

## ON FEEDING MECHANISMS AND CLEARANCE RATES OF MOLLUSCAN VELIGERS

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### Article:

The teeth of a mammal or the mouthparts of a copepod can tell a knowledgeable biologist much about that animal's feeding habits. Deductions based on the structure of ciliary bands can be at least as useful. This study is part of a larger effort to relate quantitative aspects of ciliary feeding to the morphology of ciliary feeders. Much more extensive biogeographic or taxonomic comparisons of developmental adaptations can be made when feeding capacities of larvae can be predicted from the length of cilia and the lengths of their ciliated bands.

Molluscan veliger larvae possess a lobed velum which produces both feeding and locomotory currents. Those veligers which feed on suspended particles concentrate these particles between two opposed bands of cilia which line the velar edge (Fretter, 1967 ; Strathmann, Jahn, and Fonseca, 1972 ; Thompson, 1959 ; Werner, 1955). The preoral band consists of long compound cilia which produce the swimming and feeding currents. The postoral band consists of shorter cilia which beat towards the preoral band. The combination of the two bands captures and retains particles. Between these bands is a food groove with small cilia which transport particles towards the mouth.

Veligers are tiny feeding machines which convert small eggs into larger juveniles. Parents which produce small eggs can produce large numbers of offspring, but there are costs that limit larval success as larval size is reduced. A reduced feeding capacity is one cost of a decreased larval size. This can take the form of a reduction in the clearance rate (volume of water cleared of particles per unit time) or restriction to a smaller range of particle sizes. In molluscan veliger larvae the clearance rate is likely to be limited by both the length of the velar edge and the length of the preoral cilia (Strathmann, *et al.*, 1972). The size of the particles captured is probably limited by the length of the preoral cilia.

Here we are testing the hypothesis that longer preoral cilia contribute to higher clearance rates. The test consists of comparative observations with high speed microcinematography of movements of the preoral cilia, the postoral cilia and particles captured at the velar edge. Clearance rates are calculated from these measurements. We used three species whose veligers have different lengths of preoral cilia : the oyster *Crassostrea gigas*, the nudibranch *Tritonia diomedea* and the mud snail *Nassarius obsoletus*. Movements of cilia and particles, but no particle captures, were also observed for a veliger of an unidentified species of prosobranch gastropod. Our cinefilms of feeding larvae also have extended previous interpretations of the veliger feeding mechanism.

### METHODS

Oyster (*Crassostrea gigas*) gametes were obtained by placing adults in sea water at 30° C until spawning occurred (3 to 4 hrs). The eggs were fertilized at ambient sea water temperatures (12 to 16° C). Larvae of *T. diomedea* and *N. obsoletus* were obtained from eggs laid in laboratory aquaria. The unidentified prosobranch veliger was taken from the plankton in Friday Harbor. All larvae were reared in culture dishes in the laboratory at 12 to 16° C and were fed the green flagellate *Dunaliella tertiolecta*.

Test subjects were starved for 24 hr before being filmed to promote maximum feeding rates during filming. Coverglasses were supported by plasticene feet just low enough to impede larval swimming and high enough not to impede velar cilia in the plane of focus. The larvae were usually filmed with plane of focus perpendicular to the velar edge, as in Figure 4, for velocities of cilia and particles. In some cases larvae were filmed with plane of focus parallel to the velar edge for metachronal wavelength.

Larvae were filmed with Nomarski differential interference optics with 16 or 40× objectives, a high speed cinecamera at 100 or 200 frames per second, and continuous light. A timing light exposed the margin of the film every 0.01 seconds and is accurate to  $\pm 1\%$  according to its manufacturer, the Redlake Corporation. Temperatures were maintained at 12° to 13° C with a Cloney cooling stage (Cloney, Schaadt, and Durdeen, 1970) except for some sequences of *C. gigas* filmed at 20° to 22° C.

Particles used for feeding observations were 2- $\mu\text{m}$  plastic spheres and the flagellates *Dunaliella tertiolecta* and *Monochrysis lutheri* (5 to 10- $\mu\text{m}$ ). We observed only one capture of a plastic sphere so the data on captures apply to the flagellates. High concentrations of particles were used to insure some captures in the plane of focus during high speed filming. Since particles are rapidly removed from suspension by the larvae and also settle in the confined space on a slide, particle concentrations could not be accurately determined. Therefore no cell counts were made.

Tracings of the films were made frame by frame for cilium and particle paths. All velocities were calculated from the tracings. The fraction of particles captured was calculated using all particles passing within reach of the preoral cilia from the beginning to the end of several filmed sequences.

TABLE I

Species	Egg Diameter ( $\mu\text{m}$ )	Shell length at start of feeding ( $\mu\text{m}$ )	Preoral cilium length ( $\mu\text{m}$ )
<i>Crassostrea gigas</i>	45-50	90*	30
<i>Tritonia diomedea</i>	90	145*	40
<i>Nassarius obsoletus</i>	165*	270*	70

\* Data from Costello, Davidson, Eggers, Fox, and Henley (1957), Kempf & Willows (1977), Quayle (1969), Scheltema (1967).

## RESULTS

We assume that the veligers are actively feeding whenever numerous particles are passing around the food groove to the mouth. When this occurs both the preoral and postoral bands are beating. Occasionally both bands would cease beating but we did not observe the preoral band beating while the postoral band stopped.

*Crassostrea gigas*, *Tritonia diomedea*, and *Nassarius obsoletus* are consistent with our impression that the size of veligers and the length of preoral cilia increase with egg size (Table I).

### *Velocities of cilia and particles*

Among species, the velocities of the tips of the preoral cilia in the effective stroke increase with the length of cilium (Fig. 1). It is difficult to see the bases of cilia in many filmed sequences, so radius of arc was estimated by projecting the straight section of a cilium in successive frames back to a point of inter-section. For each species the mean estimated radius of arc is greater than the lengths of those cilia which could be measured accurately. The velocities are taken from the maximum movement observed between two successive frames during the effective stroke.

Angular velocities are more convenient for comparisons among species and calculation of clearance rates. The angular velocities plotted in Figure 2 are calculated by dividing the tip velocity by the radius of arc. For cilia which are held straight during the effective stroke, the angular velocity is constant over almost the entire length of the cilium. Angular velocity may increase with cilium length (see below) but the trend is less striking than the increase of tip velocity with the length of the cilium (Fig. 1).

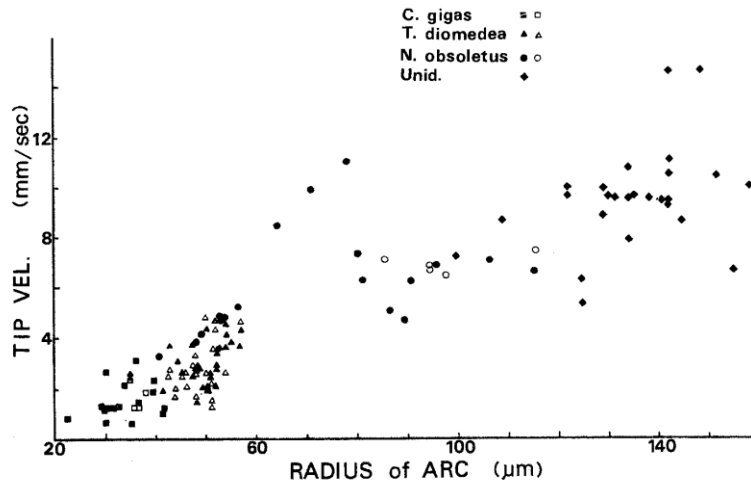


FIGURE 1. Maximum observed tip velocities of preoral cilia during their effective strokes versus radius of arc (estimate of cilium length) for veligers of *Crassostrea gigas*, *Tritonia diomedea*, *Nassarius obsoletus* and an unidentified prosobranch. Open circles are effective strokes associated with particle captures; solid circles with no capture.

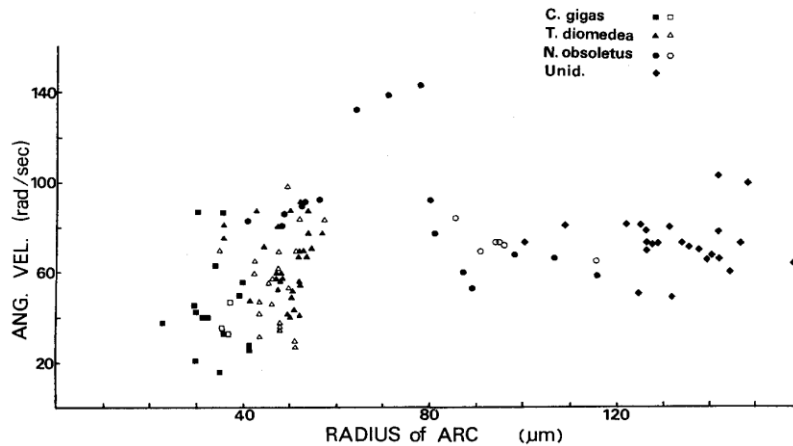


FIGURE 2. Maximum observed angular velocities of preoral cilia during their effective strokes (same larvae as in Figure 1). Open circles are effective strokes associated with particle captures; solid circles with no capture.

One-way analysis of variance of the angular velocities of the four species indicates significant differences among the species (Table II). A multiple comparison among species indicates that the species fall into three significantly different groups: *C. gigas* with the lowest mean angular velocity, *T. diomedea* in the middle, and *N. obsoletus* and the unidentified veliger with the highest mean angular velocities (Table II). Preoral cilium length increases along with the angular velocity in these three groups. Thus among species angular velocities of preoral cilia may increase with the lengths of preoral cilia, but more species must be examined to confirm this trend. The observed differences in angular velocities may be associated with the species or the taxonomic order rather than the lengths of the preoral cilia. Also, the mean angular velocity of *N. obsoletus* is greater than for the unidentified prosobranch veliger which has much longer preoral cilia. The implications of the anomalously lower angular velocity in the unidentified veliger are not obvious because this veliger was not observed to catch particles. It is nevertheless clear from these data that the small veligers are not compensating for the shorter length of preoral cilia with increased angular velocities.

Temperature could affect the rate of beat of cilia but we did not observe this. The mean angular velocity of the preoral cilia of *C. gigas* at about 20° C is only slightly greater than at 12 to 13° C, and the difference is not significant (Table III).

The preoral cilia in their effective strokes move one to three times faster than the nearby particles. We could not demonstrate that the ratio of cilium velocity to particle velocity (C/P) varies with the angular velocity of the cilium or the type of particle (Tables III, IV). In *T. diomedea* particle velocities increase and then decrease with

the distance from the base of preoral cilium (Fig. 3). The velocities were measured for particles near the middle of the effective stroke of the preoral cilia. Since velocity of the cilium increases from the base to the tip, the ratio of cilium to particle velocity should increase near the tip, but we cannot demonstrate this (Table IV, C/P versus D). Because we cannot show the existence of these possible confounding factors, we have lumped all observations on C/P for each species in a test for differences among species. Differences in C/P among species are highly significant (Table II), but the cause of the difference is not clear. The species with a substantially different ratio of cilium velocity to particle velocity is *T. diomedea*, with a mean ratio of 2 as opposed to about 1.5 for the others. The preoral cilia of *T. diomedea* are of intermediate length. We can-not show that the ratio of cilium velocity to particle velocity changes in a regular way with cilium length, cilium speed, or food particle. Therefore, longer preoral cilia, which have angular velocities greater than or equal to those of shorter cilia, move more particles and presumably more water past the preoral band of cilia.

TABLE II  
Comparisons among means for species. Ho: Means equal; reject if  $P < 0.001$

Species	Mean angular velocity (radians/sec)	(n)	Mean ratio of velocities of cilium and particle (C/P)	Range of (C/P)	(n)
<i>Crassostrea gigas</i>	32	(19)	1.6	1.1-2.1	( 6)
<i>Tritonia diomedea</i>	54	(51)	2.0	1.1-3.0	(36)
<i>Nassarius obsoletus</i>	70	(25)	1.5	1.0-2.4	(20)
Unidentified	63	(24)	1.5	1.1-1.9	(21)
Reject Ho (one way Anova) $P < 0.001$			Reject Ho (Kruskal-Wallis test) $P < 0.001$		

Groups by Student-Newman Keuls multiple comparison (reject Ho if  $P < 0.01$ ): significantly different groups are (1) *C. gigas*, (2) *T. diomedea*, and (3) *N. obsoletus* and unidentified veliger.

TABLE III  
Two sample rank tests for C/P (ratio velocities of cilium and particle) and W (angular velocity of cilium) Ho: Groups same; reject Ho if  $P < 0.05$ . Ho accepted for all tests (Mann-Whitney U, two tailed).

Species	Comparison	(n <sub>1</sub> , n <sub>2</sub> )	P
<i>Crassostrea gigas</i>	W at 12° C and 20° C	(24, 23)	>0.20
	W for captures and misses	( 3, 3)	>0.20
	C/P for captures and misses	( 3, 3)	>0.20
<i>Tritonia diomedea</i>	W for captures and misses	(19, 17)	>0.20
	C/P for captures and misses	(19, 17)	>0.20
<i>Nassarius obsoletus</i>	W for captures and misses	( 5, 16)	>0.20
	C/P for captures and misses	( 5, 16)	>0.05
	C/P for algae and 2 μm spheres	(12, 9)	>0.20
Unidentified	C/P for algae and 2 μm spheres	(16, 5)	>0.20

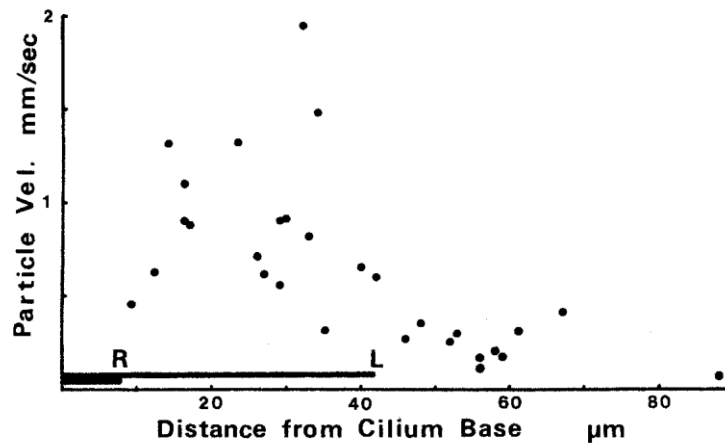


FIGURE 3. Particle velocity versus distance from base of preoral cilium for veliger of *Tritonia diomedea*. L = length of preoral cilium. R = portion blocked by recovery stroke.

## Clearance rate

The volume of water moving through the preoral band can be estimated from the above data. Our estimate combines the angular velocity ( $W$ ), the ratio of cilium velocity to particle velocity ( $C/P$ ), the length of the preoral cilium ( $L$ ), and a correction for the part of the current blocked by the recovery stroke ( $R$ ). Our reasoning is as follows. The pie-shaped area within an arc of one radian with radius equal to  $L$  is  $L^2/2$ . Subtracting the smaller pie-shaped area blocked by the recovery stroke gives  $(L^2 - R^2)/2$ . We assume that particle velocity equals water velocity, so this pie-shaped area times the angular velocity times a unit length of the velar edge divided by the ratio of cilium to particle velocities gives the volume of water passing a unit length of the preoral hand per unit time as  $(L^2 - R^2)WP/2C$ . This volume increases with the length of the preoral cilia (Table V).

TABLE IV

Regression lines for  $C/P$  (ratio of velocities of cilium and particles) against  $W$  (angular velocity) or  $D$  (distance toward base from tip of cilium)  $H_0$ : slope equals 0; reject  $H_0$  if  $P < 0.05$  (t-test, two tailed).

Species	Comparison	(n)	P
<i>Crassostrea gigas</i>	C/P versus W	(6)	> 0.50
	C/P versus D	(6)	0.10 > P > 0.05
<i>Tritonia diomedea</i>	C/P versus W	(36)	> 0.50
	C/P versus D	(36)	> 0.50
<i>Nassarius obsoletus</i>	C/P versus W	(21)	0.50 > P > 0.20
	C/P versus D	(21)	0.10 > P > 0.05
Unidentified	C/P versus W	(21)	0.50 > P > 0.20
	C/P versus D	(21)	0.50 > P > 0.20

TABLE V

Species	L preoral cilium length ( $\mu\text{m}$ )	R recovery stroke correction ( $\mu\text{m}$ )	V = $(L^2 - R^2)WP/2C$ volume through preoral band ( $\mu\text{m}^3/\text{sec } \mu\text{m}$ )	F fraction caught out of n particles	(n)	FV clearance rates ( $\mu\text{m}^3/\text{sec } \mu\text{m}$ )
<i>Crassostrea gigas</i>	30	9	8,200	0.44	(13)	3,600
<i>Tritonia diomedea</i>	40	9	21,000	0.24	(36)	4,900
<i>Nassarius obsoletus</i>	70	9	110,000	0.15	(23)	17,000
Unidentified	100	9	210,000	—	—	—

This estimate includes only the water out to the tips of the cilia and so does not include all the water moved past the velar edge. Three sources of bias may enter this estimate of water flow. First, our measured radius of arc exceeds the length of the cilia, so estimates of angular velocity may be low. Second, we assume a constant ratio of cilium velocity to particle velocity along the cilium, whereas this ratio may increase near the tip. Third, some cilia may have been pushing particles faster than the water. The first underestimates water flow; the second and third overestimate it. For the unidentified prosobranch veliger there is a fourth source of bias. Tips of its preoral cilia are often still bent in the recovery stroke as the base begins the effective stroke, so the effective length of the preoral cilium is less than indicated. The value of  $R$  is about the same for all species, as diagrammed in Figure 4, but could not be measured to the nearest  $\mu\text{m}$ . Also,  $R$  varies around the arc of the effective stroke. Despite these qualifications, the calculation gives an indication of the effectiveness of the cilia in moving water.

To convert this volume per time to an estimate of clearance rate, it is necessary to multiply by the fraction of passing particles which are actually captured. Particles further from the base of the cilia are less likely to be captured, but there is no sharply defined point beyond which no particles are captured and within which all are captured. In Figure 4 velar edges of three species are diagrammed to the same scale. The dashed lines indicate approximate paths of some particles, although the paths vary considerably even at the same distance from the base of the cilia. The films show no captures beyond the outer dashed line. Almost all the particles within the inner dashed line are captured. Particles also tend to travel across the arc described by a cilium. An effective length of cilium is there-fore not readily defined.

To obtain the fraction of passing particles which are captured, we recorded the total number of particles passing the preoral band in a filmed sequence of an actively feeding veliger for each species and noted the fraction captured ( $F$ , Table V). The sample of captures is small but the sample confirms our impression that the longer

preoral cilia are less efficient at removing particles of this size from suspension. The clearance rate is estimated by multiplying the volume passing the cilia by the fraction of particles cleared. Though longer cilia are less efficient, there is a definite gain in rate of clearance per unit length of ciliated band with longer preoral cilia.

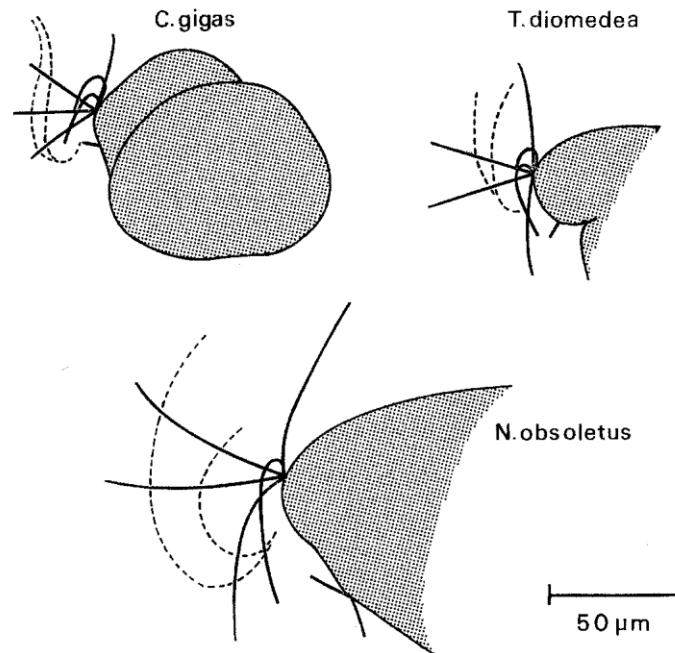


FIGURE 4. Optical section across the velar edge diagrammed for three species to same scale. Preoral and postoral cilia indicated but food groove cilia omitted. Preoral cilium shown in several positions. Dashed lines mark two particle paths (see text).

### *Mechanisms of concentrating particles*

If particles are to be concentrated, they must be moved relative to the water. We have no means of observing water movement in this study, but the observed motion of cilia and particle gives some information on the mechanism by which particles are concentrated. Several combinations of events could occur during concentration: the particles could move faster or slower than the water by either adhering to the cilia or being sieved by two adjacent cilia in their effective strokes. Our observations indicate that more than one mechanism of concentration could be operating.

The simplest hypothesis for concentration is that preoral cilia push adhering particles faster than the water during the effective stroke. In many captures, a preoral cilium overtakes a particle and then moves along next to it. This motion is consistent with the hypothesis that the cilium is pushing an adhering particle faster than the water. Captures occur in which no cilia are observed to touch the particles, but a capturing cilium may have been out of focus.

Particles reverse their direction and move from posterior to anterior into the food groove beneath the preoral cilia in the recovery stroke (Fig. 4). It seems unlikely that the particles are concentrated when they are held or moved against a posterior current here, but we cannot rule out the possibility.

Particles might also be concentrated by a sieve formed by adjacent cilia in their effective strokes. In four captures by the *Tritonia diomedea* veligers two cilia in their effective strokes were separated by an angle of less than  $11^\circ$ . The pair of cilia move next to a particle during part of the effective stroke and could be pushing it faster than the water. Since the gap between the cilia is less than the diameter of the particle, the pair of cilia may be forming a sieve. Because the depth of focus is small, these pairs of cilia may be immediate neighbors. Captures of this sort were not observed with veligers of *Crassostrea gigas* and *Nassarius obsoletus*.

Pairs of cilia separated by a small angle are not visible in most capture sequences. Adjacent preoral cilia are often separated by a large angle in their effective strokes. In such cases the metachronal wavelength rather than the distance between neighboring cilia must set the pore size of the sieve. The preoral cilia of *Nassarius*



*obsoletus* were filmed in a plane perpendicular to the plane of the effective stroke as well as parallel to it. The gap between preoral cilia in the same position of the effective stroke exceeded 20  $\mu\text{m}$  in most instances, whereas these veligers capture particles of a diameter less than 10  $\mu\text{m}$ . For veligers of this size the sieve formed by the metachronal wave is only effective for rather large particles, if it is effective at all.

Another hypothesis is that particles are retained by a sieve composed of both the preoral and postoral cilia in the latter part of their effective strokes. Under this hypothesis water in the current generated by the effective strokes would be squeezed out past the cilia of both bands at the end of the effective strokes when the tips of the opposing cilia are close together. We observed a postoral cilium tip meeting a preoral cilium tip in only one of the frames examined. Observed closest approach between preoral and postoral cilium tips in *N. obsoletus* is about 15  $\mu\text{m}$ , which is about twice the diameter of the captured particles. The actual distances may be somewhat less, however, because the closest approach can fall in the interval between frames of the film.

The films therefore indicate that the spacing of cilia does not set the minimum size for captured particles and that other mechanisms must be operating either in addition to such sieving or instead of it. The hypothesis of weak adhesion of cilia and particles is consistent with observed movements during captures ; the lower frequency of capture of particles nearer cilium tips where differences in velocities are greatest ; and the lower efficiency of capture with longer preoral cilia of equal or higher angular velocities. However, direct evidence for adhesion is still lacking.

The role of the postoral cilia in capturing particles is not clear. Occasionally particles enter the food groove past the postoral band but most captured particles do not follow this route. Yet Strathmann *et al.* (1972) found that captures by a serpulid trochophore ceased when the postoral band ceased beating but the preoral band continued beating. Possibly the postoral band is necessary for retaining particles but does not aid in concentrating them. Captured particles reverse their direction of motion where the preoral cilia end their effective stroke. The captured particles then move anteriorly into the food groove beneath the preoral cilia in their recovery stroke. The recovery strokes of the preoral cilia may be insufficient by themselves to carry the particles into the food groove and keep them there. The current from the postoral cilia may help retain particles during capture and subsequent transport toward the mouth.

## DISCUSSION

Our studies of three species of veliger larvae suggest that shorter preoral cilia clear particles from the water current more efficiently than longer preoral cilia but produce lower clearance rates per unit length of velar edge. This lower clearance rate is the result of both shorter cilia and lower angular velocities. However, larvae with longer preoral cilia may capture small particles less efficiently than large particles. Our observations with small flagellates may therefore underestimate the advantages associated with longer preoral cilia. We are not aware of any studies comparing length of preoral cilia to egg size in species of veligers, but our impression, from past casual observations and the three species reared from eggs in this study, is that veligers from larger eggs tend to have longer preoral cilia when they begin feeding. Our tentative conclusion is that veligers from smaller eggs have both a shorter velar edge and a lower clearance per unit length of velar edge, so their maximum clearance rates are lower.

The techniques of this study could be extended to more species and a greater range of sizes of food particles. A broader comparison could establish quantitative relationships between easily measured traits (cilium length and length of velar edge) and feeding capabilities (maximum clearance rate and efficiency of clearance of particles of different sizes). This would permit comparisons of feeding capabilities of larvae in numerous species which would test hypotheses on costs associated with small egg size and geographic shifts in developmental strategies.

Strathmann *et al.* (1972), using Harris' (1961) argument, speculate that with preoral cilia, which are each composed of a bundle of numerous individual cilia, cilium length could vary independently of cilium velocity. There seems to be no physical necessity for higher angular velocities with longer preoral cilia. Observations on more species are therefore needed to establish the trend found with the species studied here.

Rubenstein and Koehl (1977) have categorized the mechanisms by which suspension feeders concentrate food particles. Our observations of veligers indicate direct interception of a particle by a fiber, with the preoral cilium as the fiber. Our best guess from these limited observations is that preoral cilia overtake the particles in the latter part of the effective stroke and weakly adhere to them, pushing them faster than the water. Possibly two preoral cilia sometimes act together as a sieve. The postoral cilia probably help retain particles but do not necessarily play an important role in concentrating particles.

The veligers in this study were maintained at comfortable temperatures during filming, but they were confined on a microscope slide, exposed to bright light, and fed unnaturally high concentrations of particles. They could have reduced their rate of clearance by some means which was not detected. Bayne (1976) calculates a clearance rate of 10,000 to 15,000  $\mu\text{m}^3/\text{sec}$  per  $\mu\text{m}$  of velar edge for the veliconcha of *Mytilus edulis*. This value is based on measurement of the velum and on clearance rates calculated from rates of ingestion by unconfined veligers in a known concentration of *Isochrysis galbana*. Bayne's values fall between those determined here for *T. diomedea* and *N. obsoletus*. The shell length of 250- $\mu\text{m}$  for the *M. edulis* veliconcha falls between those of early stage *T. diomedea* and *N. obsoletus*, so Bayne's values appear to be in close agreement with our estimates, although the length of preoral cilia of *M. edulis* veligers at this stage is not given. In the worst case, if the preoral cilia of the *M. edulis* veliconcha are about the same as in the early stage *C. gigas* veligers, then our estimates of clearance rates could be one third to one half the maximum rate found by Bayne. In either case, Bayne's result indicates that our values are not far from maximum clearance rates for unconfined veligers.

Strathmann (1971) calculated clearance rates of 5000 to 10,000  $\mu\text{m}^3/\text{sec}$  per  $\mu\text{m}$  of ciliated band for echinoderm larvae feeding on *Amphidinium carteri*. This flagellate is somewhat larger than *Monochrysis lutheri*. The cilia of these larvae are shorter than the preoral cilia of *C. gigas* veligers, and the feeding mechanism is different, but the rates are in rough agreement with those determined here. As in Bayne's study, the estimate for the echinoderm larvae is based on ingestion rates of unconfined larvae.

Ratios of preoral cilium velocity to particle velocity in veligers are similar to ratios reported by Sleight and Aiello (1972), who found ratios of about 1.6, 3.3, and 4.0 near the cilium tips of *Pleurobrachia pileus* comb plates, *Mytilus edulis* gill lateral cilia, and *Stentor polymorphus* membranelles. The plot of particle velocity against distance from cilium base for the veliger of *T. diomedea* is similar to the plots of Sleight and Aiello for *Stentor* and *Pleurobrachia*, except that the velocities decrease more abruptly beyond the tips of the *T. diomedea* preoral cilia.

## SUMMARY

1. Beat of preoral cilia and particle paths were filmed for veligers of *Crassostrea gigas*, *Tritonia diomedea*, *Nassarius obsoletus* and an unidentified prosobranch. Particle captures were filmed for the three identified species.
2. Clearance rates per unit length of velar edge are estimated from the equation  $(L^2 - R^2)WPF/2C$ , where L is cilium length, R a correction for recovery stroke, W angular velocity, C/P the ratio of velocities of cilium and particle, and F the fraction of particles captured. The clearance rates are in rough agreement with Bayne's values for veligers of *Mytilus edulis*.
3. In the three identified species, longer preoral cilia clear particles at a higher rate but with less efficiency. Since veligers from larger eggs generally have both longer preoral cilia and a longer velar edge, a larger egg generally produces a veliger with a higher maximum clearance rate when the veliger begins to feed.
4. Angular velocities increase with cilium length in the three identified species of veligers but the larger unidentified species did not continue this trend.
5. Preoral cilia in their effective strokes move 1 to 3 times faster than particles travelling in about the same arc with a mean of about 1.5 times the speed of the particles. In mid effective stroke, the ratio of velocities of cilia and particles is not significantly different for captured and non-captured particles, nor does the ratio vary significantly with angular velocity of cilium. The ratio does vary significantly among species.
6. Particles passing closer to the base of the preoral cilia are more likely to be captured.



7. We hypothesize that suspended particles are concentrated when they are overtaken by preoral cilia in their effective stroke, weakly adhere to the preoral cilia, and are pushed faster than the water. Capture is completed when particles are drawn into the food groove, probably by the action of the recovery stroke of preoral cilia, the current from postoral cilia, or both.

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