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# BENTHIC BOUNDARY LAYER EFFECTS

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## Introduction

The benthic boundary layer (BBL) is a discrete layer of flowing sea water above a benthic substrate, delimited vertically by its contact with free stream flow. The degree of turbulence within the BBL and boundary shear forces exerted on the substrate are determined by the free stream velocity and the roughness characteristics at the substrate interface. Roughness elements may either be of geological origin, e.g. sand ripples of soft sediments, or of biological origin, e.g. tubes constructed by macrofauna that extend into the BBL.

Typical structure of a smooth BBL consists of a bed layer, inclusive of a viscous sublayer (laminar sublayer) closest to the substrate interface. Here, the flow is laminar and only a few millimeters thick, dictated by the free stream velocity. Next is the logarithmic layer, where mean velocity varies as the logarithm of the height above the substrate interface, and where the flow is often turbulent. In the outer layer of the BBL, turbulence decreases with distance from the substrate interface and is bounded by the free stream flow, situated immediately above it. In coastal and estuarine habitats, where many of the benthic animals discussed here live, BBL depth may vary from 10 cm to 5 m. In some conditions the BBL of coastal waters may extend throughout the water column. Such shallow environments are much influenced by tidal and wind forcing; the latter inducing oscillatory water movements in the bed layer.

A useful measure of the flow conditions for biologists is Reynold's number. It expresses the relative proportions of inertial and viscous forces within a flow as a dimensionless number. It is determined by measuring a characteristic length of a solid in flow measured in the same direction as the flow, multiplied by the velocity and divided by the kinematic viscosity of sea water. Other hydrodynamic measures useful for this presentation are lift and drag coefficients. A flat body resting on the substrate and in a flow field will experience lift due to Bernoulli's principle. This occurs because the velocity is locally higher on the upper than on the lower surface, due to the already mentioned effect of height on velocity within the BBL. The resultant pressure differences – the pressure is higher where flows are low – cause a lift force to be generated. The lift is resisted by the negative buoyancy of the body but, if exceeded as velocity increases, it is 'lifted' and carried downstream. The drag of a body in a flow field depends on the frontal area presented to the flow and the square of the velocity that it experiences.

Some examples of the wide range of taxa that can be found within the BBL are presented here. Concentrating on the epifauna and suprabenthos of the BBL macrofauna, a brief survey is made of their adaptations to the BBL environment; including examples from rocky shore, wave-exposed locations to soft sediment substrates where weak currents dominate.

## Organisms of the Benthic Boundary Layer

Many of the organisms living within the BBL are commonly found elsewhere in the sea. They include microbiota, such as viral, bacterial, and planktonic life forms, and microalgae limited by light penetration to the shallow fringes of oceans. Of two distinctive life forms of macrofauna, the first one, epifauna, is usually sampled by grab or corer, inclusive of attached, free-living, and tube-living life forms. Epifauna characteristically protrude into the BBL where they feed. The second life form group is composed of near-bottom swimmers of the BBL macrofauna. They are sampled by drawing a plankton sampler through the BBL and are defined as those animals that are retained within a 0.5 mm mesh plankton net. Typical catches consist of zooplankters, common throughout the whole water column, eggs and larvae, from some of the epifauna and suprabenthos (also referred to as hyperbenthos). The suprabenthos are bottom-dependent animals that perform regular daily or seasonal vertical migrations above the bottom. The only life forms that are unique to the BBL are epifauna and suprabenthic animals.

### Epifauna

Some examples of the major taxa of epifauna are shown in **Table 1**. Attached epifauna comprise a wide range of taxa from hydroids to cirripedes. Included among free-living epifauna are some echinoderms, decapods, and bivalves. Tube-living epifauna consist of species from a limited number of polychaete, amphipod, and tanaid families. Five types of tube builders can be distinguished on the basis of tube height (H) to tube diameter (D) ratio. The greatest difference between H/D ratios of the life forms shown in **Table 1** is between the truncated cone and spar buoy life forms. The former are short and fat ($H/D < 1$) and the latter are long and thin ($H/D > 19$). The name of the latter derives from the observation that the tube is articulated at its base so that it follows any change in flow

**Table 1** Life forms of epifauna

| *Life form* | *Examples* |
|---|---|
| Attached epifauna | Cnidaria: Hydrozoa – hydroids<br>Cnidaria: Anthozoa – gorgonian corals<br>Cnidaria: Antipatharia – octocorals<br>Bryozoa – bryozoans<br>Brachiopoda – lampshells<br>Echinodermata: Crinoidea – stalkless crinoids<br>Porifera – sponges<br>Ascidiacea – sea squirts<br>Cirripedia – barnacles |
| Free-living epifauna | Some Echinodermata, e.g. feather stars (Crinoidea), sand dollars (Echinoidea)<br>Some decapod Crustacea, e.g. sand crabs (Hippidae), porcelain crabs (Porcellanidae)<br>Some Bivalvia, e.g. scallops (Pectinidae), mussels (Mytilidae) |
| Tube-living epifauna | |
| Tube normal to flow | Polychaeta, e.g. *Lanice conchilega, Streblospio benedicti, Eudistylia vancouveri*; Amphipoda, e.g. *Ampelisca abdita, A. vadorum, Haploops fundiensis* |
| Tube opposed to flow | Amphipoda, e.g. *Ampithoe valida;* Tanaidacea, e.g. *Tanais covolinni* |
| Truncated cone tube | Polychaeta, e.g. *Spio setosa, Fabricia limnicola, Mesochaetopterus sagittarius, Phyllochaetopterus verrilli* |
| Spar buoy tube | Polychaeta, e.g. *Potamilla neglecta* |
| Complex tube | Polychaeta, e.g. *Diopatra cuprea* |

**Table 2** Densities and relative importance of suprabenthos from the Bay of Fundy

| *Taxon* | *Lower net*[a] | | *Upper net*[b] | |
|---|---|---|---|---|
| | % | *Density Number per 100 $m^{-3}$ filtered* | % | *Density Number per 100 $m^{-3}$ filtered* |
| Amphipoda, Gammaridea | 44 | 420 | 23 | 30 |
| Cumacea | 29 | 279 | 11 | 14 |
| Amphipoda, Caprelloidea | 11 | 102 | 1 | 1 |
| Mysidacea | 8 | 74 | 11 | 15 |
| Euphausiacea | 5 | 50 | 52 | 66 |
| Isopoda | 2 | 15 | < 1 | < 1 |
| Tanaidacea | 1 | 11 | < 1 | < 1 |
| Decapoda, Caridea | < 1 | 1 | 1 | 1 |

[a] 33–73 cm from sediment.
[b] 109–149 cm from sediment.

direction, like a spar buoy, and its sabellid crown filtration surfaces are thus always downstream in the flow.

### Suprabenthos

In contrast to epibenthic organisms, suprabenthic animals are represented by a narrower range of taxa, being limited to the Crustacea (**Table 2**). For example, in the Bay of Fundy, gammarid amphipods and euphausids are the dominant members representing the suprabenthos.

## BBL Flow Adaptations

Over time, the word ‘adaptation’ has come to have conflicting meanings. These include the biological process of adjustment to environmental stresses that occur within an individual’s lifetime, as well as the results of evolutionary changes that persist over more than one lifetime and produce individuals of superior survivability or reproductive capacity. To avoid confusion, the latter meaning of evolutionary adaptation is used throughout this article.

Evolutionary adaptation refers to the phenotypic characteristics of an organism, which have arisen by a process of Neo-Darwinian evolution. The adaptations of concern here are morphological, physiological, behavioral, or reproductive, in response to the physical processes characteristic of the BBL. Included in the definition are any extended phenotypic adaptations, e.g. worm tubes, that occur outside the individual body and persist as characteristic structures over many generations. An adaptation may have arisen in response to one environmental feature, and subsequently been modified for another purpose. A possible example is jet propulsive predator avoidance in scallops, modified as scallop swimming to seek a better feeding area. In the latter example, such evolutionary change from predator avoidance to free swimming may be referred to as an exaptation. Since the adaptations and exaptations occurred in the past, it is only possible to use deductive methods and circumstantial evidence in their study, thus limiting confidence in the explanations proposed.

## Life History Adaptations

Many epifaunal organisms have a complex life cycle in which the egg and larvae are the chief dispersal stages. Larval life is terminated by metamorphosis at the time of recruitment to a benthic substrate. Juvenile and adult are the main growth and gamete-producing phases of the life cycle (**Figure 1**). Because of the obviously different strategies of larval and juvenile/adult life, and therefore adaptations associated with them, they are dealt with separately.

An important function of larval life is to ensure that a sedentary adult, such as a cirripede barnacle, becomes spatially distributed to a suitable, unoccupied habitat where growth and reproduction can occur. Although larval dispersal is the major mechanism among epibenthic macrofauna, additional means of dispersal are also available during juvenile and adult life.

A characteristic feature of marine benthic larvae is their small size, in general $< 1000\,\mu m$ at all stages of larval life. Among a wide range of marine bivalve species the pediveliger larva (**Figure 1**) ranges in size from 160 to 350 μm. The pediveliger larva is the stage capable of finding and contacting a suitable substrate, and this property is referred to as competency. During larval life, small size is presumably an adaptation for passive dispersal by often

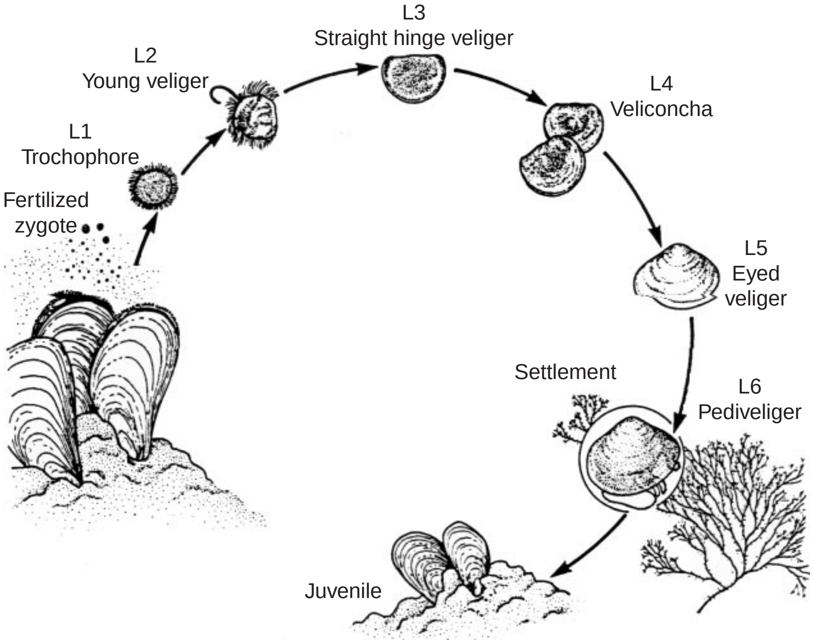

**Figure 1** Life cycle of the blue mussel, *Mytilus edulis*.

large-scale physical oceanographic forces. Concomitant features resulting from small size are the feasibility of a large number of larvae per unit of reproductive effort and limitation of swimming locomotion to ciliary means.

The distance that a dispersing larva can travel will depend largely on the time that it spends in the plankton. This can vary from a few hours for the nonfeeding, lecithotrophic larva to up to 2 years for the planktotrophic larva. The latter suspension feeds at certain stages during its life cycle and consequently sustains its stay in the plankton. The two types of larvae shown in **Table 3** appear to use contrasting strategies in determining where to settle, metamorphose, and start growth as an attached, epifaunal organism. Larvae swim at speeds characteristic of ciliary beating and low Reynold's numbers, which is in the range of $0.02–0.50\,\mathrm{cm\,s^{-1}}$. Such low speeds are sufficient for competent larvae to swim through the viscous sublayer of the BBL, so that they can contact the benthic surface guided by sensory cues, inclusive of hydrodynamics, chemicals, and/or surface roughness.

Lecithotrophic larvae (**Table 3**) spend a short time in the plankton and consequently are not dispersed far from the parental population. By contrast, planktotrophic larvae have a longer larval period and consequently can undertake longer dispersal pathways. This allows the competent larval stage to reach unoccupied habitats distant from the parental population.

Some larvae must settle on 'protruding bodies,' such as attached macroalgae, some branching corals, or man-made structures. This provides

**Table 3** Comparison of larval adaptive strategies among marine epifauna

| *Characteristic* | *Lecithotrophic larva* | *Planktotrophic larva* |
|---|---|---|
| Larval type | Larger, nonfeeding, food store | Smaller, feeding in plankton, no food store |
| Larval numbers | Few | Many |
| Larval period | Short | Long |
| Larval dispersal distance (maximum) | Short | Long |
| Inbreeding potential | High | Low |
| Biogeographic dispersal rate | Slow | Fast |
| Biogeographic range | Endemic | Pandemic (cosmopolitan) |
| Geological history of taxa | Short | Long |
| Speciation rate | High | Low |

a challenge because of the characteristic flow around the protruding structures. At higher flows, the stream lines compress the laminar sublayer on the upstream and lateral surfaces, whereas wakes occur on the downstream surface. Some coral reef larvae have developed specialized adhesive mucous threads up to 100 larval body lengths in size, which aid the competent larva to contact and firmly attach to the protruding body. In the process, coral larvae overcome the shear forces that are locally high, as well as the accelerative reaction forces characteristic of flow around protruding bodies.

## Suspension-feeding Adaptations

The function of juvenile life is to transform the recruited settlement stage to a large adult capable of producing gametes. To do this requires rapid growth, which must be fueled by a dilute diet of organic (inclusive of bacteria, phytoplankters, zooplankters, and organic carbon) and sedimentary particles in sea water, collectively called seston. The function of removal of the sestonic particles from sea water is achieved by suspension feeders in a variety of ways (**Table 4**). The characterization of **Table 4** depends on whether filtration is driven by ambient flow, as in passive forms, or by some form of energy supplied by the suspension feeder, as in active forms.

Passive suspension feeders must deflect the stream lines close enough to their filtration surfaces to enable them to capture sestonic particles by direct interception. Typical adaptations of passive forms are thus expansion of filtration surfaces and channeling flows, e.g. by polyps, tentacles, and pinnules.

By contrast, active suspension feeders provide a pump (ciliary, flagellar, muscular) or collecting device that requires muscular power to sweep and capture the seston. The operating characteristics of a representative range of pump types have been described, whereas the knowledge available regarding the precise filtration mechanism is incomplete. For taxa with mucous filter nets (see **Table 4**), the net is periodically secreted and then ingested, inclusive of the seston trapped by sieving. For taxa with a ciliary pump, such as many bivalves, the precise filtration mechanism is still unclear.

In deposit/suspension feeders, it is ambient flow, and/or seston concentration, that is the trigger to change the feeding mode. Thus, at flow velocities $< 2\text{–}5\,\mathrm{cm\,s^{-1}}$, spionid, tube-building polychaetes deposit feed by touching the elongated paired palps on the sediment surface. At faster flows, the palps become helically coiled in the downstream flow direction to optimize suspension feeding. In tellinid bivalves such as *Macoma balthica*, the extensible inhalant siphon is used to deposit or suspension feed in response to changing flow conditions. Thus, a combination of morphological/physiological and innate behavioral responses to flow changes allows these animals to feed in a wider range of flow conditions.

For barnacles of the facultative passive/active group, the cirri act passively at higher flows, but below a critical velocity of a few centimeters per second, begin active rhythmic sweeping so that the concave surface faces away in lower flows. Concave surfaces of cirri are optimum for passive suspension feeding in strong flows by direct interception and that is why the cirrus is rotated to face the oscillating flow by *Semibalanus balanoides* during passive feeding. Musculature and nervous control enables the barnacle to respond rapidly to waves by switching the cirrus to face the flow in flow oscillating conditions of wave surge and swash.

**Table 4** Classification of the filtration mechanisms of suspension-feeding epifauna

| *Classification* | *Mechanisms* | | *Examples* |
|---|---|---|---|
| | *Pump* | *Filtration* | |
| Passive | Absent | Direct interception | Sea pens, hydroids, sea whips, black coral, feather star, brittle star, sea cucumber |
| Active | Ciliary | ? | Many bivalves |
| | Ciliary | ? | Bryozoa |
| | Ciliary | Mucus net sieving | Sea squirts |
| Deposit/suspension feeder | Ciliary | ? | Spionid polychaete worms |
| | Ciliary | ? | Tellinid bivalves |
| Facultative passive/active | Cirral sweeping | Direct interception | Barnacles |
| | Maxilliped setal sweeping | Direct interception | Porcelain crabs (decapod Crustacea) |

## Adaptations to Resist Shear Stress

Rocky shores are home to epifaunal organisms such as barnacles and mussels, and experience the most extreme oscillatory movements due to wave forces. Here, 2–4 m breaking waves translate into a peak velocity of 8 m s$^{-1}$, exerting considerable shear forces at the substrate interface. This results in drag, lift, and acceleration forces on the attached macrofauna. Such forces tend to dislodge sessile organisms and are resisted in a variety of different ways. Barnacles have developed adhesives that cement the animal firmly to the rock surface. In mussels, adhesion is achieved by byssus threads produced from the foot, which attach with secreted adhesive to nearby solid surfaces. If mussels are present as densely packed reefs, the drag and lift forces are shared by the group. A similar case occurs among South African sublittoral holothurians, but here two species occur together as a mixed group. One species has degenerate tube feet and insinuates its body beneath the other, thereby gaining a surrogate means of attachment. By this arrangement, the holothurian lacking tube feet is able to extend its range from a protected to a more exposed location.

Structural adaptations linked to shear stresses include the development of an elastic body that allows form changes proportional to velocity, resulting in less drag, reduced size where flows are energetic and body strengthening by secretion of skeletal materials such as the spicules in sponges or cnidarians.

Behavioral responses to resist drag and lift forces are also common among free-living epifauna. For example, many scallop species can recess into the sediment. They do this by jetting water at the sandy sediment until a pit is made and then they settle into it. Recessed scallops experience reduced drag forces because most of the body is situated beneath the BBL, although lift forces (resisted by the buoyant weight of the animal) are still present if the upper valve is within the logarithmic flow layer. Experimental observations have suggested that larger scallops, above a critical size threshold, are at risk from drag forces during valve opening, which is required for feeding, due to an increase of the frontal area. These results are consistent with field observations that show that it is the older scallops that are recessed.

Typical stream lines around an isolated, epifaunal tube normal to the flow are shown in **Figure 2**. The conical tube of the worm *Lanice conchilega* causes resuspension of the lighter organic particles in the wake of the tube and this material becomes available for downstream capture by the tentacles of the worm. Another worm studied in detail is *Spio setosa*, which makes a truncated cone tube. The 4–6 cm high tubes have an equally wide diameter and are functional in ensuring that the worm is able to suspension feed on good quality seston. This is because at 4–6 cm in height in the BBL there is a significantly greater proportion of nutritious organic particles than closer to the sediment surface where the seston carries more heavier, denser, and non-nutritious inorganic sedimentary particles.

The fact that tube-living worms rely on the trophic advantage provided by their tubes is evidenced by the fact that they are rapidly rebuilt if they become broken or eroded during storms. Another worm, *Spiochaetopterus oculatus*, is able to adjust the height of the tube so that at low flows, tube building occurs whilst tube cutting is initiated as energetic oscillating flows commence. Tube building in this worm is achieved by the fourth paropodia selecting and gluing suitable inorganic sedimentary

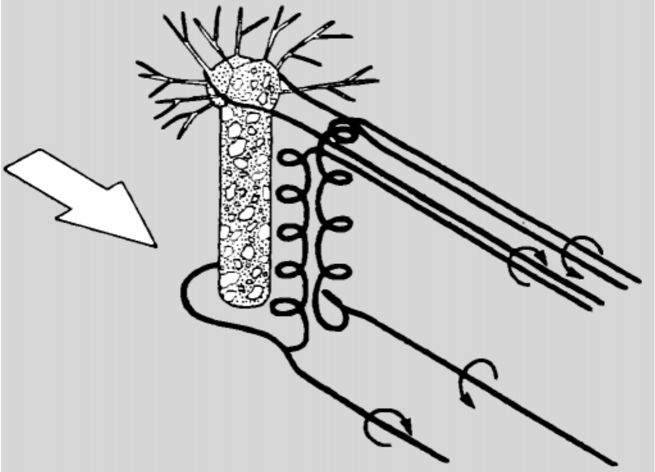

**Figure 2** Flow stream lines around the polychaete tube of *Lanice conchilega*.

**Table 5** Density and biomass of epifauna that aggregate

| *Taxa* | *Common name* | *Density (number m$^2$)* | | *Biomass (g dry m$^2$)* | |
|---|---|---|---|---|---|
| | | *Mean* | *Maximum* | *Mean* | *Maximum* |
| Molluscs | | | | | |
| *Modiolus modiolus* | horse mussel | – | 510 | 281 | 3038 |
| *Mesodesma* (1) | Turton's | 488 | 1550 | 6485 | 21 030 |
| *deuratum* (2) | wedge clam | 5890 | 12 010 | 939 | 4697 |
| *Crassostrea virginica* | American oyster | – | 4077 | – | 214 |
| *Mytilus edulis* | blue mussel | | | | |
| Rhode Is., USA | | 2139 | – | 10 962 | – |
| Baltic Sea | | 36 000 | 158 000 | 101 | – |
| *Perna perna* | green-lipped mussel | – | – | 826 | 1285 |
| Polychaetes | | | | | |
| *Owenia fusiformis* | a bamboo worm | 500 | 15 000 | – | – |
| *Lanice conchilega* | a fan worm | – | 20 200 | – | 1094 |
| *Spio setosa* | a mud worm | 408 | 2002 | 61 | 109 |
| Amphipod Crustacea | | | | | |
| *Haploops fundiensis* | ampelscid | 376 | 923 | 0.35–0.53 | 0.96 |
| *Ampelisca abdita* | ampelscid | 1360 | 73 000 | – | – |
| *Ampelisca vadorum* | ampelscid | 1307 | 1885 | – | – |

particles in place, and cutting by the setae on this segment.

There is evidence that if densely packed aggregations of tube-living epifauna exceed a critical density, they will interact with flow to produce 'skimming flow'. This implies that the flow is diverted above the tubes, which act as roughness elements. Skimming flow has important consequences for seston supply and particle settlement within the tube field, which needs further clarification.

## Aggregation as an Adaptation

Possible reasons why epifaunal organisms may occur in aggregated groups include: to exploit an optimal niche for suspension feeding, to provide protection from extreme shear forces, to provide better opportunities for successful reproduction, and to provide better protection from predators. Examples could be quoted which appear to support each reason why some epifauna aggregate, but the work is considered to be at too early a stage in its development to give a comprehensive account.

The question as to how epifauna achieve their characteristically aggregated distribution may be solved either by larvae or adults. Thus, larvae may settle near adults of the same species, guided by pheromones from the adults or by the same chemical/physical cues from the habitat that originally attracted the earlier colonizers. Many juvenile and adult epifauna are attached, and hence do not usually take part in aggregation behavior, although there are exceptions, e.g. juvenile blue mussels that may move to a secondary site after first settling on red seaweeds. Free-living epifauna, such as scallops, can swim to occupy many different niches following initial settlement as the competent larva.

**Table 5** shows examples of the population densities and biomasses of animals that aggregate as obtained by conventional grab sampling methods. The high biomasses evident in **Table 5** signify that the bivalve reefs, for example, are major producers in discrete local areas, sustained by enriched seston levels and/or optimal hydrodynamic conditions.

## Conclusions

This brief survey of the macrofauna most characteristic of the BBL, that is the epifauna and suprabenthos, leads to the conclusion that BBL physical processes have had far-reaching effects on their evolution. As the study of this subject is still so young, it is not possible to give a full account. Thus, almost nothing is known about the general biology of the suprabenthos. For example, it is not understood where they fit in the marine food web and their relative importance in it, let alone the adaptations which allow them to live in this niche. Many Crustacea, especially suprabenthic organisms, do not have a larval stage and hatch as a juvenile directly from the brooded egg.

For the larvae of epifauna, the most important adaptations appear to be associated with their small size, which permits sustained periods in the plankton and passive dispersal. The latter is made possible by adaptations to suspension feed during an extended period in the plankton. It is likely that most aggregated groups of epifaunal organisms are formed during larval settlement, but the precise behavioral mechanisms also need further study.

Benthic boundary layer adaptations of juvenile and adult life fall into the following groups:

- food collection from seston in sea water;
- resistance to the shear stresses that tend to dislodge macrofauna; and
- the building of epifaunal tubes.

Adaptations for collecting seston may have arisen in a local population to allow them to colonize or adapt to changing flow environments. Estimates of the physiological cost of operating the bivalve ciliary pump to suspension feed have been made and suggest that they are small – less than 2% of the overall energy budget. Nevertheless, the ontogenetic cost of constructing and maintaining the inline ciliary pump in the trophic fluid transport system of a bivalve must be high. To date, there do not appear to be any studies that have investigated this latter possibility.

Shear forces that try to dislodge epifauna are resisted by adaptations that include adhesives, skeletal strengthening, developing an elastic body deformation capability, and behavioral adaptations. The latter often involve changing the orientation of the body to minimize drag and lift forces.

For the few species of tube builders studied, the adaptations found seem linked to optimizing seston feeding where the quality is best. Tube building may be regarded as an extended phenotypic expression from genes that control the complex innate behavior involved in cementing sedimentary particles together. The type of sedimentary particle selected, as well as the shape and size of the tube constructed, can usually be used to identify the organism that created them.

## See also

**Turbulence in the Benthic Boundary Layer.**

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# BENTHIC FORAMINIFERA

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## Introduction

Foraminifera are enormously successful organisms and a dominant deep-sea life form. These amoeboid protists are characterized by a netlike (granuloreticulate) system of pseudopodia and a life cycle that is often complex but typically involves an alternation of sexual and asexual generations. The most obvious characteristic of foraminifera is the presence of a shell or 'test' that largely encloses the cytoplasmic body and is composed of one or more chambers. In some groups, the test is constructed from foreign particles (e.g., mineral grains, sponge spicules, shells of other foraminifera) stuck together