The Protective Reflex of *Bowerbankia* (Bryozoa): Calibration and Use to Indicate Movements of the Medium Beneath a Capillary Surface Wave

K. Wiese, F. Wollnik, and D. Jebram

Zoologisches Institut der Technischen Universität, Pockelsstrasse 10a, D-3300 Braunschweig, Federal Republic of Germany

Summary. 1. The protective polypide-withdrawal reflex of *Bowerbankia imbricata* (Bryozoa, Ctenostomata) was released by controlled oscillations of the medium (water).

2. The range of effective oscillation frequencies extends from 10 to 200 Hz.

3. The displacements at the threshold of the reflex are 120 µm (peak to peak) at 10 Hz, an average of 30 µm in the range 40–80 Hz, and 150 µm at 200 Hz.

4. The thresholds of oscillation velocity remain within the limits of 0.5 to 1.0 cm/s throughout the frequency range 10–110 Hz, which suggests that this parameter is involved in stimulus reception.

5. The "all-or-none reflex movement" of the animal was employed as an indicator of the position of a defined amount of displacement of the medium beneath a capillary surface wave; this result was compared with calculated values.

Introduction

The interface between air and water carries important imformation for many animals by virtue of its special oscillatory properties. The movement of either dead or living objects in contact with the surface film set this film into oscillations; in the frequency range 10 to 40 Hz, for example, oscillations 100 µm in amplitude at the source are transmitted over several decimeters (Markl and Wiese, 1969; Lang, 1978, 1980). These signals can be detected not only by animals in direct contact with the water surface, such as *Notonecta* and *Gerris* (Wiese, 1971; Murphey, 1971; Lang, 1978, 1980) but also – although they are attenuated – by aquatic animals at deeper levels. Among these are the clawed toad *Xenopus* (Görner, 1976), a considerable number of fishes (see in particular: Schwartz, 1971), and crustaceans (Laverack, 1962;

Mellon, 1963; Wiese, 1976). A significant factor in the communication among organisms near the surface of the water and the localization of prey by means of vibration of the medium is the degree to which this signal is transmitted from the surface to the depth in each particular case. Schuijf (1976) published a mathematical and physical description of such transmission. From this equation we learn that the depth to which interface oscillations penetrate the water depends on wavelength; the mode of movement of the water particles is also affected by the distance of the point of observation from the bottom, by the thickness of the layer of water and the presence of obstacles.

Because few experimental chambers have dimensions required for theoretical description, it seems useful to have a practical demonstration of this attenuation process.

No sufficiently small device is available at present with which the actual motion of the medium at a particular depth can be measured. Therefore we used the calibrated behavioral response of a bryozoan (Fig. 1 A), measuring 4×0.25 mm in body length and width. The suitability of these animals lies in their readily visible polypide-retraction reflex, which is elicited by movement of the medium. The *occurrence* of the reflex will indicate only strong movements of the medium, at the threshold of reflex release however – after calibration – we can read an actual value of motion at the site of the animal.

The qualitative studies of Marcus (1926) suggested that bryozoans are quite sensitive to medium oscillations; he observed that even the approach of a wire probe can cause *Electra* to withdraw its tentacular crown into its casing. Because there are no quantitative data on the sensitivity of bryozoans to such movements of the medium, the description of the conditions under which the protective reflex is released became a main topic of this paper.

Thorpe et al. (1975) resolved a long standing debate by demonstrating the presence of neural connections among the individuals in bryozoan colonies. They recorded the potentials of such neurons in *Membranipora* and *Electra;* their work provides good data on the habituation of the polypid-retraction reflex, on the latency of this response to vibration, on the correlation between stimulus strength and time the animal spends in the retracted state. Marcus (1926), Hiller (1939) and Lutaud (1969) revealed the nerve plexus of the zooids in methylenblue-stained preparations of *Electra* and *Bowerbankia*. Lutaud (1974) also published electron micrographs of cross sections through the tentacles of the polypide. The final prerequisite for a behavioral study of the withdrawal reflex was provided by one authors (D.J.) extensive experience with laboratory cultures of marine bryozoans.

Materials and Methods

1. Experimental Animals. A stolonial, ctenostomatous bryozoan, *Bowerbankia imbricata* Adams, was used because of its relatively large size and the possibility to isolate individuals from the colony (Fig. 1 A). The animals were from one strain the original specimens of which had been collected in the vicinity of the North Sea island Helgoland. The colony was propagated asexually by cutting off branches (Jebram, 1977a). The cultures were maintained in artificial seawater with a salinity of $31^0/_{00}$. The animals were fed with a mixture of protozoans called "J5" (Jebram, 1977b). Because the diatom *Phaedactylum tricornutum* Bohlin had proved a useful component (Jebram, 1975), 100 ml of a one to two week old culture of the diatom was added to 900 ml of the bryozoan food (for culture methods see Jebram, 1977a, b).

2. Stimulation by Dipole Vibration. Individuals of *Bowerbankia* were attached to the conical tip of a vertically mounted glass capillary by clamping part of the stolon in a plastic ring (Fig. 1 B). The stand supporting the holder could be positioned in the middle of a container filled with artificial seawater (salinity $31^0/_{00}$). The water displacing oscillator was a plastic sphere 10 mm in diameter, fastened to the end of a light aluminum tube. The tube was attached to the movable coil of a loudspeaker and suspended in such a way that the vibration induced by the coil occurred in the direction of the axis of the tube. The amplitude of the movement was measured with a microscope and adjusted to 250 μm peak-to-peak at all frequencies used. The oscillation was gated by a photoresistor and lightbulb arrangement (the slow heating up of the tungsten coil gradually decreases resistance of the photoresistor) so as to ensure a transient-free onset of vibration (Fig. 1 C).

The distance between the sphere surface and the nearest tentacle of the polypide was fixed so that the vibrating sphere just elicited a polypide-withdrawal response. According to Thorpe et al. (1975) and our own experience, when the stimulus near threshold, the withdrawal movement is somewhat slower than in the response to stronger stimuli, and the polypide is extended immediately after the stimulus ends. There is a proportionality between stimulus intensity and the length of time the polypide remains in the cystid after a withdrawal response (Thorpe et al., 1975; and our own obervation). The possibility that the animal might be directionally sensitive to movement of the medium was not considered in these experiments; the crown of tentacles was tilted and turned arbitrarily
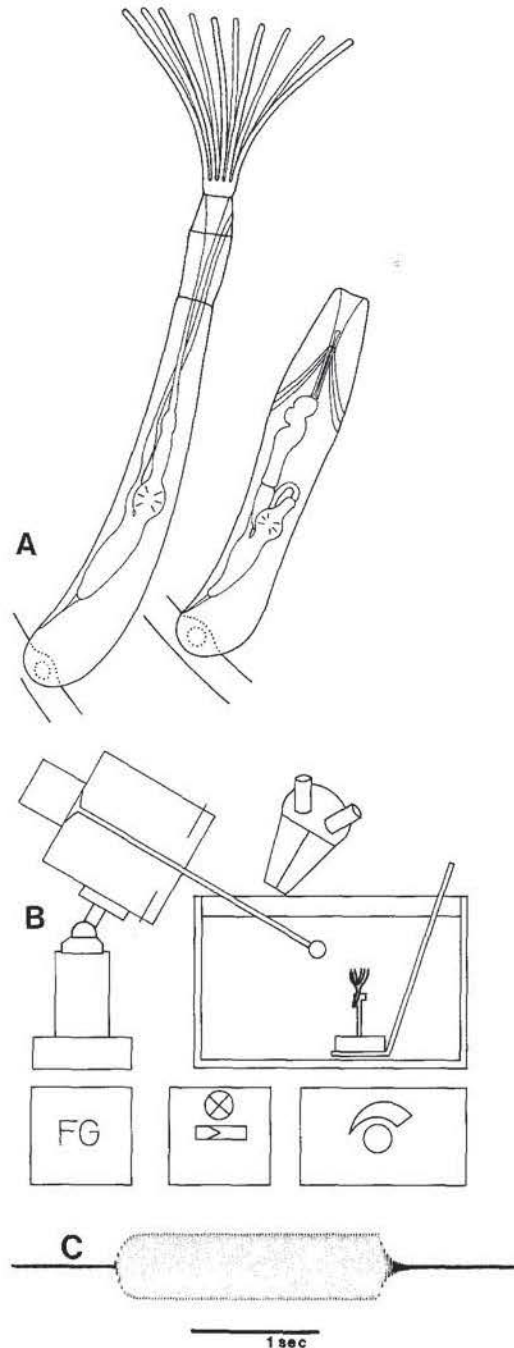
Fig. 1. A Schematic drawings of an extended and a withdrawn individual of *Bowerbankia imbricata*. The overall length of the animal, from the junction with the stolon to the tips of the tentacles, is about 4 mm. **B** The experimental arrangement. A thin aluminum tube has a 10-mm-diameter plastic sphere at one end; the other end is attached to the movable coil of a loudspeaker system. The tube is suspended by three thin, radially arranged steel wires, so that it can move only along its horizontal axis. The amplitude of its oscillatory movement is measured with a calibrated microscope. The vibrator is driven by a variable-frequency generator (*FG*) and power amplifier. The signal is turned on and off by a photoresistor illuminated by a light bulb. The slow resistance change upon lighting the bulb suppresses transients within the signal (**C**) The vibrational stimulus continues after the animal has responded

by the animals. The curve in Fig. 2, showing threshold distance over the frequency range 10–200 Hz, incorporates data from two independent observers.

Habituation of the animals under repeated stimulation (cf. Thorpe et al., 1975) made it necessary to present successive stimuli at precisely fixed intervals. The interval selected for these experiments, 2 min, was a compromise, for even after 5 and 10 min aftereffects of the preceding stimulation can be detected. After a series of reflex responses to the vibrational stimulus the animals frequently withdrew into the cystid for a prolonged period. For this reason an average of 3 animals had to be tested in order to complete each stimulus sequence.

3. Measurement of the Vibration of the Medium at Different Distances from the Sphere. These measurements, like the animal experiments, were made in a glass tank (13 × 8 × 8 cm). The sphere was underwater, with its propelling rod intersecting the water surface at an angle of about 30°. An intense beam of parallel light incident at certain angles illuminated dust particles suspended in the water. A microscope with 100× magnification was focussed on those particles that were suspended within 6 mm from the surface of and in the direction of the movement of the sphere, so that the amplitude of particle oscillation caused by sphere vibration could be measured.

4. Stimulation by Surface Waves. For these experiments, the animal holder was positioned along a vertical axis by means of a manipulator. Distance 0 was established by carefully moving the animal upward until the tentacles touched the water surface, and deeper positions were read off from the scale of the manipulator. Vertical movements of the plastic sphere positioned at the water surface generated the surface waves. The water container used in these experiments was a round glass dish 20 cm in diameter. A strip of filter paper reduced reflection of the waves from the walls. The amplitude of the waves so produced was measured at a point precisely above the bryozoan (for method see Rudolph, 1967) and adjusted to exactly 100 μm.

Results

1. The Range at Which the Animal Responds to the Vibration

With an oscillation amplitude of 250 μm the sphere can elicit the polypide-withdrawal reflex of a solitary specimen of *Bowerbankia* (Fig. 1 A, 1 B) at frequencies from 10 to 200 Hz without touching the animal. When the vibration frequency is kept constant and the sphere is moved away from the animal gradually, a position is eventually reached at which the reflex is barely triggered by the vibration of the medium. This critical distance (from the surface of the sphere to the nearest tentacle) varies with frequency of oscillation (Fig. 2). Within the frequency range 40–80 Hz the vibrating sphere triggered the reflex at distances up to 6 mm.

Our observations of *Bowerbankia* indicated that an interstimulus pause of 2 min was not sufficient to allow a polypide, after having withdrawn itself, to completely recover its readiness to respond. Indeed,
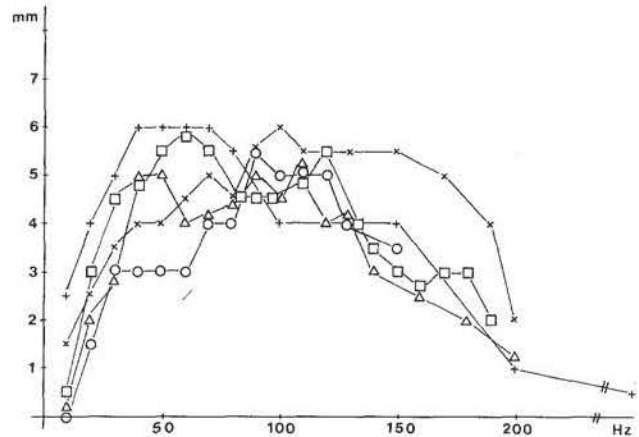
Fig. 2. Threshold curves for the protective reflex of *Bowerbankia*. Ordinate: maximal distance between animal and sphere surface at which the reflex could be released. Abscissa: frequency of sphere vibration. One series (+) was measured by K.W., and all the others by F.W.; the (×) symbols designate the curve oftained with 5-min inter-stimulus intervals rather than the customary 2-min intervals. At frequencies above 200 Hz only one trial, at 300 Hz, was made as a control. All further calculations are based on the arithmetic means of the threshold distances shown here for each frequency

habituation effects can be observed even 10 min after a stimulus has ended. For this reason one of the five series of measurements shown in Fig. 2 was done with inter-stimulus intervals of 5 min. It is evident in this curve (x) that recovery from habituation had progressed further, particularly in the range 100–150 Hz.

2. Attenuation of Motion of the Medium at Increasing Distances from the Sphere

It is clear that for a protective reflex of *Bowerbankia* to be released fairly extensive movement of the medium is required, so extensive that the movement of particles at the relevant distances from the sphere could be monitored visually. Figure 3 presents the results of measurements with the calibrated microscope in which light-reflecting particles in the water near the sphere were viewed. Along a line coincident with the rod driving the sphere, to a first approximation, oscillation frequency has no effect on attenuation; the amplitude of particle movement decreases exponentially in all cases (Fig. 3 inset).

A second experiment to determine the spatial attenuation of vibration in the direction of movement of the sphere involved measurement of the minimal oscillation amplitude necessary to elicit the withdrawal reflex. With the sphere vibrating at 80 Hz, threshold oscillation (pp)-amplitudes were measured for distances of 1, 2, 4 and 8 mm between animal and
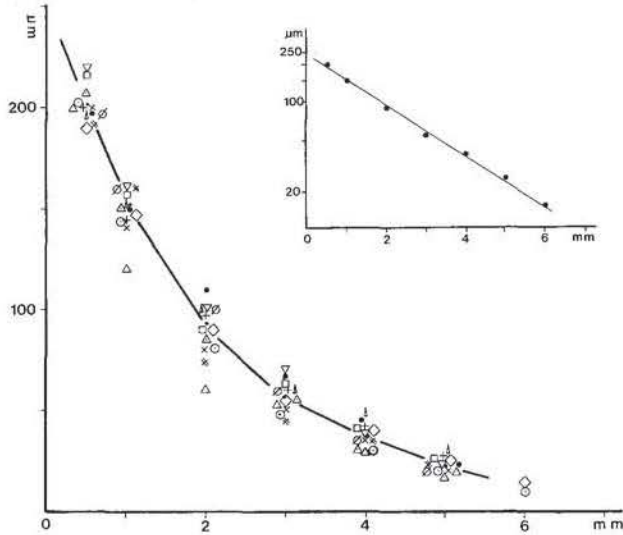
Fig. 3. Attenuation of vibration of the medium at increasing distances from the site of excitation. The vibrating sphere oscillates with a peak-to-peak amplitude ($=2A$) of 250 μm at all frequencies. At fixed distances from the *surface* of the sphere (note that in theoretical considerations the center of the sphere is the decisive point), along a line through the axis of the rod, the oscillation of light-reflecting dust particles suspended in the water was observed with a calibrated microscope. The symbols represent the frequencies tested, as follows: 10 Hz ($\triangle$), 20 Hz ($\triangledown$), 30 Hz ($\times$), 40 Hz ($+$), 50 Hz ($\triangle$), 60 Hz ($\bullet$), 70 Hz ($\square$), 70 Hz ($\odot$), 90 Hz ($\diamond$), 100 Hz ($\dagger$), 200 Hz ($\triangle$); the arithmetic mean of all the data at a given frequency is plotted as a small dot ($\cdot$); inset: demonstration of the exponential fall-off of particle displacement with increasing distance from the source of vibration

sphere surface. When the distance between the edge of one tentacle and the nearest point on the sphere was 1 mm, the threshold amplitude was 50 μm; at 2 mm it was 100 μm, at 4 mm 200 μm, and at 8 mm 450 μm.

In another experiment the 10-mm plastic sphere was replaced by a sphere only 3 mm in diameter. Again with a frequency of 80 Hz and with an amplitude of 250 μm the threshold distance for release of the reflex movement was found to be 1.2 mm (2.7 mm as measured from the center of the sphere) rather than the 4.6 mm (9.6 mm from the center) measured with the larger sphere.

3. The Displacement and Velocity of Particles Under Conditions Corresponding to the Threshold for Release of the Withdrawal Reflex

Measurements of the oscillations of the medium at different distances from the sphere and at different frequencies of vibration demonstrated that in this situation attenuation is independent of frequency. Therefore the oscillation amplitudes of the medium at different frequencies were averaged for each dis-
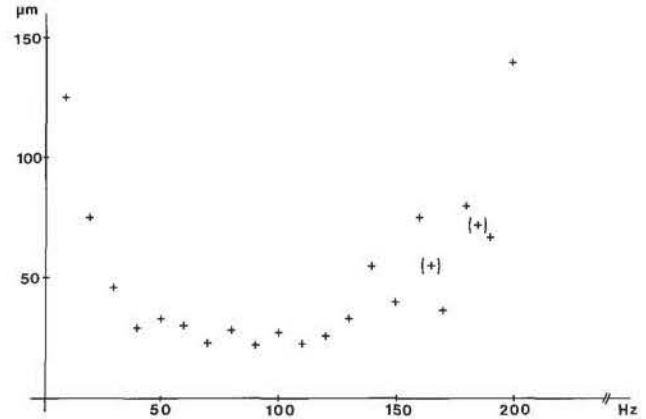

Fig. 4. Displacement ($=2A$) of the particles in the medium at the threshold for release of the polypide-withdrawal response. The large scatter of the data in the range 140–200 Hz was tentatively smoothed out by averaging the values at two adjacent frequencies and plotting the result halfway between the two original frequencies (symbols in parentheses)
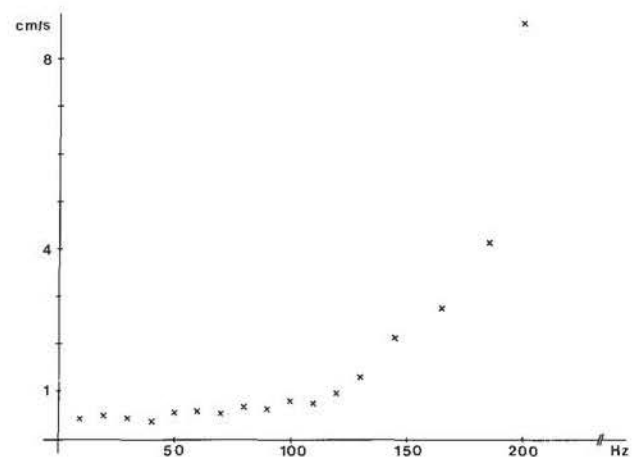

Fig. 5. Velocity of particle oscillation at the threshold for release of the protective reflex. These data were computed from those in Fig. 4 by $A \cdot \omega$, where $\omega = 2\pi f$. Note that velocities well above 0.5 cm/s are required only with frequencies of over 110 Hz

tance and these averages were used to construct an attenuation curve (Fig. 3).

This curve shows the amplitude of oscillation of the medium for each observed threshold distance. The particle-displacement thresholds for the polypide-withdrawal reflex thus derived form the curve of Fig. 4. It is evident that with 10-Hz vibration 120 μm (peak-to-peak) oscillations of the medium are required to trigger the reflex; the average value for 50–120 Hz is 25 μm; at values higher than 120 Hz the thresholds increase, reaching 140 μm at 200 Hz.

The curve in Fig. 5 was obtained by halving the threshold displacements in Fig. 4 and multiplying the result by $2\pi f (=\omega)$ so as to obtain the velocity component of particle movement. The threshold curve

for the parameter particle velocity begins with a long plateau phase in the vibration frequency range 10–110 Hz with only slight fluctuations of the threshold (between 0.5 and 1.0 cm/s). At values higher than 110 Hz the threshold values increase, reaching 9 cm/s at 200 Hz.

4. Bowerbankia as an Indicator of a Fixed Value of Water Motion

Once the magnitude and velocity of the movement required to release the reflex were known, it was possible to use *Bowerbankia* as an instrument for studying the way surface-wave motion is transmitted within a body of water. The theoretical considerations with repect to particle movement at different depths are represented by Schuijf's formula (1976):

$$\xi = \frac{A' \cdot \cosh\left(k \cdot (-z+h)\right)}{\cosh\left(k \cdot h\right)} \cdot \cos\left(kx - \omega t\right)$$

where

ξ = the horizontal component of particle movement. (If the vertical component is desired, the cosine in the formula must be replaced by sine)

A' = amplitude of the surface wave directly above the observation point

$\cosh(y) = \dfrac{e^{y} - e^{-y}}{2}$

$k = 2\pi/$wavelength of the surface wave

z = depth of the observation point below the surface; z is always negative

h = depth (surface to bottom) of the water in the vessel

$\cos(kx - \omega t)$ can be set equal to 1 whenever one is concerned only with the maximal movement of the particles.

x = radial distance of wave source from the observation point.

The attenuation curves calculated for surface waves of wavelength 5, 7, 10, 20 and 70 mm (corresponding to 60, 40, 25, 13 and 5 Hz), with amplitude at the surface 100 μm, ($=2A=A'$ of the equation) are shown in Fig. 6.

With *Bowerbankia* as the amplitude indicator the curves were derived experimentally by generating surface waves in a round glass dish so that the amplitude directly above the animal was 100 μm. With frequencies of 13, 25, 40 and 60 Hz the threshold position for the withdrawal reflex was noted; this position, in mm depth, was then converted to μm oscillation amplitude by referring to the curves in Fig. 6. In the above order of frequencies the values found
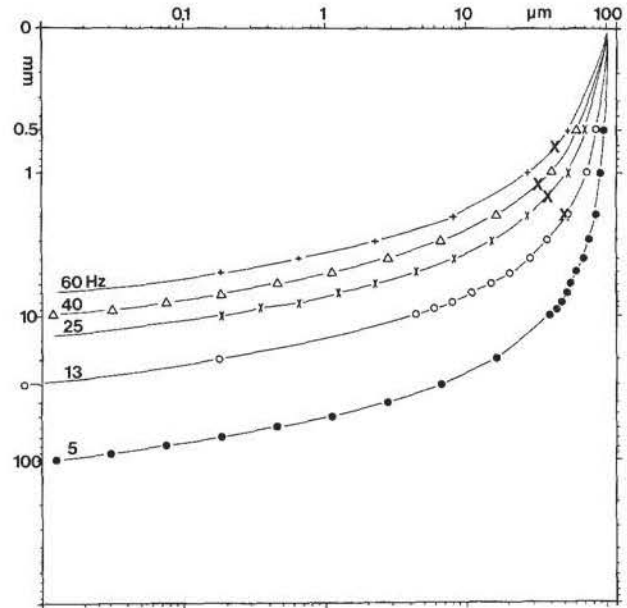

Fig. 6. Attenuation of the movement of the medium, as a capillary surface wave transmits itself into the underlying water calculated by a formula published by A. Schuijf (1976). The initial condition is a surface wave with oscillation amplitude 100 μm ($=2A$) precisely above the point for which the particle movement is to be calculated. Abscissa: particle movement expressed as oscillation amplitude. Ordinate: depth of the observation point below the water surface. The calculation was done for wavelengths of 70, 20, 10, 7 and 5 mm, corresponding approximately to the frequencies 5, 13, 25, 40 and 60 Hz. The overall depth of the water was taken to be 15 cm. Only the horizontal component of the motion was computed. The bold-faced ($\times$) symbols mark the maximal depth at which the protective reflex movement occurred in response to a surface wave of the particular frequency and 100 μm (pp) amplitude at the surface site exactly above the submerged animal

were 2.0 mm (53 μm), 1.7 mm (35 μm), 1.3 mm (30 μm) and 0.7 mm (40 μm).

Discussion

1. Release of the Protective Reflex of Bowerbankia by Vibration of the Medium

Habituation effects following a retraction response outlast even a period of 10 min (Thorpe et al., 1975). Presenting the vibrational stimulus at intervals greater than the 2 min chosen in our measurements generally lowers the threshold of the reflex response. The 5-min-interval used in one series of experiments (Fig. 2 x-symbols) shows the change in thresholds resulting from this more complete recovery.

At present two reasons can be suggested for the considerable scatter of the data among the different series (Fig. 2):

(i) It may be that the polypide as a whole, considered as a microphone that transduces movement of

the medium, has a directional characteristic; this possibility could not be controlled in our experiments, because the animals were able to alter the position of the polypides spontaneously.

(ii) On the other hand, differences in the physiological age of the zooids might perhaps cause differences in response of the protective reflex. But there can be no very pronounced inter-individual variability in responsiveness to vibration of the medium, for it would have become apparent when we changed animals within a series of measurements.

2. The Attenuation of Particle Movement with Increasing Distance from the Vibrator

Theoretically, the particle movement produced should be proportional to the volume of the oscillating body and inversely proportional to the third power of the distance between the driver and the observation point (cf. van Bergeijk, 1967). Our microscopic observations of particle movement in front of the sphere are consistent with this rule, provided that the center of the vibrating sphere is the reference point for the distance measurement. When the distance between the center of vibration and the animal was doubled, the amplitude of sphere oscillation had to be increased eightfold in order to elicit the reflex. At a distance of 6 mm an 80 Hz oscillation of 50 μm amplitude released the polypide reflex; at a distance of 13 mm, other conditions remaining constant, an oscillation amplitude of 450 μm was required to achieve the same effect.

The differences in threshold distance observed when two different sized spheres were used clearly result from the proportionality between sphere volume and the water movement generated. This relationship is evident in that the ratio R^3/r^3 (where R is the radius of the sphere and r is the threshold distance measured from the center of the sphere) is nearly equal for the two situations – 0.171 with the 3-mm sphere and 2.7 mm distance, and 0.141 with the 10-mm sphere and 9.6 mm threshold distance.

3. Magnitude and Velocity of Movement of the Medium at the Threshold for the Bowerbankia Polypide-Withdrawal Reflex

The threshold curve for displacements (Fig. 4) has a U-shape with the minimum values 25–30 μm in a broad range of frequencies from 40–110 Hz. Vibrations at 10–20 Hz and intermediate amplitude make the whole animal swing back and forth in rhythm with the vibrator: displacements of more than 100 μm in amplitude are required to release the reflex.

The increased threshold in the range 10–40 Hz is surely of practical importance in the animal's habitat, where, although they are not exposed directly to the surf there are variations in the water flow owing to the pressure fluctuations caused by wave motion. Bryozoans feed by means of longitudinal rows of motile cilia on the frontal-median line and on the sides of the tentacles; the current these cilia produce flows into the polypide at an estimated 1–2 mm/s. Again, the animal needs a mechanism to protect the reflex from beeing released by low frequency or steady fluid movements.

Markl (1973) pointed out that the movement of the bodies of even small organisms (1 cm or less) in water generates a field (the near field) within which the medium follows the organism's motion. The velocity component of this field effectively stimulates vibration receptors and thus reveals the presence of the vibration-generator (cf. Tautz, 1979). In this situation the velocity parameter is kept constant over a considerable range of the threshold curve (Fig. 5), whereas the displacement of the medium must be relatively large, particularly at frequencies around 10 Hz, to release the protective reflex.

Essentially nothing is known about the amplitude and frequency range of the vibrations produced by either the predators of *Bowerbankia* or any other organisms that share its habitat. It is interesting, however, to note that the locomotion of the fairly large ciliate *Glaucoma* (although it definitely does not inhabit the biotope of *Bowerbankia*) was found by Kolle-Kralik and Ruff (1967) to generate maximal near field velocity of the medium in the frequency range from 45 to 65 Hz.

4. Penetration of a Body of Water by Surface Waves

When the *Bowerbankia* protective reflex was used to indicate position of threshold water displacement resulting from a surface wave, that displacement was in general found at the distance below the surface predicted by Schuijf's (1967) equation (Fig. 6), except for the vibration at 13 Hz. The fact that the density of the medium used (artificial seawater with a salinity of 31⁰/₀₀) is greater than is assumed in the calculation evidently has no appreciable effect on attenuation underwater; there is no clear difference between prediction and measurement. In the case of the 13-Hz surface wave there are various conceivable reasons for the discrepancy between the displacement threshold of reflex release determined during the calibration procedure and the threshold value (boldface (x) symbol) read from the corresponding curve of Fig. 6. Among the reasons are the steepness of the threshold

curve in the 10 to 20 Hz-range (Fig. 4), the scatter of the data on which the threshold curve was based (Fig. 2), and the possibility of interference phenomena within the container at this relatively long wavelength.

It is possible that water pressure has an influence on vibration sensitivity of the bryozoa; if so, it would not affect the present data, because all measurements were made at water depths between 0 (surface) and 5 cm below; rather, the velocity dependent receptor mechanism (Fig. 5) hints at a bristle- or cilium-type sensor structure which is unlikely to respond to pressure.

The question of the transmission of surface waves into the underlying water has received some attention previously (Markl and Wiese, 1969) in connection with the site of the vibration receptors used by *Notonecta* to localize prey. The equation derived then, $r^2 = \frac{k}{\omega} \cdot A \cdot e^{-ky}$ (with reference to Sommerfeld, 1947), has proved to be wrong in two respects: First, a mathematical expression describing reduction of a linear quantity can not be equated with a quadratic quantity; second, the description does not take into account that the overall depth of the water and the nearness of the observation point to the bottom also affect magnitude and direction of particle movement.

The protective reflex of *Bowerbankia* is a sensitive indicator of 0.5–1.0 cm/s near field particle velocity and 25–30 μm water displacement (at 40–110 Hz), and it has the advantage that it can be observed with the naked eye. Unfortunately, for many applications in studies of the behavioral physiology of aquatic animals, it would be more useful to detect displacements in the region of 0.1 μm. We have also tentatively examined the potential of another biological preparation, the water current receptors on the crayfish carapace, which do respond to displacements of this order. In this case however, the indicator is a relatively inconspicuous increase in the discharge rate of the sense cell, rather than a readily visible "all-or-none" behavioral response.

References

Bergeijk, W. van: Introductory comments on lateral line function. In: Lateral line detectors. Cahn P. (ed.), pp. 73–81. Bloomington: Indiana University Press 1967

Görner, P.: Source localization with labyrinth and lateral line in the clawed toad (*Xenopus laevis*) in: Sound reception in fish. Schuijf, A., Hawkins, A.D. (eds.), pp. 171–182. Oxford: Elsevier 1976

Hiller, S.: The so-called nervous colonial system in Bryozoa. Nature (London) **143**, 1069–1070 (1939)

Jebram, D.: Effects of different foods on *Conopeum seurati* (Canu) (Bryozoa Cheilostomata) and *Bowerbankia gracilis* Leidy (Bryozoa Ctenostomata). Doc. Lab. Geol. Fac. Sci. Lyon **3** (1), 97–108 (1975)

Jebram, D.: Experimental techniques and culture methods, Chapt. 8. In: Biology of bryozoans. Woollacott, R.M., Zimmer, R.L. (eds.), pp. 273–306. New York: Academic Press 1977a

Jebram, D.: Culture media and diets for Bryozoa. In: CRC Handbook series in nutrition and food, Vol. II, Sect. G. Rechcigl, M., Jr. (ed.), pp. 77–92. Cleveland, Ohio: CRC-Press Inc. 1977b

Jebram, D.: Interrelations of nutrition, food uptake and growth in bryozoans. In: Advances in bryozoology, Abbott, M.B., Larwood, G.P. (eds.), pp. 121–140. London: Academic Press 1979

Kolle-Kralik, U., Ruff, P.W.: Vibrotaxis von *Amoeba proteus* im Vergleich zur Cilienschlagfrequenz der Beuteltiere. Protistologica **3**, 319–323 (1967)

Lang, H.H.: Die Unterscheidung zwischen Beute und Artgenossen durch den Rückenschwimmer *Notonecta glauca* mit Hilfe von Oberflächenwellen. Verh. Dt. Zool. Ges. 1978, p. 163

Lang, H.H.: Surface wave discrimination between prey and non prey by the Back Swimmer *Notonecta glauca* L. (Hemiptera, Heteroptera). Behav. Ecol. Sociobiol. **6**, 233–246 (1980)

Laverack, M.: Responses of cuticular sense organs of the lobster *Homarus* I. Hair peg organs as water current receptors. Comp. Biochem. Physiol. **5**, 319–325 (1962)

Lutaud, G.: Le "plexus" pariétal de Hiller et la coloration du system nerveux par le bleu de méthylène chez quelques Bryozoaires Chilostomes. Z. Zellforsch. **99**, 302–314 (1969)

Lutaud, G.: Le plexus pariétal des Cténostomes chez *Bowerbankia gracilis* (Leydi) (Vésicularines). Cah. Biol. Mar. **15**, 403–408 (1974)

Marcus, E.: Beobachtungen und Versuche an lebenden Meeresbryozoen. Zool. Jahrb. Abt. Syst. Ökol. Geogr. Tiere **52**, 1–102 (1926)

Markl, H., Wiese, K.: Empfindlichkeit des Rückenschwimmers *Notonecta* für Oberflächenwellen des Wassers. Z. Vergl. Physiol. **62**, 413–420 (1969)

Markl, H.: Leistungen des Vibrationssinnes bei wirbellosen Tieren. Fortschr. Zool. **21**, 100–119 (1973)

Mellon, D.: Electrical responses from dually innervated tactile receptors on the thorax of the crayfish. J. Exp. Biol. **40**, 137–148 (1963)

Murphey, R.K.: Motor control of orientation to prey by the water-strider *Gerris remigis*. Z. Vergl. Physiol. **72**, 150–167 (1971)

Rudolph, P.: Zum Ortungsverfahren von *Gyrinus substriatus*. Z. Vergl. Physiol. **56**, 341–375 (1967)

Schuijf, A.: Variation of hydrodynamic parameters with depth in capillary gravity waves. In: Sound reception in fish. Schuijf, A., Hawkins, A.D. (eds.), p. 183. Oxford: Elsevier 1976

Schwartz, E.: Die Ortung von Wasserwellen durch Oberflächenfische. Z. Vergl. Physiol. **74**, 64–80 (1971)

Sommerfeld, A.: Mechanik der deformierbaren Medien, p. 163ff. Wiesbaden: Dieterichs'sche Verlagshandlung Wiesbaden 1947

Tautz, J.: Perception of particle oscillation in a medium – An unorthodox sensory capacity. Naturwissenschaften **66**, 452–461 (1979)

Thorpe, J.P., Shelton, G.A.B., Laverack, M.S.: Electrophysiology and coordinated behavioural responses in the colonial Bryozoan *Membranipora membranacea* (L.). J. Exp. Biol. **62**, 389–404 (1975)

Wiese, K.: Das mechanorezeptorische Beuteortungssystem von *Notonecta*. J. Comp. Physiol. **78**, 83–102 (1972)

Wiese, K.: Mechanoreceptors for near-field water displacements in crayfish. J. Neurophysiol. **39**, 816–833 (1976)