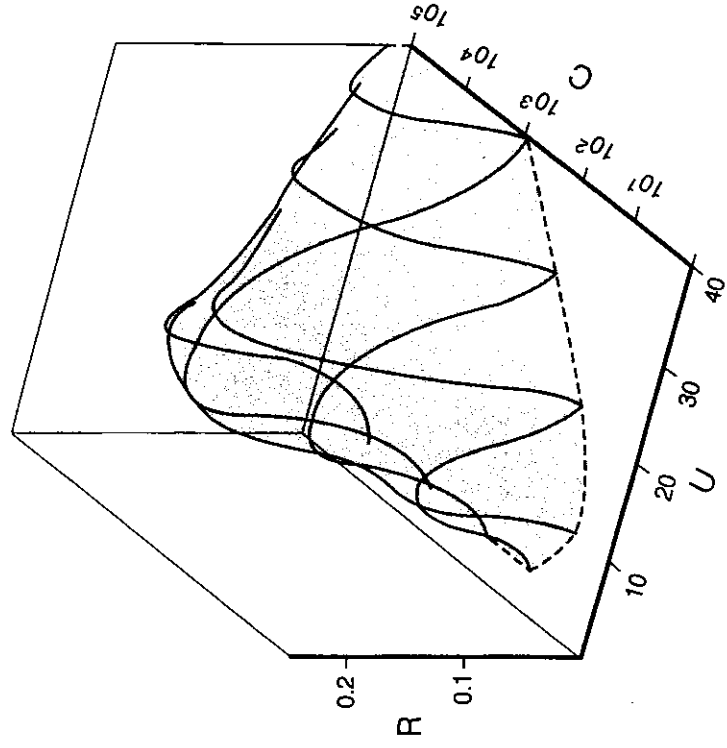


Figure 4.5 The seston uptake rate,  $R$ , as arbitrary units, is a function of velocity,  $U$ , in  $\text{cm} \cdot \text{s}^{-1}$ , and seston concentration,  $C$ , as cell number  $\cdot \text{ml}^{-1}$  of *Chroomonas salinus* (Wildish et al. 1992).

valves would suggest that the pressure defect would be relatively small in the vicinity of the exhalant, which will lie in the turbulent wake of the scallop. The bulk stream velocity required to give a stagnation pressure of  $1.0 \text{ mm}$  of water is  $14 \text{ cm} \cdot \text{s}^{-1}$ . Because the flow through the trophic fluid transport system is laminar, the volumetric flow is linearly related to the external pressure difference (see Jørgensen et al. 1986a). If the scallop's ciliary pump can generate a pressure difference of  $1.0 \text{ mm}$  of water, the volumetric flow through the animal can be doubled by an external pressure difference of the same magnitude. How the ciliary pumping system of other bivalve molluscs would respond to extreme pressure differences caused by ambient flow is not clear. As has been demonstrated by Wildish and Saulnier (1993), by direct video viewing of the exhalant siphon, the live scallop reacts behaviorally by partially closing the mantle and valves in order to resist the external pressure

Table 4.4. Scallop seston uptake rates as affected by flux, seston concentration, and velocity.<sup>a</sup>

Seston concentration cells · ml <sup>-1</sup>	Velocity cm · s <sup>-1</sup>	Flux rate cells · cm <sup>2</sup> · s <sup>-1</sup>	Seston uptake rate µg Chl a · g wt · h <sup>-1</sup>
10	50	500	0
100	5	500	0.018
	50	5,000	0
1,000	5	5,000	0.09
	50	50,000	0
10,000	5	50,000	0.30
	50	500,000	0.24
100,000	5	500,000	15.0

Source: Extrapolated from Wildish et al. (1992).

<sup>a</sup>Note: Seston is a unialgal culture of *Chroomonas salinus*.

difference. This results in a reduced volumetric flow rate of inhaled seawater for filtration and hence feeding rate at increased velocities.

If the scallop is reversed with the inhalant pointing downstream, the velocity at which the ambient pressure differential is just balanced by a ciliary pump delivering a 1.0-mm head is, as noted previously, 14 cm · s<sup>-1</sup>. For a head of 2.0 mm, the required velocity is 20 cm · s<sup>-1</sup>. The reversed live scallop must maintain its ciliary pumping work rate but, in the unfavorable pressure conditions, cannot maintain its filtration throughput, as suggested by Jørgensen (1990) in mussels. Evidence that growth rates of live scallops forced to oppose unimodal flume velocities >12 cm · s<sup>-1</sup> is reduced is presented by Wildish and Saulnier (1992).

In addition to velocity, seston concentration itself has been shown by Wildish and Saulnier (1993) to interact to influence the degree of valve and mantle edge opening, as indicated by seston uptake (Table 4.4). For a unialgal culture of *Chroomonas salinus*, filtration rates by individual, starved scallops were maximized at a cell concentration of  $\sim 1 \times 10^3$  cells · ml<sup>-1</sup> and at a constant ambient velocity of 8 cm · s<sup>-1</sup>. Flume experiments in which velocities and seston concentrations were widely varied (Wildish et al. 1992) and giant scallop filtration rates determined show that the maximum uptake rate occurs at  $\sim 25$  cm · s<sup>-1</sup> when the optimum seston concentration ( $\sim 10^3$  cells · ml<sup>-1</sup> of *C. salinus*) is offered. Presumably, at this optimum point, giant scallops are filtering near the maximum intrinsic capacity of their pump. The ambient velocity at which scallops

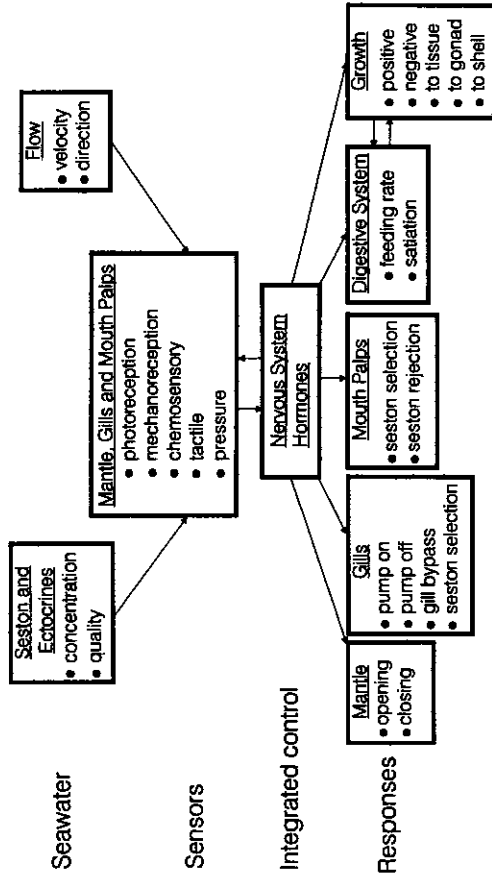


Figure 4.6 Environmental/physiological model of giant scallop feeding and growth (Wildish and Saulnier 1993).

stop filtering is directly proportional to seston concentration (Fig. 4.5). At seston concentrations greater than the optimum, sufficient ration can be obtained at lower clearance rates, and at both  $10^4$  and  $10^5$  cells · ml<sup>-1</sup> of *C. salinus*, filtration was still occurring at up to 45 cm · s<sup>-1</sup>. This was the maximum velocity achievable with the recirculating Vogel-LaBarbera type flume used in these experiments (Wildish et al. 1992).

The demonstration that giant scallop filtration rates are controlled by at least two independent environmental variables, velocity and seston concentration (Fig. 4.5), suggests an integrated environmental-physiological model for feeding and growth (Wildish and Saulnier 1993). This model (Fig. 4.6) depends on a constant output ciliary pump whose filtration rate can be controlled by closing/opening valves and mantle edge according to changes in these environmental variables. The evidence also indicates that velocity and filtration only continue if it is nutritionally advantageous for the scallop. This implies central physiological control, perhaps by the nervous system, in which the bioenergetic profit and loss can be optimized.

The model incorporates evidence that ectocrines (substances released from cells which elicit chemosensory responses in target organisms) associated with seston alter the filtration response by causing closing/



opening of the valves, which automatically control volume throughput. Ward, Cassel, and MacDonald (1992) showed that filtration of the giant scallop is stimulated by preferred species of microalgae. When toxic dinoflagellates were fed to giant scallops, they caused valve clapping and closure (Shumway et al. 1985a). Little is known about the structure of sensors involved in the physiological control of feeding in the giant scallop (Beninger 1991).

Surprisingly few authors have investigated the effect of velocity on mussel filtration/feeding or growth rates. Walne (1972) claimed that growth rate in blue mussels *Mytilus edulis* was positively linked to increasing volumetric flow in the range tested (50–700 ml·min<sup>-1</sup> in 2.4-L capacity boxes). On the other hand, Hildreth (1976) claimed that the pumping rate of blue mussels was unaffected by volumetric flows from 33 to 700 ml·min<sup>-1</sup>. These studies have led to some confusion (e.g. Vogel 1981), but, in both cases, the mixing characteristics within the experimental chambers, the degree of refiltration by the mussels, or velocities near the mussel inhalant were not determined, although the latter are likely to have been <1 cm·s<sup>-1</sup>, and the results remain apparatus specific and not referable to the much wider range of velocities experienced in the field. Walne's (1972) results could be explained by small velocity increases helping to remove seston-depleted water near the mussel.

Preliminary measurements of blue mussel filtration rates as a function of velocity in the range 6–38 cm·s<sup>-1</sup> have been made by Wildfish and Miyares (1990) in a recirculating Vogel–LaBarbera flume of 90-L capacity. The velocity measurements were made with the aid of a small rotor of 11 mm diameter (see Chap. 2) placed in front of the mussel inhalant, with the mussel firmly attached by the valve to the flume floor so that the siphons opposed the flow. At velocities in the range 6–25 cm·s<sup>-1</sup> and at a constant seston concentration of 10<sup>4</sup> cells of *Chroomonas salinus*·ml<sup>-1</sup>, filtration rates were inversely related to velocity. At velocities >25 cm·s<sup>-1</sup> and at the same seston concentration, the filtration rate was zero or a small percentage of the maximum possible at 6 cm·s<sup>-1</sup>. Although these results could be interpreted as part of a unimodal function of velocity where only the c and d stages were observed, the velocity range tested needs to be widened and seston concentrations tested need to be varied before a conclusion can be reached.

Growth studies in which velocity is varied while keeping seston concentration constant are not available for blue mussels. The flow range examined by Wildfish and Kristmanson (1985) in growth experiments with blue mussels of 0.1–3.89 cm·s<sup>-1</sup> is not considered wide enough to

detect the unimodal response of feeding/growth to velocity. Bayne, Thompson, and Widdows (1976) suggested that the relationships among velocity, filtration rate, seston concentration, and respiration rate in mussels need to be elucidated, but as far as we are aware, this has not been done.

Seston concentration also affects the filtration rate of *Mytilus edulis*. An optimum rate at 75–200 × 10<sup>3</sup> cells of *Phaeodactylum tricornutum*·ml<sup>-1</sup> was obtained in static seawater test conditions (Foster-Smith 1975). An indirect method was used to determine this with animals of 45–52-mm shell height and 2.56– to 4.00-g wet weight. The mean filtration rate was 1.47 ± 0.20 L·h<sup>-1</sup> per individual or 0.39 ± 0.04 L·h<sup>-1</sup>·g<sup>-1</sup> wet weight. Widdows, Fieth, and Worrall (1979), working with the same species and a similar indirect technique, showed that filtration rate was a unimodal function of the natural seston concentration (expressed as dry weight per litre, inclusive of sedimentary particles, and therefore not relatable to Foster-Smith's results). The optimum seston concentration increased as animal size became larger. Riisgård and Randlov (1981) also studied the filtration rate of *Mytilus edulis* over a wide range of concentrations of *Phaeodactylum tricornutum*. They found that filtration was independent of seston concentration between 1.5 × 10<sup>3</sup> and 30 × 10<sup>3</sup> cells·ml<sup>-1</sup>, but at higher concentrations there was a decrease in filtration. At seston concentrations lower than 1.5 × 10<sup>3</sup> cells of *P. tricornutum*, a decrease in filtration rate resulted from inhalant and valve closing.

Seston quality is a factor which has been extensively investigated in relation to filtration and feeding in the blue mussel. *Mytilus edulis* is considered to be an indiscriminate active suspension feeder whose filtration rate is not usually stimulated by ectocrines (Ward and Targett 1989), although seston quality, e.g. exudates from toxic dinoflagellates, may directly inhibit filtration or cause valve closures (see review by Shumway and Gainey 1992; Ward and Targett 1989). Some bacteria have also been reported to be inhibitory to filtration in the blue mussel (Birbeck and McHenery 1982; McHenery and Birbeck 1986; Birbeck, McHenery, and Nottage 1987). Ward and Targett (1989) have suggested that the response mechanism involves epicellular ectocrines which are cues for particle selection after capture but before ingestion. This response would be integrated by the nervous system, which then reduced, or shut, the valves, thus limiting or stopping filtration. Such a response would be consistent with the model shown in Fig. 4.6. One criticism of the work done on the effect of seston quality on bivalve filtration is that ambient flows around the feeding bivalve have not been simulated, and

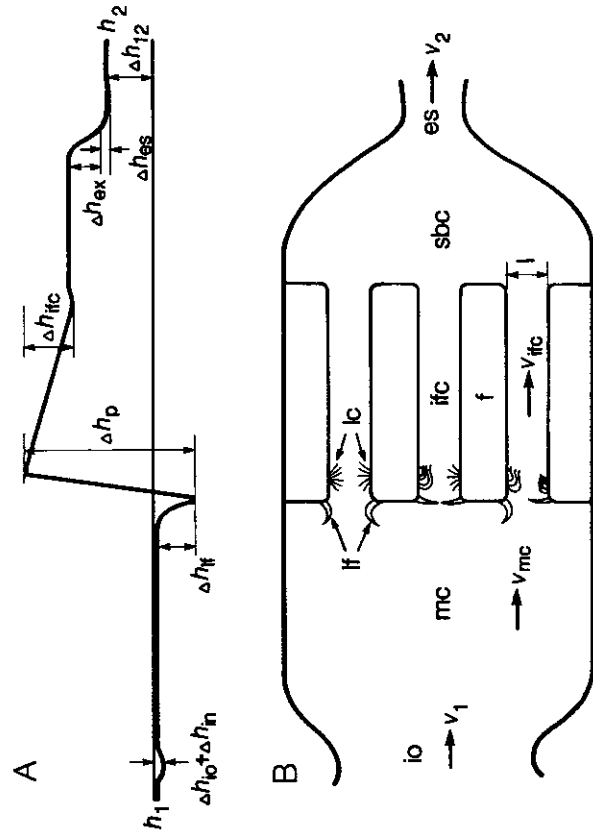


Figure 4.7 Diagrammatic representation of the blue mussel pump with typical static pressures (Jørgensen et al. 1986a) at points along the trophic fluid transport system: A, relative pressure heads; B, diagram of pump;  $h_1$  and  $h_2$  hydrostatic pressures at inlet and outlet;  $\Delta h_{12}$ , difference between  $h_1$  and  $h_2$ ; or back pressure; in, and ex, inlet and exit losses of pressure; io, inhalant opening; mc, mantle cavity; lf, laterofrontal cirri; p, pump; lc, lateral cilia; ifc, interfilament canal; f, filament; sbc, suprabranchial cavity; es, exhalant siphon; l, interfilament canal width;  $v_1$  and  $v_2$ , velocities at inlet and exhalant.

it remains to be seen whether this would change the conclusions already reached.

Jørgensen et al. (1986a) have provided a hydrodynamic model of the blue mussel pump useful in estimating inhalant and exhalant pressures. Pumping power is created by the metachronal beating of lateral cilia which are located at the upstream ends of the interfilament canals. There are resistances associated with various parts of the trophic fluid transport system, and these were estimated from their dimensions by Jørgensen et al. (1986a) to be of the order shown in Fig. 4.7. The pump characteristic was calculated from estimated resistances, pressure changes of the whole system, and volume flow rates to give the relationships among pump power, pressure heads, and volumetric flow rate (see Jørgensen et al. 1986a).

The measurement of bivalve pump characteristics, e.g. velocities at

inhalant and exhalant, is rendered difficult by the rapidity of opening/closing of the mantle walls. According to Jørgensen and Ockelmann (1991), when this occurs, ciliary beating (in young, transparent-valved individuals) abruptly stops when the exhalant closes and immediately begins beating once the exhalant opens again. Apart from this, velocity distribution in the exhalant is that of laminar flow in a tube with midpoint velocities twice that of the bulk velocity. The difficulties involved in direct measurements of velocity or pressure at exhalant openings were emphasized in Chapter 2.

Pumping rate varies with the degree of valve gaping or, more precisely, with the degree of openness of the inhalant and exhalant siphons (Foster-Smith 1976). Maximally open siphons produce the maximum pumping rate. Retraction of the siphons causes a shortening of the gill axes and thus of the demibranchs, which results in a reduced lumen diameter of the interfilament canals (Jørgensen 1990). Complete siphon retraction and closing reduce the distance between the extended tips of opposing lateral cilia from  $\sim 10\mu\text{m}$  to zero; this is suggested to be a general property of suspension feeding bivalve gills (Jørgensen and Riisgård 1988). Jørgensen (1990) concludes that pump power and volumetric capacity are probably direct functions of interfilament canal width, which is ultimately controlled by valve gaping and the linked degree of siphon retraction.

The relationship between seawater viscosity and the pumping rate of blue mussels (Jørgensen, Larsen, and Riisgård 1990) clearly shows the dependence of pumping rate on kinematic viscosity at different ambient temperatures. This effect was considered to be due to the resistance to water flow in the interfilament canals of the trophic fluid transport system. Jørgensen and Ockelmann (1991) showed that in young mussels lateral cilia beat with a mean frequency of  $\sim 10\text{Hz}$  at  $14^\circ\text{C}$  to  $\sim 15\text{Hz}$  at  $20^\circ\text{--}21^\circ\text{C}$ , corresponding to a  $Q_{10} \approx 2$ . Rapid changes of temperature in intact mussels are reported by Jørgensen (1990) not to lead to obvious effects on the pumping rate, despite the increased ciliary beating.

Physiologists interested in the energetics of filter feeding in bivalves such as mussels (e.g. Bayne and Newell 1983) have hypothesized that filtration is internally controlled, e.g. by gut fullness, to maintain a constant feeding rate over a wide range of environmental conditions. Although not supported by direct evidence, it is commonly held (Winter 1978) that ciliary pumping by bivalves is energetically expensive. Internal physiological control of filtration would thus be homeorheostatic by allowing the conservation of energy required for ciliary beating. An

alternative view formulated in Jørgensen (1990) is that ciliary pumping (see also Jørgensen et al. 1986b) is inexpensive and, anyway, maintained at a constant rate irrespective of the pump output (see also Chap. 9, the section, Ultimate questions). Differences in pump output, and hence filtration rate, were a simple function of the degree of openness of the valves and siphons (Jørgensen 1990). Some additional evidence is available for Jørgensen's view; for example, Wildish and Saulnier (1993) found that the scallop exhalant opening area was a function of ambient velocity consistent with regulation of valve closure to control seston uptake and growth rates by velocity. Stenton-Dozey and Brown (1994) also found that in the South African clam *Venerupis corrugatus* the degree of siphon openness correlated positively with clearance rates and that increasing clearances were achieved without an increase in respiration rate. Both competing hypotheses outlined are compatible with the environmental-physiological model of feeding proposed by Wildish and Saulnier (1993).

### Bryozoans

The phylum Bryozoa consists of colonial forms, usually attached to the substratum as an encrusting, stolonate, or bushy growth. The individual zooid of the colony is protected by a non-living chitinous skeleton, sometimes strengthened by calcareous secretions. The characteristic tentacle-bearing lophophore is the structure concerned with suspension feeding.

Observation of feeding Bryozoa in a static experimental system, where the seawater was slowly mixed by a peristaltic pump, was undertaken by Best and Thorpe (1983) in *Flustrellidra hispida*. This species is an epiphyte of the brown macroalga *Fucus serratus*, which is found in the lower intertidal zone of the Isle of Man. The experimental method involved viewing the lophophore at 1000 $\times$  magnification with a stereomicroscope to observe the rate of movement of the seston particles (= *Tetraselmis suecica* of ~10- $\mu$ m diameter at all densities up to  $2 \times 10^5$  cells·ml<sup>-1</sup>). Because the particles were moving quickly across the field of view, it was necessary to tune an oscilloscope trace to the same speed so that from the distance travelled (= field of view diameter), a particle speed could be calculated. Results showed that starved *Flustrellidra* could increase the seston particle speed if increased concentrations were supplied by up to 130%. Best and Thorpe (1983) noted that speeds were variable within the lophophore and further investigation revealed that particles located at the centre of the lophophore had the greatest speed. Rates of particle

movement depended on ciliary currents generated by cilia present on the lophophore tentacles and ciliary speed varied in time, related to satiation. Best and Thorpe (1986) extended their investigations to five other species locally available around the Isle of Man. They found that starved zooids also responded to increased seston concentration by increasing the ciliary flow and that this resulted in a higher capture rate of a preferred food particle. They also found that feeding current velocities were positively linked to the lophophore height because increased tentacle length increases the number of cilia available to drive seawater through the lophophore.

Okamura (1984, 1985) has studied the effects of ambient flows on feeding of *Bugula stolonifera*, an arborescent species, and *Conopeum reticulatum*, an encrusting species. *Bugula* and *Conopeum* were present on floating docks in the Pacific Ocean off California. Feeding success was determined by using latex beads (mean diameter of  $11.9 \mu\text{m} \pm 1.9 \mu\text{m}$  standard deviation [SD]) offered at 1120–1190 beads·ml<sup>-1</sup>. Feeding experiments were of 20-min duration during which there was no settling out of the beads in the flume. The beads captured by individual zooids were counted after treatment with sodium hypochlorite, which left the exoskeleton and beads intact. Small *Bugula* colonies showed inhibition of feeding success for individual zooids at the higher flow velocity tested (10–12 cm·s<sup>-1</sup>). Okamura (1984) suggests that this is because the sestonic particles are moving at a greater speed past the lophophore, making it more difficult to divert the streamlines into the lophophore. In addition, it is suggested that once they are in the lophophore, it may be more difficult to retain the particles for a sufficient time to effect transfer to the mouth as a result of the drag force caused by the current. Larger, more bushy *Bugula* did not show this effect of velocity on feeding because flows are decelerated as they pass through the branches, the colony changes its shape, and central or downstream, flow-protected zooids are the ones feeding at the greatest rate. In addition to flow protection, Okamura (1984) thought that the lack of flow inhibition in bushy forms could be due to a greater availability of seston because of the poor feeding effectiveness of upstream zooids and perhaps greater ciliary pumping by the flow-protected zooids.

In the encrusting bryozoan *Conopeum reticulatum*, which were grown on glass microscope slides in the field, feeding experiments were conducted in the laboratory by placing slides normal to the flow in a small recirculating flow tank. Feeding success was determined as for *Bugula* and tests were made at three velocities: slow (1–2 cm·s<sup>-1</sup>), intermediate

(4–6 cm·s<sup>-1</sup>) and fast (10–12 cm·s<sup>-1</sup>). The results show an inverse relation of feeding with velocity, and both large and small colonies were unable to accumulate beads at higher rates. At low and moderate velocities, zooids from larger colonies were more effective in feeding than small colonies, perhaps because the larger number of zooids could better divert seawater to the colony.

Subsequently, Okamura (1987, 1990) tested the interactive effects of particle size and velocity on the feeding success of Californian Bryozoa. She was able to show in *Bugula stolonifera* that medium and large particles (14.6 ± 1.0 and 19.1 ± 1.1 μm) were ingested at rates greater than small particles (9.6 ± 0.5 μm). Flow influenced the particle size ingested by *B. stolonifera* so that this bryozoan fed preferentially on larger particles at the highest flow tested (10–12 cm·s<sup>-1</sup>). Particle size alone affected the feeding success of *Bugula neritana*; the medium and larger particles were preferred. The mechanism of selective feeding may involve size-dependent particle behavior, active selection, or rejection involving alternative feeding mechanisms such as tentacle flicking.

#### Sieving suspension feeders

Mucous filter nets have been found in a wide range of taxa, including ascidians, appendicularians (Flood and Fiala-Médioni 1982), some vermiform gastropods (Hughes 1978), and polychaetes such as *Nereis diversicolor* and *Chaetopterus variopectatus* (Wells and Dales 1951; Riisgård 1989, 1991).

Ascidians, or sea squirts, are attached benthic animals which may be solitary or colonial and are characteristically suspension feeders. A single feeding zooid of the colonial ascidian *Clavelina* species (Fig. 4.8) has two openings – the buccal siphon for inhaled flow and the atrial siphon for exhalant flow. The pharyngeal side walls are punctuated by gill slits or stigmata. The inhaled flow is generated by cilia lining the stigmata which cause inhaled seawater to pass around the pharynx, through the stigmata to the atrium, then out via the atrial siphon. Sestonic particles are captured on a mucous net which is secreted by the endostyle and the whole thing periodically ingested. When feeding conditions are suitable, the endostyle continuously produces the mucous net.

Randløv and Riisgård (1979) have studied the effect of sestonic particle size (in the range 1- to 7-μm equivalent spherical diameter) on the fractions retained by *Ascidia aspersa*, *Molgula manhattensis*, *Clavelina lepadiformis*, and *Ciona intestinalis*. The small particles used originated

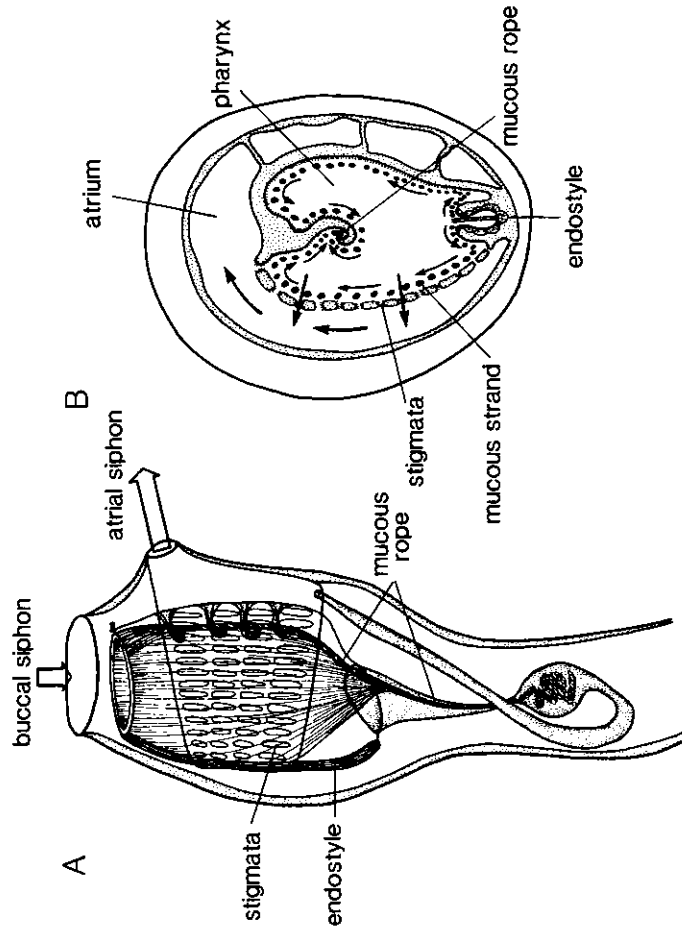


Figure 4.8 A, Single feeding zooid of *Clavelina*; B, transverse section of *Clavelina* (Carlisle 1979).

from those already present in the seawater system. Cultures of *Monochrysis lutheri* and *Dunaliella marina* were added at a concentration of  $1 \times 10^4$  cells·ml<sup>-1</sup> to increase the seston size range. Samples were collected from the inhaled and exhalant areas as in Møhlenberg and Riisgård (1978) and the concentration determined in an electronic particle counter/sizer. Results showed that seston of equivalent diameter in the range 2–3 to 7 μm were completely retained, while particles of <1 μm diameter had a particle retention efficiency of ~70%. Within the experimental error likely in measuring mesh size and retention efficiency, the results provide support for the hypothesis that food capture in these ascidians is by sieving. Fiala-Médioni (1978), working with at least one of the same species, *C. intestinalis*, suggested that up to one-third of *Monochrysis lutheri* (6–10 × 2–3 μm in size), offered as food at  $20 \times 10^6$  cells·l<sup>-1</sup> and  $15 \pm 1^\circ\text{C}$ , passed through the filter. As Randløv and Riisgård (1979) point out, this result was not obtained by direct observation of

retention efficiency but by calculation from direct observation of pumping rate and indirect observations based on particle clearance rates, and so may be inaccurate.

Robbins (1984) studied the effect of particle concentration on feeding of *Ciona* and *Ascidella* spp. and found that ingestion was reduced at higher concentrations of fuller's earth (mean particle diameter of 25–30  $\mu\text{m}$ ). This was a result of a reduction in pumping rate and an increase in the frequency of squirting, but there was no change in retention efficiency, which remained at 100%. Squirting is a sudden muscular contraction of the zooid which causes excess sestonic food to be rejected from the pharynx.

The ascidian pump has been analyzed in a manner similar to that of the mussel by Riisgård (1988). The pump in *Syela clava*, by comparison with that in the mussel, is a much lower pressure/energy system. Flow through the filter is calculated to be  $0.03 \text{ mm} \cdot \text{s}^{-1}$  and the pressure drop across it to be  $0.069 \text{ mm H}_2\text{O}$  (using a net dimension of  $1.4 \times 5.4 \mu\text{m}$ , this value has been recalculated; see Riisgård 1989). The maximum pressure rise in the trophic canal system is  $1.2 \text{ mm H}_2\text{O}$ . The pumping rate is reduced by closing the atrial siphon, but this does not automatically reduce pressure, as it does in bivalves, because the stigmata cilia may continue to beat. Factors which result in the cessation of ciliary beating include a lack of sestonic particles or direct physical disturbance of the ascidian.

Most of the ascidians which have been studied are found in the nearshore continental shelf area. Carlisle (1979) reports that some continental slope stalked ascidians such as *Bolteniopsis* are specialized for opposing a steady external current and passively receive seawater and seston in a much enlarged buccal siphon. Concomitantly, there is a great reduction in the branchial basket, which may no longer be needed as a pump. Another example is provided by a stalked ascidian, *Syela montereyensis*, which is adapted to oscillating wave surge channels of exposed shores of the Pacific Ocean on the U.S. West Coast (Young and Braithwaite 1980). Characteristic of this species of *Syela* is a spar buoy system (see Chap. 6) in which wave forces passively reorient the stalked ascidian (Fig. 4.9) which is articulated near its base so that the buccal siphon faces the flow either on the onshore wave or on its back surge. It was shown by field experiments that the time required for seawater to pass through the trophic fluid transport system depends on ambient velocity conditions. It was also found that seawater was pushed through by dynamic force from waves, perhaps assisted by viscous entrainment. It

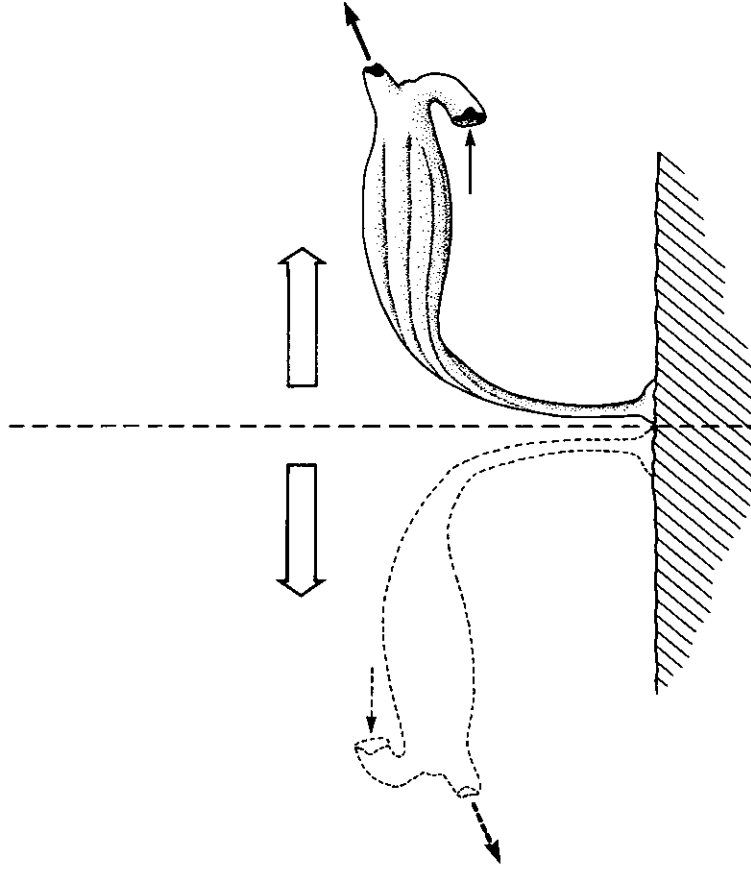


Figure 4.9 *Syela montereyensis*: responses to oscillating flows (Young and Braithwaite 1980).

is thus possible that these specialized ascidians are combined passive-active suspension feeders. Manahan et al. (1982) have shown that this species can remove free amino acids from seawater, although the importance of dissolved organic matter in its nutrition remains unclear.

Other species of considerable interest are polychaetes such as *Chaetopterus variopedatus* and *Nereis diversicolor* which are both capable of producing mucous nets and capturing microscopic food, probably by sieving. *Chaetopterus* lives in a parchmentlike tube secreted by the epidermis and attached to stones, or in soft sediment in a U-shaped burrow (Fig. 4.10). The parapodia of segments 14, 15, and 16 are disc shaped and beat to produce a flow of water through the tube. Flow direction is always from the head to the tail. The mucous net used in sieving food particles is produced by the modified parapodia of the

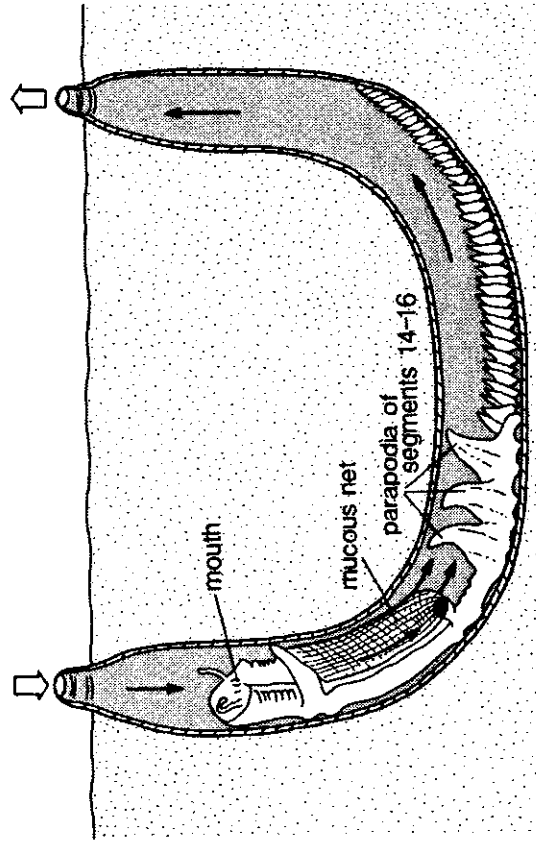


Figure 4.10 Life form of *Chaetopterus variopedatus* in soft sediments (Flood and Fiala-Médioni 1982).

twelfth segment. The ciliated dorsal groove and cuplike organ of the thirteenth segment gather the mucus and roll it into a food ball. When the ball is sufficiently large, the parapodia stops pumping and the food, plus mucus, is transported anteriorly by cilia in the dorsal groove to the mouth for ingestion.

The *Chaetopterus variopedatus* pump is a muscular one. Riisgård (1989) has used his constant-level chamber to investigate these worms from the Swedish west coast. The methods employed were similar to those used with mussels (Jørgensen et al. 1986a) and ascidians (Riisgård 1988). Video recordings of *Chaetopterus* confirmed that the mechanism involved a positive displacement pump and that parapod beating decreased with increasing back pressures. Imposed back pressures set up in the constant-level chamber caused the worm to reverse itself in the tube. The maximum pressure rise in the tube and the total head loss are approximately twice those in bivalves and five times those in ascidians, consistent with the filter area's being relatively smaller than in those species. The pressure drop across the mucous net as estimated by the Tamada-Fujikawa equation requires knowledge of mesh opening size

and diameters of the mesh fibres. Estimates made by Jørgensen et al. (1984) of mesh size based on observations of particle retention efficiency at different particle sizes suggest that the *C. variopedatus* mucous net meshes are three times larger than suggested by Flood and Fiala-Médioni (1982). This results in a pressure drop estimate of 0.7 mm (Jørgensen's estimate) versus 3.0–4.5 mm of water for the mesh size suggested by Flood and Fiala-Médioni (1982). Even with the lower estimate, the pressure drop across the net in the tubicolous worm is several times greater than in the ascidian.

A field study of the pumping activity of the facultative sieving suspension feeder *Nereis diversicolor* was reported by Videl et al. (1994), who used a phototransducer system to record long-term seasonal patterns of pumping activity indicating filtration activity. Observations showed that the worms also go to the sediment surface to deposit-feed on benthic diatoms just after low tide at one, but not the other, Danish location studied. During the summer, *Nereis* was suspension feeding for 50%–100% of the time, and this behavior seemed to be triggered by a threshold chlorophyll a concentration of  $1\text{--}3\ \mu\text{g}\cdot\text{L}^{-1}$ . During the spring and autumn when chlorophyll a was scarce, the filtration activity occurred only 5%–20% of the time.

#### Facultative active suspension feeders

In some benthic suspension feeders, the filtration-feeding behavior changes with velocity so that at low velocities active filtration occurs, while above a critical higher velocity passive suspension feeding occurs. Although LaBarbera (1984) lists some ascidians – e.g. *Syella monteryensis* (Fig. 4.9), some brachiopods, and some sponges – in this category, their filtration/feeding responses to velocity have not been adequately examined. The status of these forms is considered to be unclear, although tentatively they are placed in a separate combined passive-active category (discussed later, in the section, Combined passive-active suspension feeders). The taxa best known as facultative active suspension feeders are the cirripede barnacles, but some decapod Crustacea also have representatives in this category (Trager et al. 1992).

#### Barnacles

It was determined by Crisp and Southward (1961) that changes in velocity can alter the type of feeding behavior of a number of adult cirripede

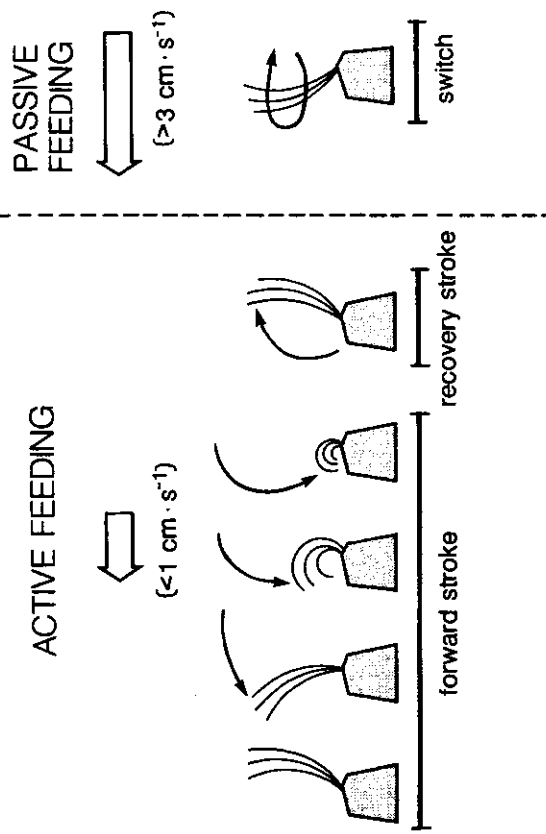


Figure 4.11 Active and passive feeding in *Semibalanus balanoides* (Trager et al. 1990).

barnacles. They described a fast-beat rhythmic sweeping of the cirri through slowly moving seawater and a non-rhythmic full extension of the cirri held rigidly opposed to the direction of flow when the ambient flow was more energetic. These different means of suspension feeding correspond to active suspension feeding at low velocity and passive suspension feeding at higher velocities. Barnacles, such as *Semibalanus balanoides*, are found on those rocky intertidal Atlantic Ocean shores where tidal currents and wind-wave activity are usually energetic and are constantly changing. In a flume study of this species, Trager et al. (1990) investigated the effect of velocity near the barnacle of up to  $9\text{ cm} \cdot \text{s}^{-1}$  on feeding behavior. The recirculating flume (capacity 15 L) had a sophisticated electronic controller which could reverse the propeller, thereby creating oscillating flows with sine wave acceleration or deceleration. Velocity was measured from dark field, laser optical pathway video frames of sestonic particle movement taken at known intervals. The mean velocity at which adult cirripedes changed from active to

passive feeding was determined (Fig. 4.11) to be  $3.10 \pm 0.73\text{ cm} \cdot \text{s}^{-1}$  ( $\pm\text{SD}$ ). The actual range of switch velocities from 22 experiments was  $1.84\text{--}4.83\text{ cm} \cdot \text{s}^{-1}$ . From Fig. 4.11, it can be seen that the active cirral beating involved rhythmic movements in the same direction as the slow flows (individuals positioned carinorostally to the flow). In passive feeding, the cirral fan is held rigidly into the flow so that the concave surface is opposed to it. If the flow direction and position of *S. balanoides* were as described previously, passive feeding involves reversal of the cirral fan through  $180^\circ$ . Trager et al. (1990) could make the cirripedes "dance" (change the orientation of their cirral fans) by rapidly changing the flow direction in the flume. This suggests that the response is controlled by the nervous system with accelerating or decelerating flows acting as the stimulus to cause the reflex responses observed. Further work by Trager, Hwang, and Strickler (1992) using a recirculating computer-controlled oscillating flow tank confirmed that in two species of barnacles, *S. balanoides* and *Sarignium milleporum* (from the Red Sea), flow oscillation frequencies in the range  $0.16\text{--}0.65\text{ Hz}$ , with flow velocities ranging from  $6.2$  to  $12.1\text{ cm} \cdot \text{s}^{-1}$ , stimulated reorientation of the cirral fan. Reorientation occurred during passive feeding so that the concave surface of the fan always faced upstream, where it is known to be most efficient at capturing suspended particles. Behavioral anticipation of flow change appeared to be based on water deceleration that occurred during the oscillation cycle. Trager et al. (1992) also showed that barnacles subjected to increasing oscillation frequencies spent less time in passively filtering and relatively more in removing particles filtered and in re-orienting the fan. Thus, the ratio between the time spent feeding to non-feeding activity depended on the wave oscillation frequency so that at high oscillation frequencies less time was available for filtration.

Hunt and Alexander (1991) have used an endoscope developed for medical research to observe movements of the mouth parts and cirral fan of a tropical cirripede, *Tetractita squamosa*, collected from the east coast of Australia. They were able to show that a wide range of particle sizes, including zooplankters and microplankton, were filtered and utilized as food. They include a description of the ultrastructure of the thoracic appendages and how they are used in capturing the various prey sizes. A more detailed description is provided of six different cirral activity patterns, including that of the passive and active cirral fan behavior described by previous authors.

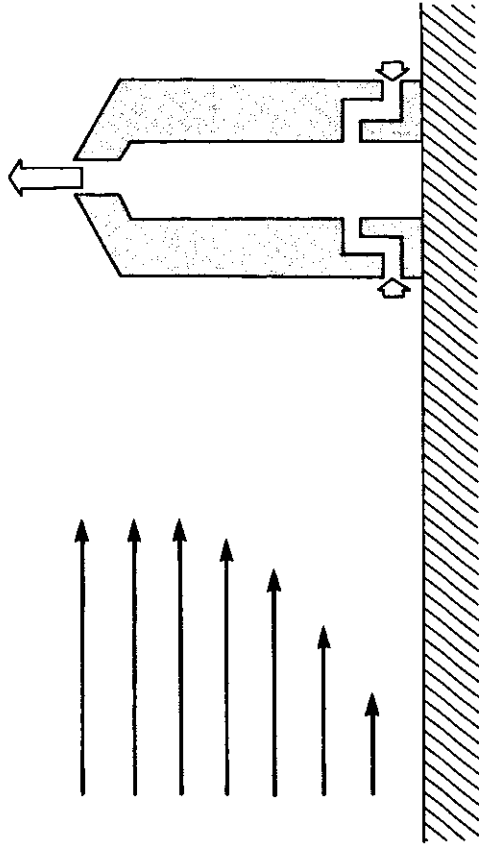


Figure 4.12 Diagrammatic view of a model sponge in a flow where a benthic boundary layer is present (Vogel and Bretz 1972).

#### Combined passive-active suspension feeders

Unlike in facultatively active suspension feeding, in which ambient velocity conditions provide the environmental switch to signal change from, or to, passive feeding, in combined passive-active suspension feeding the passive and active mechanisms appear to continue simultaneously.

#### Sponges

Model studies were undertaken by Vogel and Bretz (1972) in sponges, which have many small incurrent openings through the body wall. These openings connect to the spongocoel and an excurrent opening or osculum which opens dorsally in the animal so that it is high in the benthic boundary layer (Fig. 4.12). Besides an active flagellar pumping, passive flow in the sponge is induced by the Bernoulli effect resulting from the velocity and consequent pressure differences at the incurrent and excurrent openings caused by their different positions within the benthic boundary layer. Experiments with live erect sponges *Halichondria bowerbanki* obtained from the Massachusetts coast, were made at ambient flows from 0 to  $10\text{ cm}\cdot\text{s}^{-1}$  (Vogel 1974). Flow measurements at 4 mm into the osculum and 3 cm in front of the sponge were

made to record the osculum and ambient velocities, respectively. By immersing live sponges in freshwater, it was possible to inhibit choanocyte pumping. At zero velocity, live *Halichondria* of 3.1 cm height  $\times$  1.2 cm diameter produced an internal flow measured at the osculum of  $2.5\text{ cm}\cdot\text{s}^{-1}$ . As ambient flows were increased, both normal live and choanocyte-inhibited live *Halichondria* increased internal flows at the same rate proportional to ambient velocity. At ambient flows  $>6\text{ cm}\cdot\text{s}^{-1}$ , most of the total flow through the spongocoel was due to passive flow induction. Vogel (1974) thought that active pumping in *Halichondria* was unaffected by ambient flow and merely added on to the passive flow, which was directly related to the Bernoulli effect and ambient velocities. Further results using similar methods (Vogel 1977), but on eight species of live sponges obtained from Bermuda, showed similar results. In this case, the velocity measurements were made in the field at depths of 1–2.5 m, without removing the sponges. The osculum flow rates (when ambient flow = 0) obtained were much higher than obtained in the lab studies with *Halichondria*. For example, in *Verogia fistularis* and *Haliclona viridis*, the osculum flow rate was  $21\text{ cm}\cdot\text{s}^{-1}$ , whereas in *Ircinia fasciculata* it was  $11\text{ cm}\cdot\text{s}^{-1}$ . These results may have differed from the laboratory ones because of difficulties in handling the sponge and in simulating suitable environmental conditions.

Riisgård et al. (1993) examined the effects of temperature on filtration rates in the sponges *Halichondria panicea* and *Haliclona urceolus* by using a direct and an indirect method. The sponge pump characteristics were also estimated by a model and methods previously employed (Famme, Kristensen, Larsen, Møhlenberg, and Riisgård 1986a). The maximal operating point of the pump was  $0.673\text{ mm H}_2\text{O}$ . The pump work was less than 1% of the respiratory output, suggesting a very low energy cost for filtration in sponges. Because of this low cost, Riisgård et al. (1993) considered it unlikely that passive increments to flow as postulated by Vogel and Bretz (1972) would be relatively important.

Vogel (1978) has postulated that a now extinct fossil group present in the Cambrian period – the Archaeocyanthids – may have been purely passive feeders relying on strong local currents to supply seawater for passive suspension feeding in the manner described for modern sponges.

#### Lampshells

LaBarbera (1977) proposed that active suspension feeders such as lampshells or brachiopods may use ambient flows to “augment or even



supplant their active pump," as has been suggested for sponges. Model studies showed that induction of water movement through the dead valves of *Terebratulina unquicula*, *Terebratalia transversa*, and *Laqueus californianus* did passively occur at ambient flows of  $2\text{--}4\text{ cm}\cdot\text{s}^{-1}$ . It is also known that brachiopods may actively pump at zero flows. However, as pointed out by LaBarbera (1977), there is no evidence available to show that the filtration rate increases as ambient velocities are increased.

The bilateral symmetry of brachiopods (Chap. 6) with two incurrent openings  $180^\circ$  apart allows them to utilize oscillating flows if the anterior-posterior axis of the valves is aligned parallel to the current direction. There is also evidence that some lampshells can behaviorally reorient to flow direction by means of pedicel musculature (see Chap. 6). LaBarbera (1977) proposed that passive flow augmentation through the brachiopod lophophore resulted in increased feeding rates and/or in increased availability of dissolved oxygen and removal of wastes. Vogel and Bretz (1972) and LaBarbera (1977) suggested that their *ambient velocity passive enhancement theory* could apply to other species, e.g. scallops. An independently derived theory, the *inhalant/exhalant pressure field theory*, was proposed by Wildish et al. (1987) to explain behavioral orientation to flow direction by scallops, which might also apply to brachiopods. Certainly, in future studies, both theories should be considered in designing experiments and testing specific hypotheses. According to the inhalant/exhalant pressure field theory applied to brachiopods, the lampshells would be considered as active suspension feeders, and the low exhalant flows measured by LaBarbera (1981) in still water indicate that the ciliary pump is much less effective than in bivalves. Exhalant velocities of *Terebratulina unquicula*, *Terebratalia transversa*, and *Laqueus californianus* ranged from  $0.2$  to  $1.2\text{ cm}\cdot\text{s}^{-1}$  and flow within the trophic fluid transport system was laminar. Referring to Fig. 6.5, the following orientation mechanisms are possible:

- A. When the exhalant flow directly opposes the ambient flow direction and when the ambient flow pressure exceeds the ciliary pump pressure either extra work must be done by the pump to overcome it or the valves partially close (as in scallops) to reduce the differential.
- B. With the exhalant downstream with respect to ambient flow direction and as the flow builds up so that the external pressure tends to force flow across the ciliary pump at a rate faster than that maintained by the cilia alone, then either the valves partially close to reduce it or filtration retention efficiency declines.
- C. In this orientation the valves present the maximum amount of drag opposing the flow.

D. The valves present minimal drag to the flow and, as in C, the inhalant and exhalant can be oriented optimally for either uni- or bidirectional flows. These represent suggestions (see Chap. 6, the section, Sessile epifauna, for an alternative view) and should be worked up further as null and alternative hypotheses for experimental testing.

### Deposit-suspension feeders

Some species of benthic infauna have the ability to switch between deposit and suspension feeding. Ambient flow velocity is the environmental cue thought to trigger the change of behavior. Thus at low velocities, these animals feed on particles present on the sedimentary surface, while at higher velocities, they switch to suspension feeding.

### Spionids

The tube-building spionid polychaetes are characteristically able to switch from deposit to suspension feeding. The switch seems to encompass a range of velocities from  $<2$  to  $5\text{ cm}\cdot\text{s}^{-1}$  when a worm population is sampled (Taghon, Nowell, and Jumars 1980; Taghon and Greene 1992). For *Pseudopolydora kempii japonica* and *Boccardia pugettensis*, increasing velocity causes an asymptotic rise in the number of worms which are suspension feeding. Thus 50% of worms are suspension feeding at  $\sim 1.7$  for the former species and  $4.5\text{ cm}\cdot\text{s}^{-1}$  for the latter species (measured  $0.3\text{ cm}$  above the bottom). Partly because a wide enough range of velocities was not used in the flume experiments of Taghon and Greene (1992), their results do not provide sufficient detail to determine whether a unimodal feeding response to velocity exists.

Miller, Bock, and Turner (1992) have extended observations to *Spio setosa* in a flume oscillating flow. The sinusoidal flows produced in the working section were characterized by the maximum free-stream velocity reached in each excursion. The percentage of worms suspension feeding (that is palp coiling) in still water is zero, rising to  $\sim 90\%$  at  $6.5\text{ cm}\cdot\text{s}^{-1}$  and thereafter dropping off (maximum velocity tested of  $\sim 10\text{ cm}\cdot\text{s}^{-1}$ ). The feeding response shown by populations of *S. setosa* appears to be unimodal with respect to maximum oscillation velocity, but the absence of higher velocity tests prevents drawing conclusions. In another experiment, the percentage of *Spio* showing palp coiling was observed at five maximum free stream velocities ( $6.8\text{--}30\text{ cm}\cdot\text{s}^{-1}$ ). In this

experiment, the flows were increased every 10 min and the palp coiling of 19 individual *Spio* observed. Again, a unimodal response is suggested with a lower percentage of worms coiling at 6.8 and the two highest velocities tested: 24 and 30 cm · s<sup>-1</sup>. To establish firmly the oscillating velocity threshold from deposit to suspension feeding and the worms' responses to higher flows, a wider range of velocities should be tested. When one, or both, tentacles of spionids are lost to sublethal predation, Lindsay and Woodin (1995) have shown experimentally that such worms can still deposit feed directly from sediment surfaces.

### Bivalves

Some species of the bivalve molluscan family Tellinacea, although mainly sediment interface deposit feeders, may, under some environmental conditions, subsurface deposit feed or suspension feed. Levinton (1991) suggests the following classification for tellinaceans:

- *Swash rider suspension feeders*, intertidal species such as *Donax* which migrate on sandy beaches to maintain moist and relatively unexposed sediments
- *Sandy bottom suspension feeders*, intertidal and nearshore subtidal species with relatively large ctenidia specialized for suspension feeding
- *Sandy-mud bottom switching feeders*, intertidal and nearshore subtidal sandy-mud species such as *Macoma* and *Scrobicularia*, some species of which can switch between deposit and suspension feeding.

Of the latter group, Hughes (1969) studied the suspension feeding of *Scrobicularia plana* by using the direct method of measuring pumping rate in apparatus designed by Drinnan (1964). Filtration rates were estimated independently by indirect measurement of seston depletion in 100-ml dishes containing one *Scrobicularia*. In these studies, no attempt was made to investigate the effect of flow and the environmental factors causing deposit to change to suspension feeding. In the study by Levinton (1991), the feeding behavior of three Pacific species of *Macoma* from the San Juan Archipelago – *M. nasuta*, *M. secta*, and *M. unguinata* – was studied with respect to water flow and sediment transport. These studies were done in an annular flume and showed that deposit feeding was inhibited by increasing velocities (only three free-stream velocities, ~10, ~25, and 33–36 cm · s<sup>-1</sup> were tested). This involved a decrease in deposit feeding radius from the siphon hole because the inhalant was withdrawn as velocity was increased. Levinton (1991) observed a loss of control of the inhalant siphon (quivering/flopping over) at a free-stream velocity between 10.5 and 12.0 cm · s<sup>-1</sup>, suggesting that drag on the siphon is sufficient to overcome its normal functioning.

### Summary

The following criteria can be used for assessing the completeness, or lack thereof, of our knowledge of the physiological mechanisms of filtration in benthic suspension feeders:

- That velocity has been accurately measured near the appropriate filter or inhalant opening of the trophic fluid transport system over a sufficiently wide range of ambient velocities and directions
- That the volumetric flow which enters the filter or inhalant is known
- That the retention efficiency of the filter is known.

Most suspension feeders have not been studied over a sufficiently wide range of velocities to determine effects on filtration, feeding, or growth and, consequently, conclusions about the general applicability of the unimodal function model may be premature. Some hypotheses concerning filtration of benthic macrofauna which require further experimental testing are summarized in Table 4.5.

Of the few species that have been studied adequately with respect to velocity, inclusive of passive (the sea pen *Ptilosarcus quernei*, gorgonians of the genus *Pseudopterogorgia*, the crinoids *Oligometra serripinnia* and *Antedon mediterranea*) and active suspension feeders (scallops, *Argopecten irradians*, *Placopecten magellanicus*, plus a few species of Bryozoa), all appear to fit the unimodal model. The cause-effect mechanisms at each response stage of the model are poorly understood and require further experimental investigations. These studies need access to controlled flows in flumes (see Chap. 2) with well-defined boundary layer flows which simulate field flows as closely as possible. In general, in stage a transport limitation of filtration can be expected, in stage b this effect is absent and ambient velocity has no influence on filtration, whereas in stage c filtration inhibition related to velocity can be expected. In active suspension feeders, the filtration responses may also be interactively linked to seston concentration and quality, making them complex and often difficult to interpret.

As far as we are aware, there have been no studies which investigate the effect of a wide range of flume-controlled ambient velocities on filtration or feeding of sieving suspension feeders (Table 4.5, number 1), and a unimodal response hypothesis probably applies to most groups considered. The exact nature of the compound passive-active suspension feeding group is still in doubt because, in order to establish firmly that passive supply of seawater to the organism is of physiological consequence, it must be demonstrated in live animals that enhanced filtration associated with enhanced ambient velocity results in increased growth

Table 4.5. Some hypotheses related to filtration of benthic suspension feeders which need further experimental testing.

No.	H <sub>0</sub> /H <sub>1</sub>	Description	Reference
1	H <sub>0</sub>	The filtration rate of sieving suspension feeders is unaffected by velocity	Vogel (1981) LaBarbera (1984)
	H <sub>1</sub>	The filtration rate of sieving suspension feeders is a unimodal response of velocity	This analysis
2	H <sub>0</sub>	Combined passive-active pumping does not enhance filtration/growth rates	
	H <sub>1</sub>	Combined passive-active pumping enhances filtration/growth in some sponges and brachiopods	
3	H <sub>0</sub>	The energetic cost of ciliary pumping in bivalves is directly proportional to pump power output	Winter (1978) Jørgensen (1990)
	H <sub>1</sub>	The energetic cost of ciliary pumping in bivalves is small and does not vary with pump power output	
4	H <sub>0</sub>	Filtration or growth rate in brachiopods and scallops is not affected by their orientation to flow	Vogel and Bretz (1972), LaBarbera (1977) Wildish et al. (1987), Wildish and Saulnier (1993)
	H <sub>1</sub>	Filtration or growth in brachiopods and scallops is controlled by their orientation with respect to flow direction	

(Table 4.5, number 2). The critical experiments required to establish this have not yet been carried out. The question of the energetic costs associated with ciliary pumping in bivalves (number 3, Table 4.5) is peripheral to the arguments presented in this chapter, although we return to this subject in relation to the evolution of the ciliary pump in Chapter 9 (the section, Ultimate questions).

Another interesting unanswered question concerns the ambient velocity passive enhancement and inhalant/exhalant pressure field theories and their possible applicability to both brachiopods and scallops. As proposed, the hypothesis (Table 4.5, number 4) does not appear to be incisive in its ability to provide support for one or the other of the two

competing theories. Published data of seston uptake in scallops (Wildish et al. 1987) do support H<sub>1</sub> in hypothesis number 4 (Table 4.5). Utilizing the principle of multiple hypotheses – if the unimodal response for scallops outlined earlier is valid – the most likely applicability of the passive enhancement theory is in the “a part” of the unimodal response, i.e. from 0 to ~3 cm · s<sup>-1</sup>. Thus the goal of an experimental test would be to determine whether small increases in flow serve only to remove localized seston depletion due to dilution with pre-filtered seawater around the animal, or whether the flow provides a direct subsidy to the scallop’s active pumping, as is required by the passive enhancement theory.

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