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**LABORATORY EXPERIMENTS ON PUMPING AND FILTRA-
TION IN *MYTILUS EDULIS* L. USING SUSPENSIONS OF
COLLOIDAL GRAPHITE.**

Laboratory Experiments on Pumping and Filtration in *Mytilus edulis* L. using Suspensions of Colloidal Graphite.

by

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Abstract

Pumping and filtration of colloidal graphite and shell movements of *Mytilus edulis* from Carlingford Lough, Northern Ireland, were recorded in the laboratory.

Pumping and filtration rates fluctuated widely even in undisturbed animals.

Long term recordings demonstrated an inverse relationship between pumping rate and filtration efficiency.

The effects of light, tidal cycle, particle concentration, temperature and salinity on pumping rate have been examined.

Periods of light and dark did not affect pumping rate nor was there evidence for any intrinsic tidal rhythm in feeding. Pumping increased to a maximum at graphite concentrations of 20-25 mg/l. The rate prior to the addition of graphite influenced the response at certain particle concentrations.

Filtration was most efficient at 18.5°C and decreased above 22.5°. Pumping steadily increased to a maximum at 22.5°. Filtration of acclimated mussels was maximal at 25-34‰ whilst feeding ceased at the extreme salinities of 15 and 50‰.

Introduction

The gills and associated pallial organs of *Mytilus* permit the filtration, sorting and ingestion of particulate material. Each ctenidium is 'W' shaped in section and consists of two rows of elongated reflected filaments which form the ascending and descending limbs of the filament. Adjacent filaments are connected by ciliary junctions so that all the filaments are joined together to form gill plates each consisting of two lamellae formed from all the ascending and descending limbs respectively. In all, therefore, four pairs of lamellae lie within the mantle cavity. Lamellae are further united by cords of interlamellar tissue. Several ciliary tracts lie along each ctenidial filament. The frontal cilia on the outer side convey particles along its length, the latero-frontal cilia along each side form a sieve across the ostia or spaces between filaments whilst the lateral cilia lie between each filament and produce a current of water through the ostia. Abfrontal cilia along the inner side of the lamellae also have a pumping function.

Lateral and abfrontal cilia maintain a flow of water through the inhalent aperture between the unfused mantle edges, across the gill lamellae into the interlamellar spaces and thence into the suprabranchial chamber and exhalent opening. As water passes through the ostia the latero-frontal cilia remove particles from suspension and convey them to the frontal cilia. These in turn transport material to marginal grooves at the free edge of each lamella. Material transported along these grooves is further sorted by the ciliated labial palps and from there it passes via the oral grooves to the mouth.

The rate at which water passes through the gills is controlled by the degree of separation of the mantle edges, size of the ostia, beat frequency of the lateral and abfrontal cilia and the activity of the adductor muscles.

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The rate of flow in turn appears to affect the frequency of the latero-frontal ciliary beat and presumably therefore filtration rate (Dral, 1967). Whilst Davids (1964) thought that a high pumping rate may reduce the efficiency of particle retention he had insufficient evidence to reach any definite conclusion though Tammes and Dral (1955) found no relationship between pumping and filtration rates. Their methods, however, interfered with normal shell and mantle movements and thus pumping rates. Unfortunately many workers fail to distinguish between pumping and filtration and little information is available concerning the relationships between the two.

MacGinitie (1941) suggested that filtration is carried out by means of a mucous sheet which completely covers the gills during feeding. Whilst several other workers supported this theory, assuming that changes in filtration rates were caused by changes in the distribution of the sheet, Nelson (1960) criticised the theory on the grounds that the mucus would be drawn into the ostia and prevent the proper functioning of the lateral cilia. Owen (1964) suggested that the beating of the frontal and latero-frontal cilia would tend to disperse any mucus sheet over them. Verwey (1952) believed that the latero-frontal cilia might act as a sieve, sorting being carried out by the frontal cilia. Although Tammes and Dral (1955) observed that the latero-frontals were sticky and particles tended to adhere to their surface, Dral (1967) found that in non-filtering mussels the latero-frontal cilia have no adhesive properties and the efficiency of the gill filter is lowered by shifting the range of beat of these cilia so that they no longer completely bridge the ostia. This ability to vary the efficiency of the gill makes any direct correlation between gill structures and filtration difficult. However, it is apparent that the size of the ostia limits the passage of large particles whilst for those particles which can pass through the spaces between the latero-frontal cilia retention depends on chance interception by the adhesive mucous covering of the beating cilia. Between these two extremes in size, particles can be retained or rejected as required.

In this investigation *filtration rates* (the amount of water filtered free of particles per unit time) *pumping rates* (the total amount of water passing across the gills per unit time) and *shell movements* have been recorded simultaneously in the laboratory. Techniques have enabled long-term observations to be made under simulated regimes of cyclical immersion and emersion, light and dark periods and other conditions normally encountered in the natural environment. The possible effects of such conditions on feeding rates and ultimately on growth and reproduction in natural mussel populations in Carlingford Lough will be considered in a subsequent publication.

Materials and Methods

Two essentially different methods have previously been employed to determine feeding rates in bivalves. The classical *indirect method* (e.g. Fox, Sverdrup and Cunningham, 1937; Jørgensen, 1955; 1960) measures filtration and pumping from the rate of removal of particles in the medium surrounding the experimental animal. Pumping rate is calculated from the assumption that all particles suspended in the water passing over the gills are retained. This assumption, however, cannot be justified since *filtration efficiency* (the percentage of particles actually retained) varies considerably. Filtration rates determined by this method must also be suspect. Bivalves rapidly reduce the concentration of particles in suspension and whilst the use of large volumes of media minimise such rapid changes this necessitates more sensitive means of assessing particle concentration. This has been achieved by using radioactively labelled particles (e.g. Smith, 1958; Allen, 1962). However, thorough mixing of the suspension to prevent the establishment of local concentration gradients also recirculates particles deposited in the pseudofaeces, giving rise to anomalously low filtration rates. Furthermore, the necessity of avoiding dispersion of the pseudofaeces prevents direct aeration of the medium which is essential for normal filtration. Haven and Morales-Alamo (1970) have overcome the problem of variation in particle concentration by using a flowing water system (see also Tenore and Dunstan, 1973; Walne, 1972). Oysters were placed in troughs of slowly flowing water and the particles entering and leaving the troughs were counted and measured with a Coulter Particle Counter. Unfortunately, only filtration rates could be measured by this technique. Winter (1969, 1973) also describes a method whereby the particle concentration can be maintained at a constant level throughout the course of the experiment.

In this investigation a *direct method* was used to measure pumping and filtration rates (see also, Tammes and Dral, 1955; Drinnan, 1964). Here a flexible rubber cone is fitted to the shell in order to collect the exhalent water. In the case of *Mytilus*, which lacks prominent siphons, disturbance to the mantle is minimal whilst the extremely elastic cone offers little resistance to shell movements. Drinnan (1964) found that oysters and mussels fitted with cones pumped vigorously, grew normally and spawned upon stimulation. The restrictions imposed by the rubber cone are probably far less than those imposed by overcrowding or fouling organisms present on many shells.

Cones were made from the fingers of surgical gloves as the rubber was extremely elastic and bonded well to the shell using Bostik impact adhesive. Mussels used in the experiments were collected from the shores of Carlingford Lough, County Down, still attached to small stones or shell fragments. All fouling organisms were removed from the shell and shell length measured. Only mussels of 5 cm shell length were used. The cone was glued over the shell so as to contain the posterior-lateral region of the mantle. A cotton wool plug was inserted under the edge of the cone at the posterior shell margin to prevent leakage and a cotton thread was glued to the posterior-ventral region of the shell. Those animals not used immediately were kept in shallow trays of aerated sea water.

Fitting the rubber cones and attachment to the recording apparatus caused considerable initial disruption to normal feeding behaviour though rapid feeding characterised by a high pumping rate and frequent shell movements began shortly after immersion. Over a period of 6-12 hours the pumping rate decreased to a minimum and shell movements became fewer. Mechanical disturbance of the mussel in the experimental chamber caused a similar disruption to the normal feeding pattern. Animals, therefore, were left attached to the apparatus for two days before recording began, care being taken at all times to avoid disturbing the experimental animal.

The apparatus used in the current investigation is illustrated in Fig. 1. Aerated sea water at constant temperature was delivered by pump A from a large reservoir to a constant head unit B. Chamber E was thus supplied with a steady flow of water via siphon C. Tube F acted as a weir, returning excess water to the reservoir. The experimental animal G was attached to tube H by the rubber cone; care was taken to ensure a water-tight joint. Tube H was of large bore to minimise resistance to the passage of water pumped into the second chamber D. Tap R was closed and the chamber allowed to fill with water. Both chambers were tilted by means of the adjusting screw O so that with tap J open water was almost on the point of overflowing down tube I. Thus, with tap J closed, water pumped by the mussel caused an overflow down this tube. It was possible to check for leakage by forcing the mussel to close and then raising the water level in E above that in D with screw O. No water should then be discharged from tube I when tap J was closed.

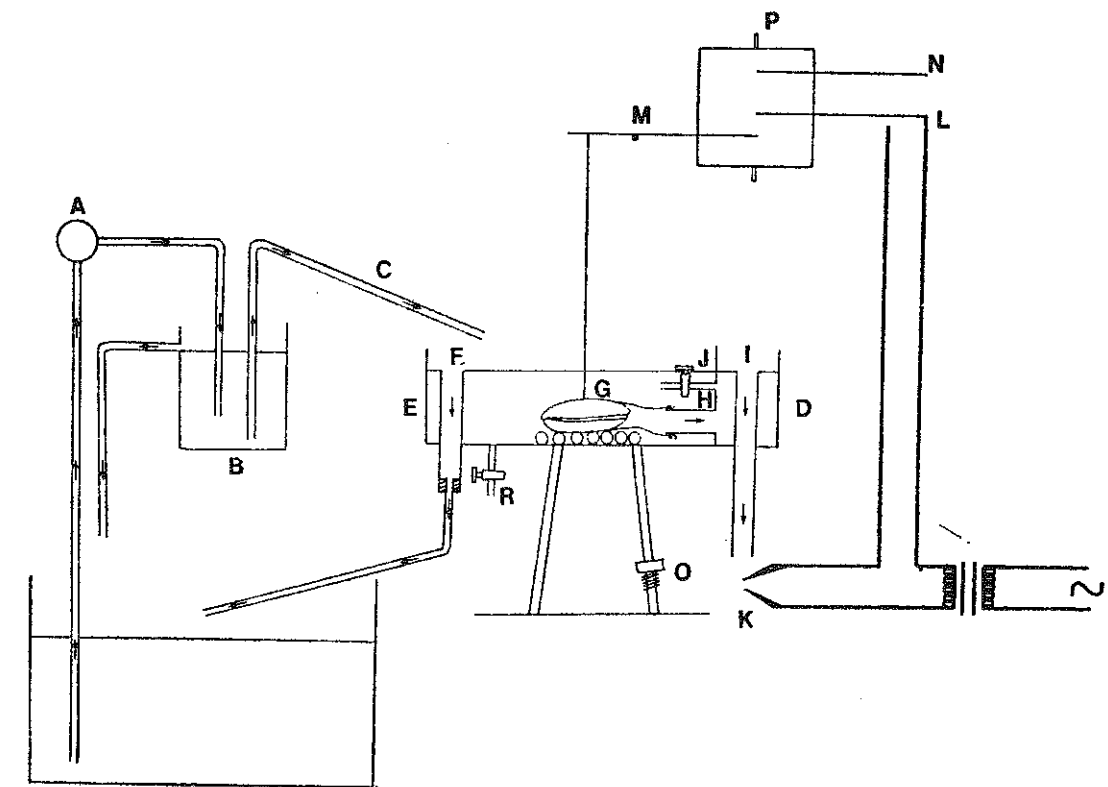


Fig. 1. Apparatus used to record pumping rates and shell movements.

An electrode method previously used by Davids (1964) was used to record short term variations in pumping rates. Water pumped by the mussel was measured as the number of drops of known volume produced per unit of time. Two carbon electrodes K were positioned beneath tube I so that the passage of each drop completed the circuit. This was recorded by the electromagnetic marker L on the kymograph drum P. At the same time marker M traced shell movements—undue tension in the thread connecting the mussel to the lever was carefully avoided. Time intervals were also recorded on the kymograph by the marker N.

Several other materials were tried as electrodes but in most cases rapid deposition of salts prevented conduction after a relatively short time. Carbon functioned most efficiently when used in a 12 volt/1 amp circuit. For experiments where instantaneous recording of water flow was unnecessary an automatic siphoning chamber (Collier and Ray, 1948) was placed between the outflow tube and the electrodes. This device was adjusted to discharge water in 10 ml aliquots thereby simplifying calculations of pumping rates recorded over long periods.

The above method of recording was unsuitable for experiments involving simultaneous measurements of pumping and filtration rates as gradual electrolysis of the electrodes caused dispersion of carbon particles into the medium. In filtration experiments, therefore, pumped water was collected in a graduated cylinder and measured directly.

Filtration rates were estimated by comparing the concentration of suspended particles in chamber E with that discharged from tube I. When frequent readings were required, the accuracy of the method depended on a rapid flow of water through chamber D. Preliminary tests demonstrated that when pumping was in progress, dye introduced into the chamber was totally discharged in a few seconds.

The medium used in filtration studies was a suspension of 5 mg/l. of "Aquadag" colloidal graphite in seawater. In seawater the diameter of the graphite particles increases from 1-2 μ to 2-3 μ within half an hour and flocculated after 5-6 hours (Jørgensen and Goldberg, 1953). Suspensions were first prepared in distilled water and aerated for 24 hours to remove traces of ammonia. These suspensions were then mixed with the seawater in the reservoir of the apparatus and allowed to circulate throughout the system before each experiment. In experiments exceeding 4 hours the suspension was renewed without disturbing the experimental animal.

Graphite concentrations were measured by means of an Eel colorimeter at a wavelength of 608 m μ using a seawater blank. The concentration of "Aquadag" was proportional to the optical density of the suspension.

Natural sea water filtered through glass wool was used for most experiments but where particle-free water was required seawater was first filtered using sintered glass filters (porosity 5) which removed all particles above 1.4 μ diameter. Salinities were adjusted by adding distilled water or "Instant Ocean".

Results

Pumping and filtration rates of individual mussels were extremely variable. Short term variations in pumping rates frequently corresponded to changes in the gape of the shell valves although pumping sometimes stopped without any significant change in the position of the valves. In Fig. 2 two examples of typical kymograph traces illustrate the disruptive effect of shell movements on pumping. In Fig. 2A steady pumping ceased prior to adduction. The shell did not close completely and pumping resumed as the valves were returning to their former gape. When adductions occurred in rapid succession (Fig. 2B) short periods of pumping were normally recorded between each partial closure. Complete and prolonged closure rarely occurred in undisturbed mussels. When a disturbance did cause complete closure the shell did not reopen for some time.

Shell movements generally coincided with periods of pumping. This was especially evident in mussels which were pumping sporadically as in Fig. 3. For most individuals frequency of adduction was approximately proportional to pumping rate. Adduction frequency alone, however, did not give a true picture of the extent and duration of each partial shell closure and its use as an indicator of pumping intensity was therefore avoided. Furthermore, vigorous shell movements also occurred during periods of byssus secretion. Here pumping was very irregular and did not correspond to the frequency of shell adduction.

Filtration efficiency—the percentage of particles filtered—varied over relatively short periods. In Fig. 4 frequent readings illustrate the rapid changes which occurred simultaneously in pumping rate and filtration efficiency. In short term experiments of this kind, no immediately obvious relationship between pumping and filtration could be demonstrated but when recording was extended over longer periods as in Fig. 5 an inverse relationship became apparent. Thus an increase in the pumping rate resulted in a decline in the percentage of particles removed from the inhalent water.

The frequent variations in pumping rate and filtration efficiency which were an integral part of the feeding behaviour pattern caused considerable difficulty when attempting to distinguish experimentally induced changes in feeding from the normal pattern under constant conditions. However, the use of the direct method enabled prolonged observations to be made on each mussel. This greatly aided the detection of small changes from the normal feeding pattern or responses which developed gradually.

Preliminary observations suggested that pumping generally ceased for short periods when shadows passed over the mussel in the chamber. Such changes in pumping resulted from total or partial shell closure in response to rapid changes in light intensity. The direct effect of light on pumping was investigated by exposing actively feeding animals to alternating 12 hour periods of light and dark. In Fig. 6 the pumping behaviour of an individual mussel is shown during a period of five simulated days and nights. Although pumping rates varied considerably there was no immediate response to the transition from light to dark or vice versa and no significant difference was recorded between the volumes of water pumped.

The effect of simulated tidal cycles on pumping was observed in mussels taken from mean tide level where six hours of emersion normally alternate with six hours immersion. The rubber cones were fitted during the period of exposure and the tidal rhythm was continued in the laboratory by periodically filling and draining the chamber. Fig. 7 shows the pumping rates and frequency of shell adductions recorded throughout two tidal cycles. Pumping began within a few minutes of immersion and increased to a maximum within three to four hours. Pumping was halted by emersion but the shell did not shut immediately and movements continued for some time. There was no evidence that this enforced tidal rhythm in pumping persisted in conditions of continuous immersion. Pumping activity was normally sporadic but the intervals between maxima were extremely variable and did not coincide with the tidal cycle at the shore level from which the mussels were collected.

Particle concentration had a marked influence upon feeding behaviour of the experimental animals. In Fig. 8 it will be seen that pumping declined when natural seawater was replaced by water free of particles over 2 μ in diameter. Pumping eventually ceased in particle-free water and long periods of inactivity were infrequently punctuated only by short spells of pumping. The addition of certain concentrations of colloidal graphite caused an immediate acceleration in pumping. The introduction of 15 mg of graphite per litre produced a sevenfold increase in the volume of water pumped (Fig. 9). The increase, however, was only temporary and

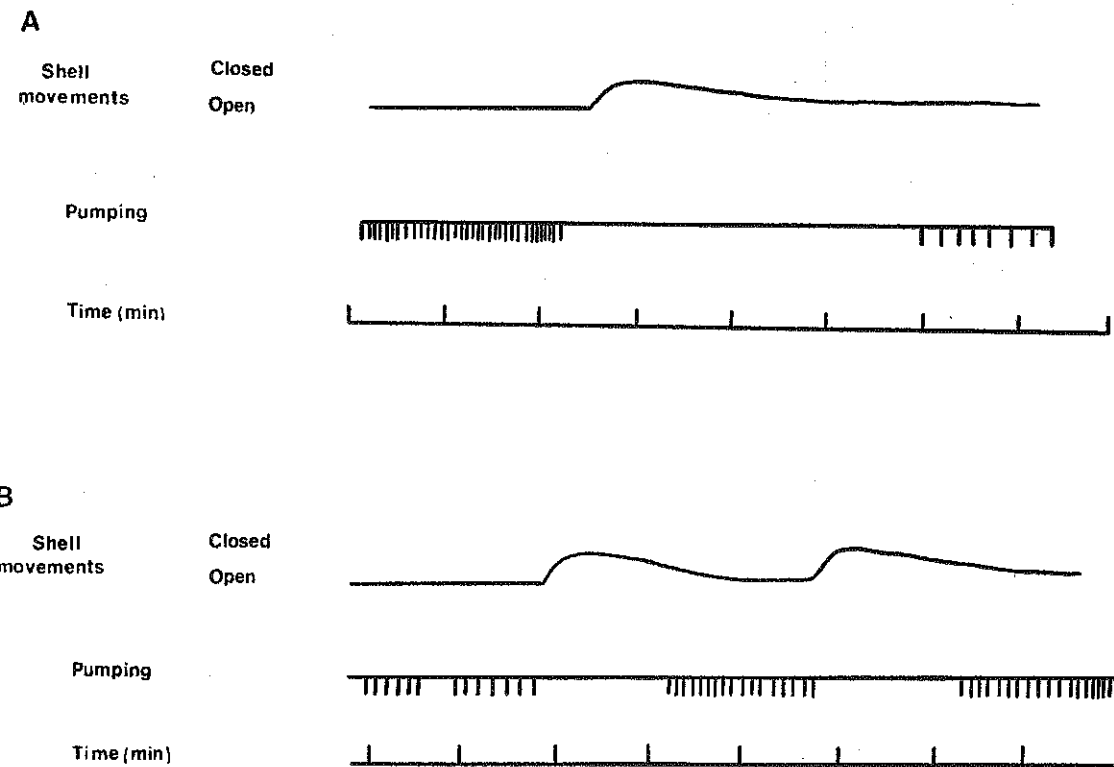


Fig. 2. Kymograph traces of shell movement and pumping rates. Time traces are in minute intervals and pumping is registered in 0.098 ml aliquots.

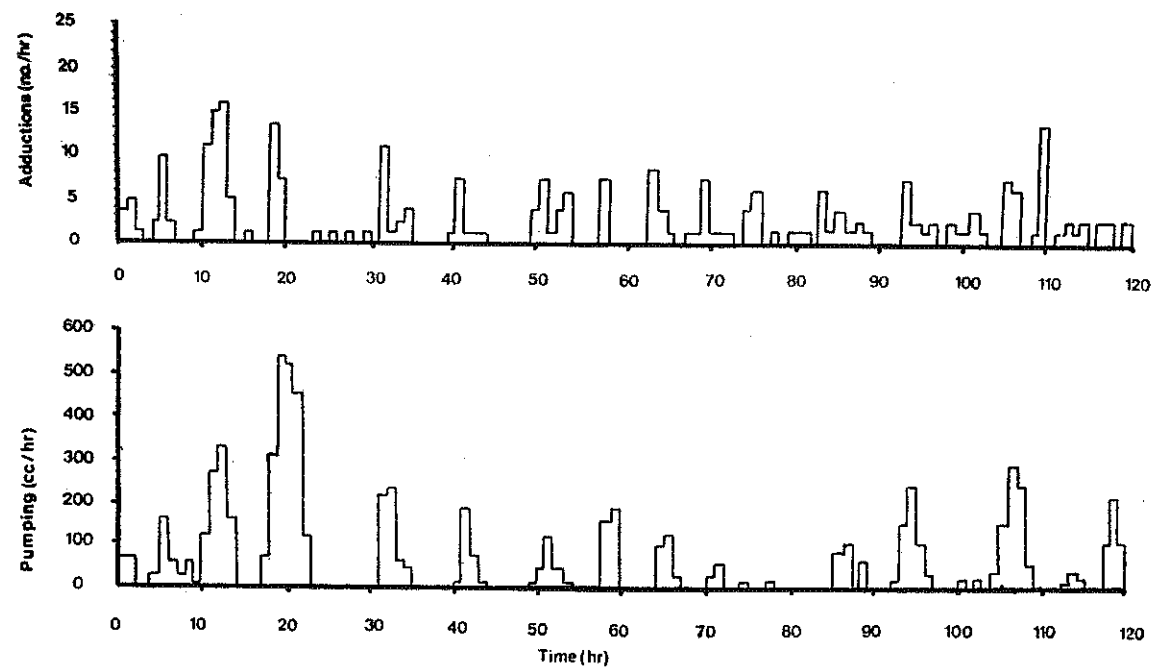


Fig. 3. Typical histograms of adduction frequency and pumping rates for a single mussel over a 5 day period.

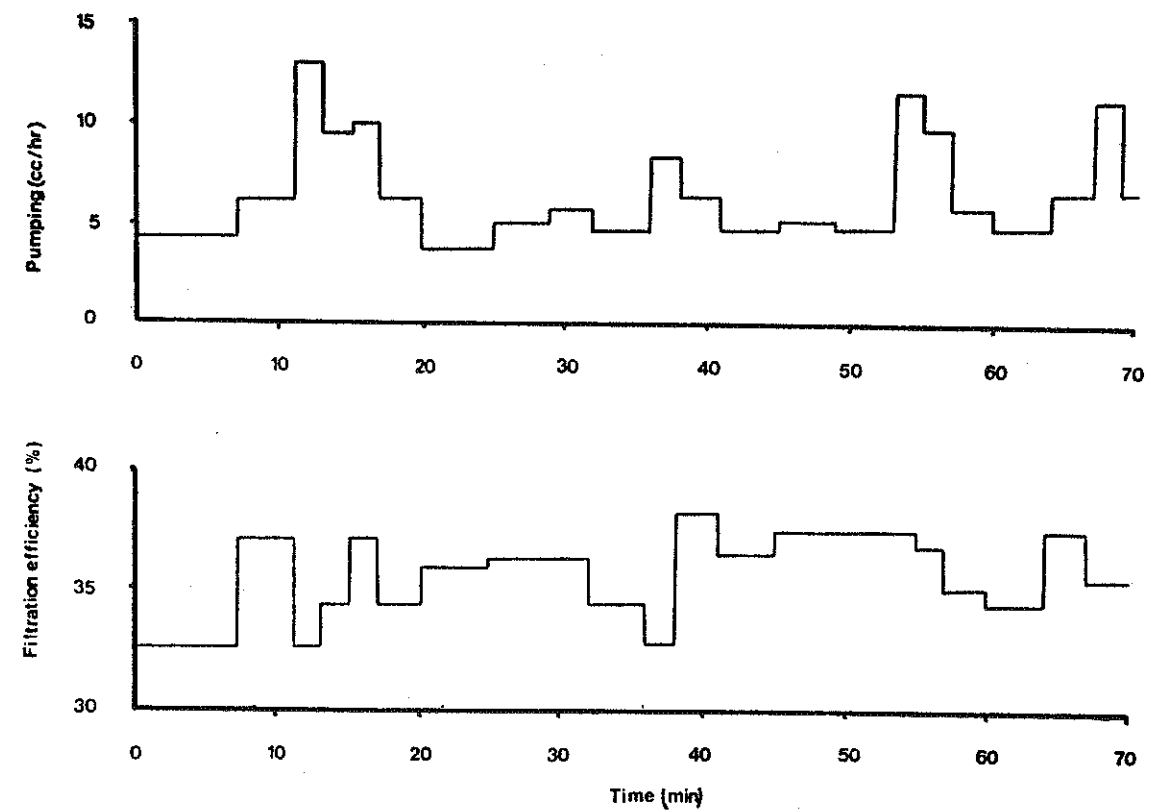


Fig. 4. Short term variations in pumping rate and filtration efficiency of a single mussel in a suspension containing 5 mg/l of colloidal graphite.

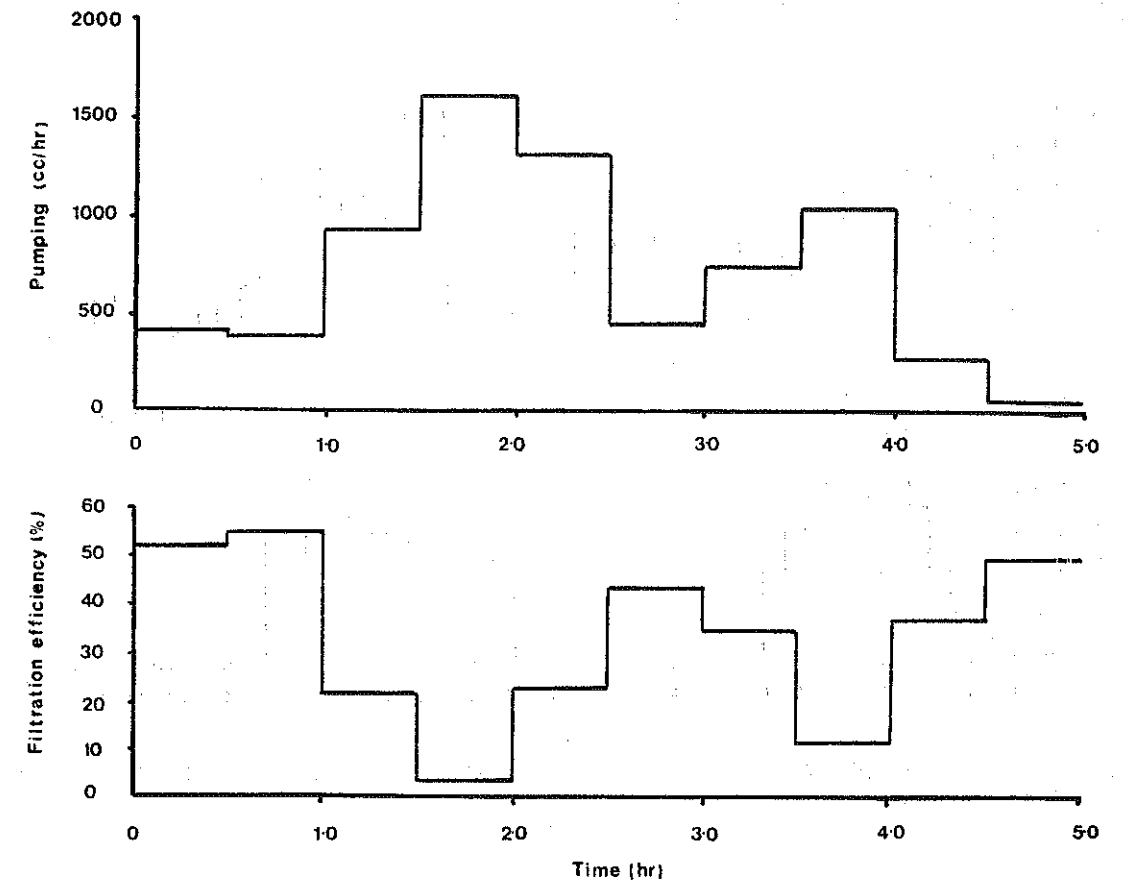


Fig. 5. Pumping rate and filtration efficiency of a single mussel recorded over 30 minute intervals in 5 mg/l of colloidal graphite.

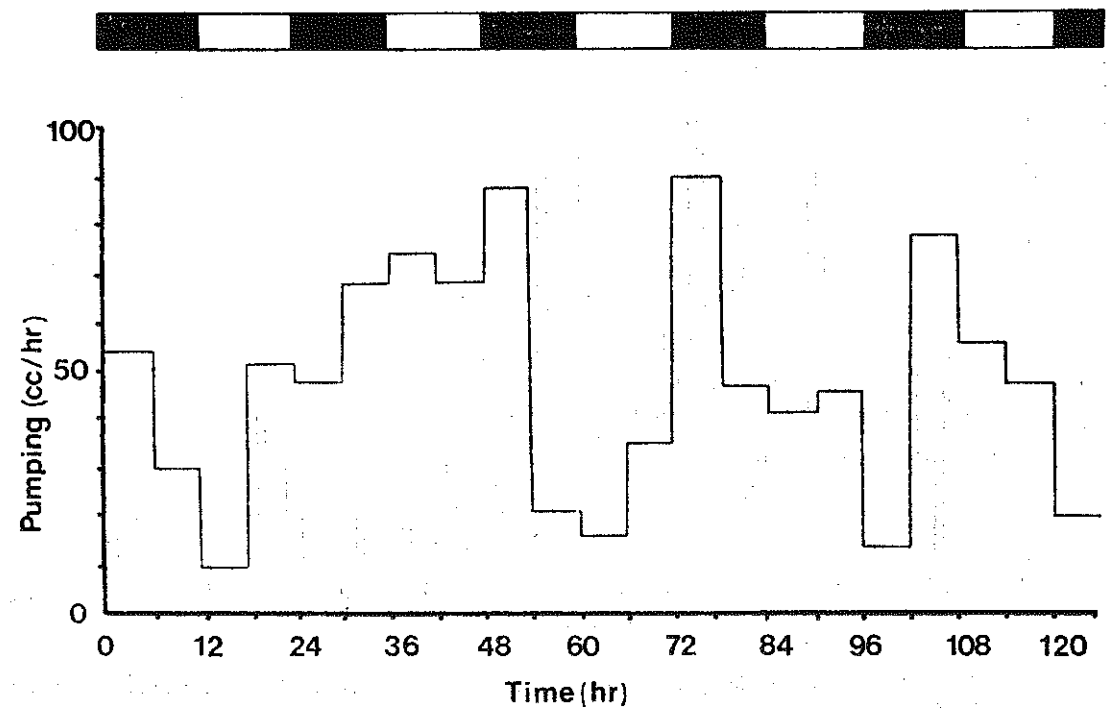


Fig. 6. Pumping rate of a mussel exposed to alternating 12 hr. periods of dark and light over a period of 5 days.

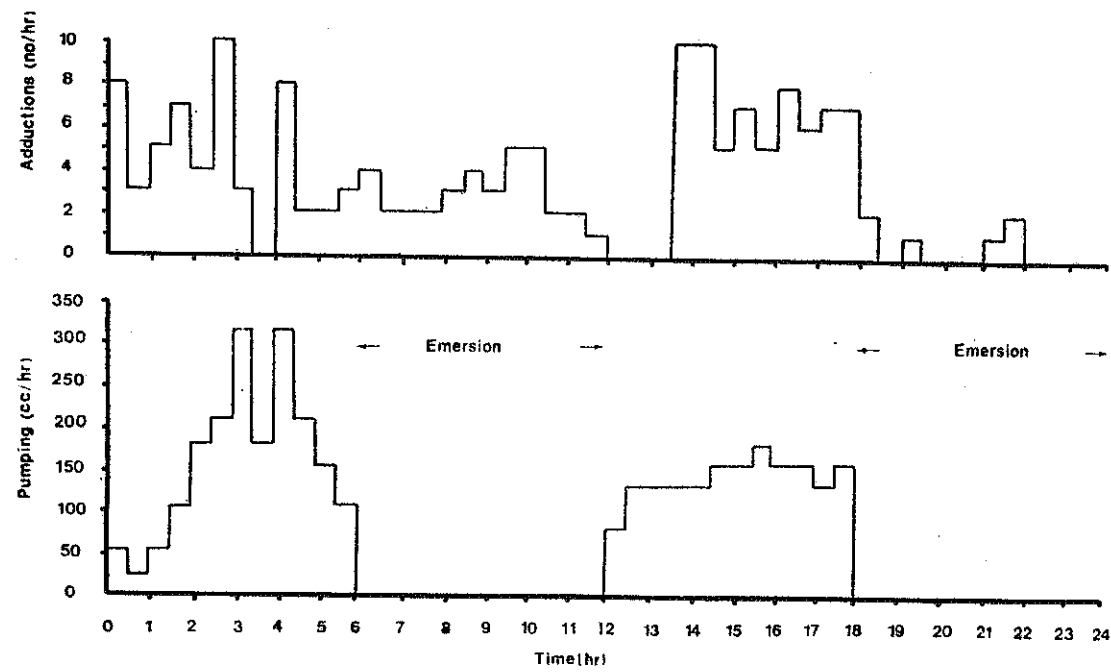


Fig. 7. Pumping rate and adduction frequency of an individual mussel during two simulated tidal cycles (alternating 6 hour periods of immersion and emersion).

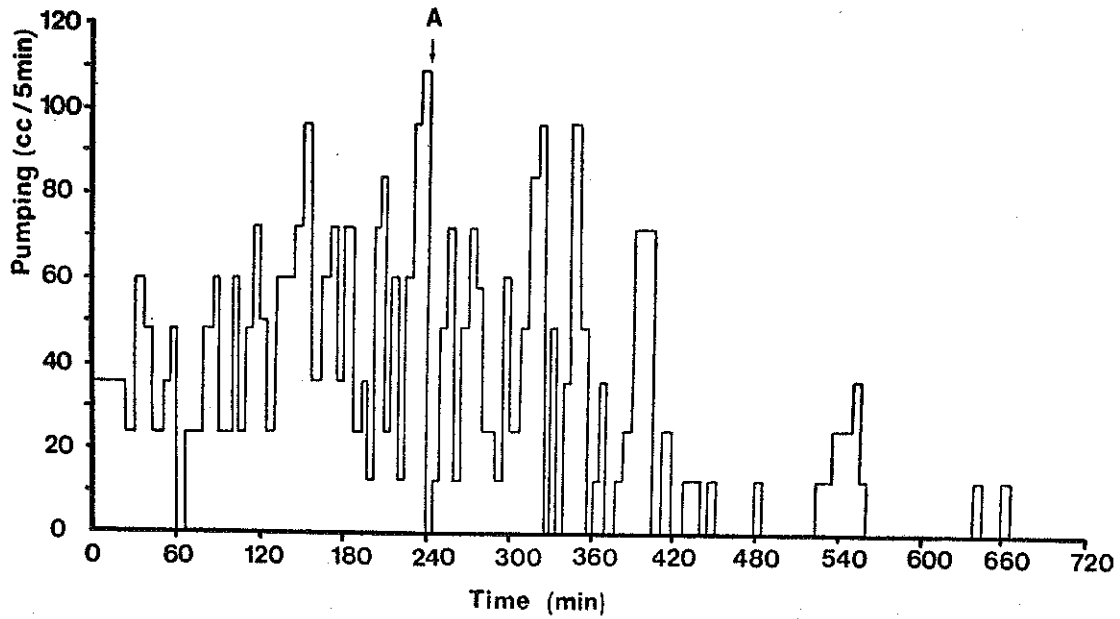


Fig. 8. The effect of the absence of suspended particulate material on pumping rate. Point A marks the transition from natural to particle-free sea water.

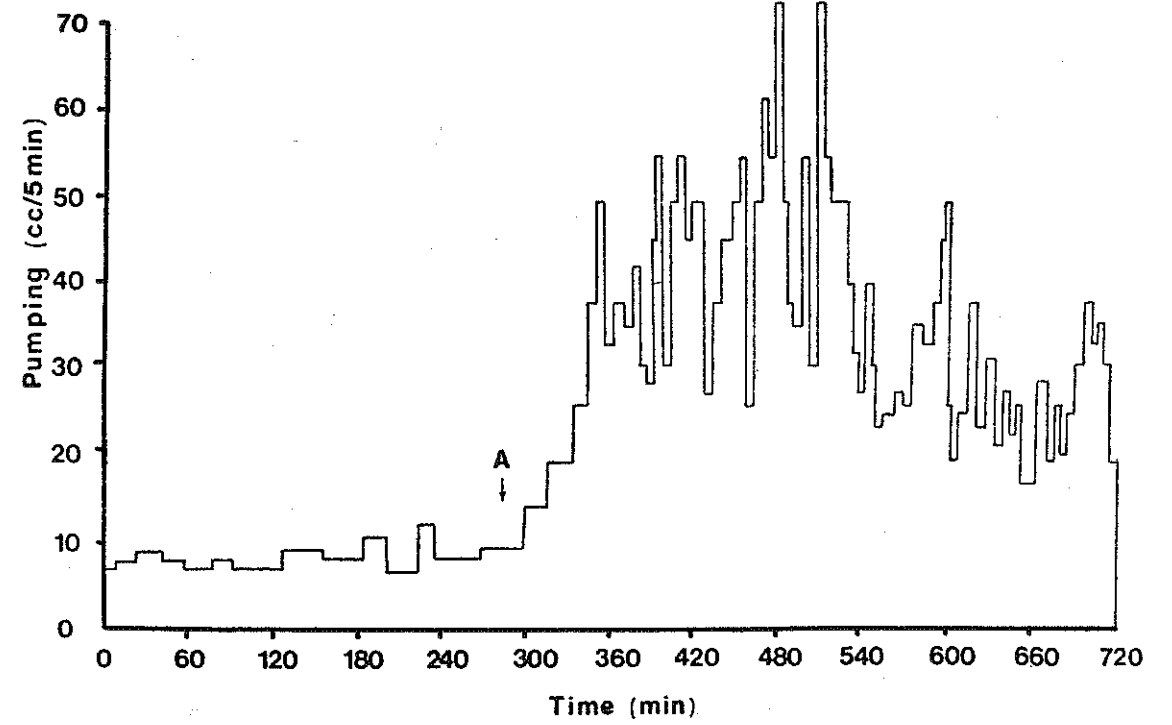


Fig. 9. Stimulation of pumping by adding colloidal graphite (15 mg/l). Point A marks the time of addition.

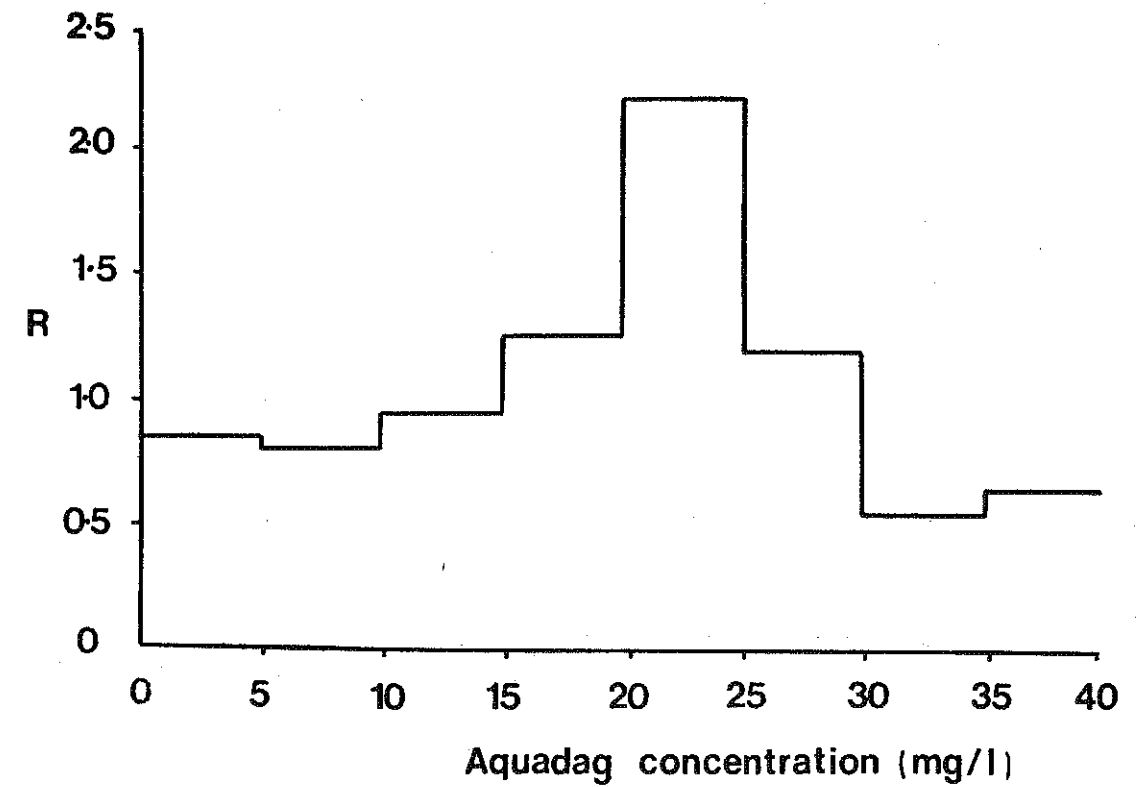


Fig. 10. The effect of concentration of colloidal graphite on R where R = pumping rate after the addition of graphite : rate prior to its addition.

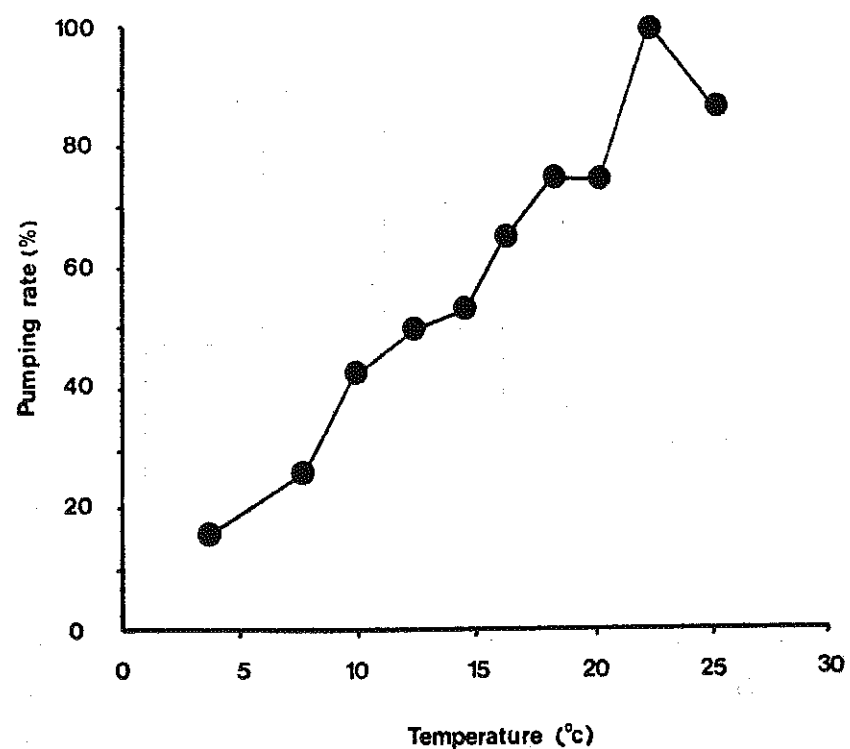
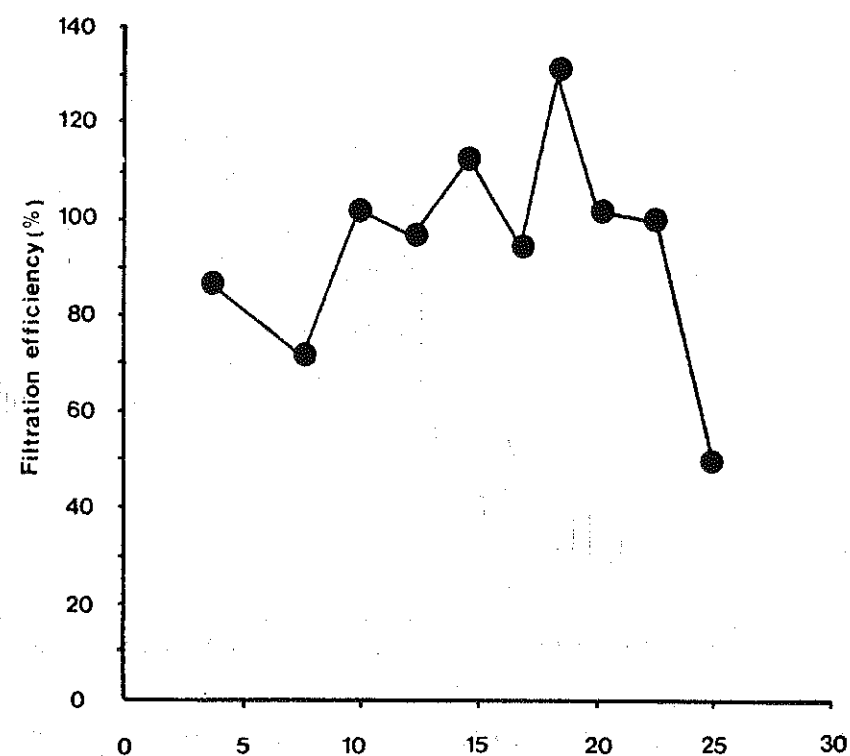


Fig. 11. Filtration efficiencies and pumping rates of mussels acclimated for 4 days to temperatures from 4-25°C. Values are expressed as a % of the value at 22.5°C.

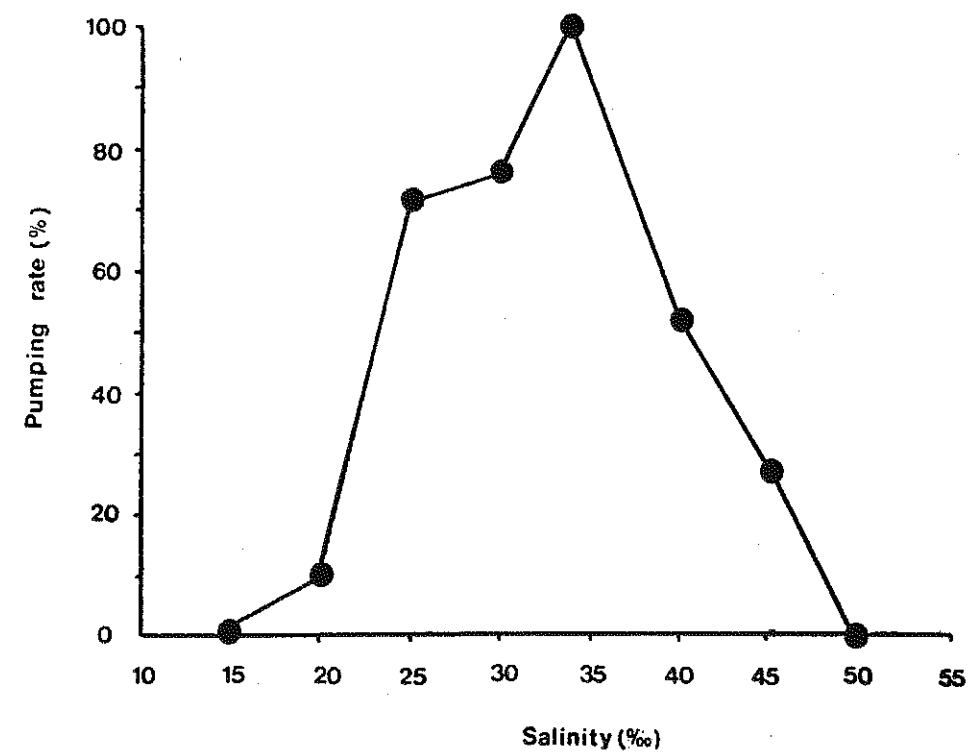
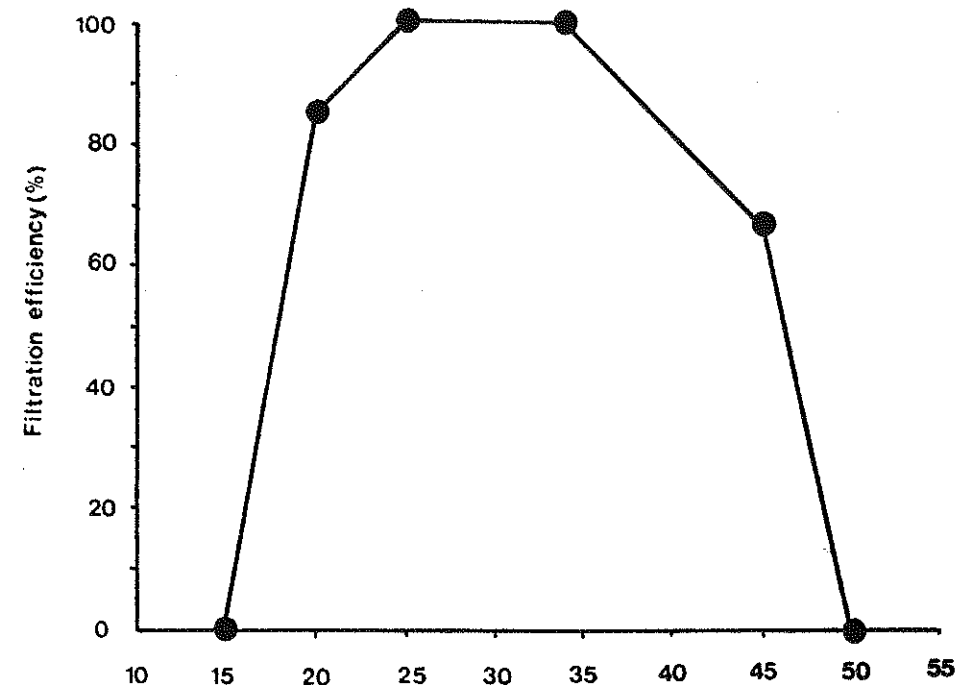


Fig. 12. Filtration efficiencies and pumping rates of mussels acclimated for 7 days to salinities from 15-50‰. Values are expressed as a % of the value at 34‰.

pumping gradually fell as the animals became acclimated. Not all graphite concentrations stimulated pumping. In Fig. 10 the ratio (R) of the pumping rate during the hour before, to that during the hour following the addition of graphite was plotted against the concentration of graphite used. Pumping rates of 5-6 individuals were averaged for each concentration used in order to reduce the errors due to individual variations over the two hour period. No stimulation occurred until the concentration was in the range of 15-30 mg/l. with maximum R values at concentrations between 20-25 mg/l. At higher concentrations pumping was considerably inhibited.

The pumping rate before the introduction of graphite influenced the response when concentrations were at the threshold of stimulation. When added as the pumping rate was decreasing, no stimulation occurred and pumping continued to decrease even though graphite at the same concentration caused an increase in pumping of individuals which had previously been pumping steadily. Thus, from these and other observations it seems that the initial pumping rate may determine whether a suspension produces an increase or decrease in pumping when the graphite concentration is at or only slightly above the threshold level for stimulation.

Temperature had a considerable effect on filtration and pumping. Elevation of temperature produced an increase in filtration efficiency and pumping rate of mussels acclimated over four days to temperatures from 4-25°C (Fig. 11). Filtration is most efficient at 18.5°C although the increase in efficiency with temperature is small. However, temperatures above 22.5°C caused a sharp decline in filtration. Pumping rates showed a steady increase with temperature to a maximum at 22.5°C.

Mussels which had been acclimated to salinities from 15-50‰ for 7 days were used to determine the effect of salinity on pumping rates and filtration efficiency at a constant temperature of 10°C (Fig. 12). Filtration efficiency was relatively high over a wide range of salinities with a maximum occurring between 25-34‰. The values of filtration efficiency at 15 and 50‰ were zero as no water was pumped through the gills. Although animals ceased pumping when exposed to extremes in salinity, the shell did not close and pumping was resumed when the salinity was readjusted to 34‰.

Discussion

Despite the numerous investigations undertaken on different aspects of feeding in bivalves few workers have attempted to analyse filtration rates in terms of filtration efficiency and pumping rates. The almost constant filtration rate frequently recorded in mussels (e.g. Winter, 1973, p.327) is partly a consequence of the inverse relationships between filtration efficiency and pumping rate. During vigorous pumping the filtration efficiency may be reduced due to the rapid saturation of the latero-frontal cilia by the increased influx of particles. Additionally, Dral (1967) found that the frequency of the latero-frontal ciliary beat is reduced by increasing the flow of water over them. Thus, both the rate of particle influx and the strength of the water current probably have a direct bearing upon filtration efficiency. It is essential, therefore, in analysing filtration that account be taken of variations both in pumping and filtration efficiency.

Hamwi and Haskin (1969) in a study of the feeding behaviour of *Mercenaria mercenaria* found a linear relationship—which Verduin (1969) showed to be curvilinear—between pumping and respiratory rates. They concluded from their results that oxygen demand rather than feeding regulates pumping rate. However, Krogh (1959) concluded that pumping rate is more closely related to feeding than to respiration since oxygen uptake is small compared with the volumes of water filtered. Frequent variations in pumping rates were recorded in this investigation despite continual vigorous aeration of the medium.

Adductor muscle activity was shown to directly affect pumping rate in *Mytilus*. Pumping rarely occurred without being accompanied by frequent shell movements. The tendency for the frequency of shell adduction to vary with pumping rate supports the conclusion of Drinnan (1964) that rapid adduction caused "backflushing" of the ctenidia thus preventing the accumulation of particles likely to block the ostia. Morton (1970) considered phasic adductions in *Cardium edule* to have three major functions—expulsion of faeces and filtered water from the exhalent siphon, ejection of pseudofaeces from the inhalent siphon and squeezing the stomach to force the contents into the digestive diverticulae. Ejection of faeces and pseudofaeces by rapid adduction was not observed in this investigation. Faeces were deposited without any increase in the exhalent current and often in the absence of shell movements. It is possible, however, that rapid shell movements associated with active feeding assist the passage of food into the digestive diverticulae and at the same time "back-flush" the ctenidia.

Intrinsic rhythmicity in pumping and filtration has been observed in certain bivalves. Chappuis and Lubet (1966) detected short-term "pseudo-rhythms" in pumping in *Mytilus edulis* and *M. galloprovincialis* which appeared to be controlled by an intrinsic activity rhythm in the neural ganglia. Similar rhythms were present in animals observed in this study though the pattern varied from day to day. Rao (1954) found that *M. edulis* and *M. californianus* exhibited cyclical variations in filtration rates in phase with the tidal cycle which persisted in constant conditions of light and immersion in the laboratory. Bennett (1954) recorded a similar persistent rhythm in shell movements in *Mercenaria mercenaria* associated with an additional diurnal rhythm with periods of maximum and minimum activity during the afternoon and early morning respectively. The summation of the periodicities of the two cycles was related to a lunar cycle. Persistent tidal rhythms of oxygen consumption have also been observed in *Mytilus edulis* and *Pecten maximus* by Gompel (1938). However, the presence of inherent tidal rhythms in pumping have been denied by Loosanoff and Nomejko (1946) for *Crassostrea virginica* and by Chappuis and Lubet (1966) for *Mytilus edulis* whilst a tidal rhythm in filtration was found to be absent in the latter by Theede (1963). During the present study rhythms in pumping were observed in some individuals but even when marked rhythmicity was apparent there was no obvious correlation with the tidal cycle at the animal's place of origin. The periodicity of the rhythm not only varied from one individual to another but also with time. A slight mechanical disturbance such as might be expected to occur in the natural habitat, generally caused major changes in the pattern of pumping. Thus, intrinsic tidal rhythms could be disadvantageous since minor disturbances could radically alter the time available for feeding in the natural environment especially in littoral populations. It appears in fact that the mussel is an opportunistic feeder readily adjusting its behaviour in order to maintain optimum feeding efficiency. Feeding began almost as soon as the animal was immersed and continued until emersion. Fox, Sverdrup and Cunningham (1937) and Theede (1963) concluded that mussels filtered more rapidly after prolonged emersion whilst Schlieper (1959) found that gill cilia exhibited an increased activity for several days after three days in nitrogen saturated water. In *Mya arenaria* the rate of oxygen utilisation after exposure was proportional to the time of emersion (Van Dam, 1935) and in *Lasaea rubra*, a bivalve adapted to life in the upper shore, respiration resumed at the normal rate after exposure (Morton, Boney and Corner, 1957). Thus it appears that certain intertidal bivalves replenish the depleted oxygen levels in the body on immersion by rapidly circulating water over the respiratory surfaces. After prolonged exposure, pumping rates are increased in response to elevated respiratory demands and such behaviour might be expected to persist in conditions of constant immersion in the laboratory.

Dodgson (1928) observed that mussels tended to remain open and continue feeding in darkness or very subdued daylight but were not always open during the day especially at low temperatures. When temperature was not unusually low, shell movements of *Crassostrea virginica* were not influenced by rhythmical light changes of day and night (Galtsoff, 1928). Webb (1930) and Loosanoff (1942) reached the same conclusion for *Ostrea edulis* and *Mytilus edulis* respectively. Loosanoff and Nomejko (1946) also found that changes in illumination did not stimulate a pumping rhythm in *Ostrea virginica*. The present study failed to reveal any diurnal differences in pumping though contrary to Loosanoff's (1942) findings pumping was disrupted by partial or total shell closure when a shadow passed over the mussel. This reaction to light could be of some survival value in protecting the mussel from potential predators.

Temperature has a marked influence on pumping in *Mytilus* but its effect on filtering efficiency is less obvious. Pumping reached a maximum at 22.5°C in acclimated mussels. Gray (1928) has shown, however, that the amplitude and rate of beat of gill cilia in *M. edulis* continue to increase with temperature with maxima at 33 and 37.5°C respectively. However, pumping rate is controlled not only by ciliary activity but also by other factors including gape of the shell valves (Hopkins, 1931). The opening between the valves of *Ostrea gigas* is widest at 20°C whilst at higher and lower temperatures the valves tend to close and restrict water intake. Thus pumping rates at different temperatures are a function not only of ciliary activity but also shell gape. Shell movements, however, were so infrequent that assessments of the average distance between the valves at each temperature proved impracticable.

The optimum temperature for filtration efficiency in *Mytilus* was 18°C which is again considerably lower than the temperature for maximum activity of latero-frontal cilia. This may be partly due to the inverse relationship between filtration efficiency and pumping rate. Increase in the latter with temperature would reduce filtration efficiency, which is itself increasing due to increased ciliary activity. A temperature would be reached where the pumping rate prevents any further increase in filtration efficiency. Nevertheless, it may be erroneous to assume that increased ciliary activity is correlated with improved filtration efficiency. Whilst Gray (1928) found that the rate and frequency of ciliary beat are maximal between 30-40°C, Dral (1957) has pointed out that filtration efficiency also depends on the range of beat of the cilia. Thus, the degree of ciliary activity may not be the only temperature dependant factor controlling filtration. Hopkins (1935) in discussing Gray's findings concluded that the different temperature optima concerned in the activity of single cilia emphasises the complexity of the activities resulting in a single curve of gross activity at different temperatures. Although referring essentially to pumping, Hopkins' statement must also apply to the ciliary mechanism involved in filtration.

At 4°C pumping was only 15% of the maximum rate at 22.5°C whereas filtration efficiency remained relatively high at 86%. *M. edulis* is reported to function normally—pumping and ejecting faeces and pseudo-faeces—at temperatures as low as -0.5°C. Galtsoff (1928) states that some cilia in isolated pieces of gill tissue from *Ostrea gigas* continue to beat until frozen but that low temperatures disrupt the coordination of the ciliary beat. Theede (1963) recorded filtration in mussels at 2°C whilst Loosanoff (1958) found that *Crassostrea virginica* pumped at temperatures as low as 1-1.7°C although true faeces were rarely formed below 2-3°C. Menzel (1955) however, found no ciliary activity in *C. virginica* gills below 4°C and concluded that several physiological races exist in relation to the minimum temperature for ciliary activity. Segal, Rao and James (1953) considered that differences in ciliary response to temperature need not be racial but could result from phenotypic acclimation. Theede (1963) has demonstrated differences in filtration rates of mussels acclimated to different temperatures.

Pumping rate and filtration efficiency of mussels acclimated to different salinities were maximal at 34‰, variations from this optimum causing a decline in pumping and, to a lesser extent, in filtration efficiency. No pumping occurred at the extreme salinities of 15‰ and 50‰ although natural populations are found in salinities as low as 4.5‰ (Heinonen, 1962). Renzoni (1963) and Theede (1963) conclude that the optimum salinity for filtration was that of the natural habitat but that this could be adjusted within certain limits. Although acclimation was carried out over a period of seven days it is thought that adjustment to low salinities is an extremely slow process becoming progressively more difficult as the limits of tolerance are approached. As *M. edulis* is an osmoconformer, dilution of the medium causes marked changes in the physiological balance of the acclimated tissues. Schlieper and Kowalski (1957) in a comparison of mussels native to habitats with salinities of 30‰ and 15‰ found that animals living in low salinities had higher rates of oxygen consumption and lower ciliary beat frequencies. As salinity decreases, a point is reached where reduced pumping rates can no longer meet the increased respiratory demands. Thus, oxygen consumption rather than ciliary activity may be the limiting factor at low salinities.

It has already been pointed out that ciliary activity is not the only factor controlling pumping and filtration. Unfortunately shell gape was too variable to allow any definite conclusions to be reached as to its effects on the flow of water across the gills. Nevertheless, it was observed that the shell generally remained open at 15‰ and 50‰ even though pumping was not occurring. Complete closure was recorded at 10‰ and 55‰ and also when salinity was rapidly increased or decreased from the optimum. This probably results from the inability of the tissues to adjust to extreme or rapidly changing salinities. Freeman and Rigler (1957) found that in *Scrobicularia plana* the valves opened more readily in seawater isotonic with the tissues than in higher or lower concentrations.

Pumping rates of experimental animals were found to be largely dependant on the concentration of particulate material. However, Flugel and Schlieper (1962) and Theede (1963) have shown that apart from particulate material certain solutes can exert a considerable effect on ciliary activity in *Mytilus*. In the present investigation the effects of particle free sea water on pumping were examined by using water previously filtered to remove all particles above 1.4 µ diameter. Under such conditions pumping rapidly decreased, stopping altogether in some animals. The valves remained open, and if periods of pumping occurred they were generally short and infrequent. It would appear, therefore, that particulate material present in natural seawater in the form of plankton and fine detritus stimulates and maintains pumping. Whilst extremely low concentrations of particulate material in natural seawater is perhaps uncommon some samples of water collected during winter failed to stimulate prolonged periods of pumping and it is possible that this behaviour is a means of conserving energy during periods when particulate food is scarce. However, in addition to feeding on particulate material it is becoming increasingly clear that many invertebrates including *Mytilus* (Pequignat, 1973) are capable of taking a significant part of their diet from dissolved organic nutrients providing these are continually supplied in their environment. The relative importance of this potential food source and its bearing on such factors as growth and reproduction is clearly an area in which much critical research is urgently required.

The mantle margin of *Crassostrea virginica* has been shown to be sensitive to chemical and mechanical stimuli (Loosanoff and Engle, 1947) triggering feeding activity when stimulated by the addition of particulate material. The immediate response to graphite particles in *Mytilus* suggests that the stimulus may be purely mechanical, the response increasing with concentration. At higher concentrations, however, the pumping rate shows a sharp decline eventually ceasing altogether at concentrations approaching 100 mg/l. A similar decrease in pumping and filtration rates in mussels and other bivalves has also been recorded with high concentrations of live microorganisms (Loosanoff and Engle, 1947; Rice and Smith, 1958; Davids, 1964; Morton, 1971). Winter (1973) found that within a specific range of algal concentration the filtration rate is regulated in such a way that the amount of algae filtered is more or less constant. Variations in food concentration in the natural environment can perhaps be compensated for by regulating the filtration rate and this could be a significant factor in accounting for the success and wide distribution of *Mytilus*.

Responses to graphite at the threshold concentration for stimulating pumping were extremely variable. Pumping behaviour prior to the addition of graphite determined whether an increase or decrease in pumping activity would occur (see also Loosanoff, 1961 for *Crassostrea virginica*). Stimulation of the experimental animal produced a cycle of increased pumping which lasted several hours. Once this accelerated pumping was induced the mussel seemed incapable of reacting to other stimuli and the further introduction of graphite during such periods of increased pumping failed to induce an additional acceleration. When pumping is at its normal minimal rate the animal is in a condition receptive to stimulation and increases its pumping rate in response to the introduction of graphite.

This discussion has covered aspects of the feeding behaviour under a variety of environmental conditions. However, feeding might be controlled, in part at least, by intrinsic physiological factors. Tsujii and Ohnishi (1957), Rice and Smith (1958), Theede (1963), Coughlan and Ansell (1964) and Morton (1971) have shown that pumping rates are related to body weight or shell length in several bivalves including *Mytilus*, small individuals pumping more rapidly per unit weight or length than larger individuals. Dodgson (1928) observed that under similar temperature conditions mussels cleared water more rapidly in September-October than in February-March and considered that this may be due to gonad development. It could, however, be due to the relative amounts of food present in seawater at different times of the year. Rao (1953) however, found that ovigerous individuals pumped erratically and although Verwey (1952) states that temperature is the operative factor controlling seasonal variations in feeding, Theede (1963) showed that filtration rates in *Mytilus* were higher in spring than in late summer at the same temperature.

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